

**INTERNATIONAL CONFERENCE ON
SUSTAINABLE CONTRIBUTION OF FISHERIES
TO FOOD SECURITY**

Kyoto, Japan, 4-9 December 1995

organized by the

GOVERNMENT OF JAPAN

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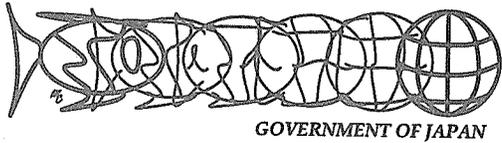
**FOOD AND AGRICULTURE ORGANIZATION
OF THE UNITED NATIONS**

**IMPACTS OF PREDATOR - PREY RELATIONSHIPS ON
HARVESTING STRATEGIES AND MANAGEMENT**

By

Michael Sanders

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IMPACTS OF PREDATOR - PREY RELATIONSHIPS ON HARVESTING STRATEGIES AND MANAGEMENT

EXECUTIVE SUMMARY

The major predators of fish (including non-commercial species) are the fish themselves. Predation by man is substantially less, roughly the same level as other mammals. Predation represents an important process in the regulation of fish populations, but predator-prey interactions and their effects on fish resources are very diverse and complex and require in-depth study. The situation is further complicated by the non-equilibrium nature of both the local and ecosystem environments in which predation and competition occur. In reality, the world's fisheries are targeted at both predator and prey assemblages. Attaining most beneficial use requires knowledge of the interactions, the ecosystem effects, and bio-economic modelling in the multi-species context.

This paper examines predator-prey interactions as a component of the regulation of fisheries resources. It includes observations on the impact and scale of predation in marine and freshwater ecosystems, approaches to including predation effects in mathematical modelling of single- and multi-species fisheries, and provides examples of how these effects have been incorporated in management advice and in harvesting strategies.

Predation can have a significant impact on marine and freshwater ecosystems. The reduction of the large baleen whales in the Antarctic meant a greater abundance of krill in the short term through reduced mortalities from predation. Subsequently there was population growth among the remaining baleen whales, seals, seabirds and squid. Similar effects can be observed in freshwater ecosystems, in seal predation on marine organisms, and in predation on eggs and larvae. Some of the more dramatic effects of predation at community level occur when species are introduced into freshwater lakes. An example is the destruction of the haplochromine cichlids of Lake Victoria after the Nile perch was introduced.

The harvesting of marine mammals is a special case, in view of the aesthetic and moral constraints being imposed by public opinion. The continuing recovery of most marine mammal populations, however, has created the dilemma of whether to continue the near total ban on harvesting, or to permit limited harvesting under carefully controlled conditions. Much more study is required to understand the consequences of these alternatives to the maintenance of balanced ecosystems. The public needs to be better informed of the extent of recovery of these populations and the ecosystem effects, in order to permit a more reasoned discussion of the costs and benefits (aesthetic, social and economic) of the alternative approaches.

The scale of predation is reported for the following: cod, tuna, marine walleye pollock, mammals, cephalopods, and birds. The magnitude of shrimp predation in the waters of Greenland is presented as an example.

The annual consumption of northern shrimp by Pacific halibut was estimated as 1 300 tonnes for 1990 and 1 100 tonnes for 1991. The consumption of shrimp by redfish was estimated to be 33 600 tonnes in 1990 and 8 700 tonnes in 1991. The nominal catch of shrimp in the two years was about 52 000 tonnes and 58 000 tonnes respectively.

Attempts have been made to incorporate the effects of predation in fisheries models. Extensions to single species assessments take into account the effects of cannibalism and the repercussions for stock size, recruitment, yield and management strategies. Single species models can also be extended into simple multi-species models. In an example of the interactions between Norway lobster and cod in the Irish sea, where these are the two most valuable species and where cod accounts for an estimated 88% of all predation on the lobster, it was concluded that cod exploitation should be kept as high as possible (while taking care to avoid declining recruitment) to reduce predation and increase lobster yield.

Other multi-species models are more complex. The ICES approach consists of two models. The first is MSVPA (Multi-Species Virtual Population Analysis), which is used to estimate the past stock numbers, the past predation mortality coefficients and the parameters to compute them, and the past fishing mortality coefficients. It takes as its primary inputs the total numbers caught by age group by all fishing fleets, the food consumption rates and prey preferences of the predatory fish, and individual weights by age for all the species. The second model is MSFOR (Multi-Species Forecast), which is used to predict future yields, stock numbers and biomass, and future predation mortality coefficients. Its inputs are the outputs from the MSVPA (stock numbers, predation and other fixed parameters), estimated or assumed recruitment, and assumed future fishing mortalities.

Two case studies of the application of multi-species models are given. In the example of hake and anchovy stock in the northwest Mediterranean, the conclusion favoured management that maximized yields of the predator, hake. This is largely due to the higher price that hake commands. Moreover the incorporation of a predator-prey interaction into the assessment did not provide any further insights beyond that available from a single species assessment. The important results were from the single species VPA applied to hake, particularly in respect to quantifying the extent of potential benefit from having an age at first capture of 4 years (equivalent to a length of about 40 cm).

Owing to the complexity of multi-species ecosystems, harvesting strategies should not be oversimplified. The idea that the total production of a system can be increased by fishing down the predators, and then harvesting the more abundant prey lower down in the food web, does not seem to work in practice.

As fishing increases on the apex predator, its role as a regulating agent on the abundance of the lower trophic species is replaced, at least in part, by the next predator down; the older individuals of which are able to move into a higher trophic level than formerly.

The extent to which this happens is increased when there are many competing predators on the same group of prey. Furthermore, as the natural effect of predators is to regulate the abundance of the prey, the substantive and selective removal of predators will be de-stabilizing, as reflected by increased variation in the abundance of the prey. Selective removal of the prey, on the other hand, will be detrimental to the predators, although less so if alternative prey are available.

The economics of predator-prey harvesting also need to be assessed. Flaaten (1989) combined a simple biological model involving a single predator and a single prey from May et al. (1979), with economically independent harvesting sectors, one for each of the two species. As expected, harvesting the predator in this very simple situation increased the harvestable stock of the prey, and harvesting the prey reduced the harvestable stock of the predator.

In the case where the prey is inexpensive-to-catch and valuable, and the predator is expensive-to-catch trash, he concluded that it may be economically justified to subsidise the harvesting of the predator.

In the reverse, when the predator is inexpensive-to-catch and valuable, and the prey is expensive-to-catch and trash, the increase in the harvestable stock of the prey resulting from the harvesting of the predator, may make it economic to harvest the prey when previously it was not. This would occur, however, at the expense of the fishery on the predator.

Examples are provided of predation effects being incorporated into management advice for marine fisheries. In the Northeast and Northwest Atlantic, capelin catches are restricted to leave enough as food for the higher valued cod. In contrast, anchovy and pilchard continue to be heavily exploited in the Southeast Atlantic even though they are valuable forage fish for the higher value hake and other predators. Other examples include harvesting of the South African fur seal, and culling of grey seals in Scotland.

The policy and institutional implications of multi-species management need to be examined. Three problems, in particular, are highlighted: fishermen restricted (as through licensing) to exploiting certain species may become disadvantaged; fishery resources are often shared with other apical predators (whales, seals and birds); and institutional problems arise when species come under the jurisdiction of several independent agencies.

Nevertheless, there is certain to be an increasing trend toward studying and managing fish stocks in a multi-species context, and in some cases toward managing the ecosystem where they belong. In multi-species fisheries, the search for economic viability will continue to be the dominant influence on the strategies used to harvest predator-prey stocks.

When the predators have a much higher per unit price than the prey, as is usual, the harvesting strategies will give preference to sustainable exploitation of the predators, with the yields from the prey stocks being of lesser importance.

In conclusion, research to support multi-species management is necessary, but will not be equally relevant across all fisheries. Research will depend on how well established species interactions are, its cost effectiveness in complex ecosystems, and appropriateness in cases where single species assessments might be adequate. Whatever emphasis is given to the research, it will be essential to model the effects in its full bio-economic context. At least some minimum understanding of the species interactions and the abiotic factors will be needed. As appropriate, this should include a fuller understanding of predator-prey relationships, natural climatic processes, ecological responses, and the impacts of exploitation and management.

IMPACT DES RELATIONS PREDATEURS-PROIES SUR LES STRATEGIES D'EXPLOITATION ET L'AMENAGEMENT DES PECHEES

RESUME

Les principaux prédateurs des poissons (espèces non commerciales incluses) sont les poissons eux-mêmes. La prédation par l'homme est nettement moins importante et a approximativement la même ampleur que la prédation imputable aux autres mammifères. Si la prédation joue un rôle de premier plan dans la régulation des populations de poissons, les relations entre proies et prédateurs et leurs incidences sur les ressources halieutiques sont extrêmement diverses et complexes et nécessitent donc une étude approfondie.

La situation est encore compliquée par le fait que les milieux où se déroulent prédation et compétition, que ce soit à l'échelle locale ou à celle des écosystèmes, ne sont pas en état d'équilibre. En fait, à l'échelle mondiale, l'exploitation porte à la fois sur les assemblages de prédateurs et de proies. Pour utiliser au mieux les ressources halieutiques, il est indispensable de mieux connaître les interactions proies-prédateurs, et l'impact des écosystèmes et d'élaborer des modèles bio-économiques qui tiennent compte du caractère plurispécifique des ressources. L'article examine les interactions proies-prédateurs en tant que facteur de régulation des ressources halieutiques. Il fournit des observations sur l'impact et l'échelle de la prédation dans les écosystèmes marins et d'eaux douces, des indications sur les approches visant à intégrer les effets de la prédation dans les modèles mathématiques mono- et plurispécifiques et des exemples sur la prise en compte de ces effets dans les avis en matière d'aménagement et de stratégies d'exploitation.

La prédation peut avoir une incidence considérable sur les écosystèmes marins et d'eaux douces. La réduction du nombre de grands cétacés à fanons dans les eaux de l'Antarctique s'est traduite à court terme par une plus grande abondance de krill du fait de la diminution de la mortalité par prédation. Cela a eu pour conséquence d'accroître le nombre de baleines à fanons, de phoques, d'oiseaux de mer et de calmars. Des effets semblables peuvent s'observer dans les écosystèmes d'eau douce, dans le cas de la prédation d'organismes marins par des phoques et dans celui de la prédation des oeufs et des larves. A l'échelle d'une communauté, certaines des conséquences les plus frappantes de la prédation se manifestent à la suite de l'introduction de nouvelles espèces dans des lacs. On peut évoquer l'exemple de l'élimination des cichlidés haplochromis du lac Victoria après l'introduction de perches du Nil.

L'exploitation des mammifères marins constitue un cas particulier, compte tenu des pressions esthétiques et morales exercées par l'opinion publique. La reconstitution régulière de la plupart des populations de mammifères marins a toutefois engendré un dilemme : faut-il continuer à interdire presque toute exploitation ou peut-on autoriser une exploitation limitée dans des conditions strictement contrôlées.

Seules des études beaucoup plus poussées permettront de mieux comprendre les conséquences de ces deux possibilités pour la préservation de l'équilibre des écosystèmes. Le public doit être mieux informé de la reconstitution de ces populations et de ses effets sur les écosystèmes, de façon à permettre une appréciation raisonnée des coûts et bénéfices (sur le plan esthétique, social et économique) des options d'alternatives.

L'article fait état de l'échelle de la prédation exercée sur les animaux suivants : morue, thon, morue du Pacifique occidental, mammifères marins, céphalopodes et oiseaux. L'ampleur de la prédation des crevettes dans les eaux du Groenland est donnée à titre indicatif. La quantité de crevettes nordiques consommées annuellement par les flottes du Pacifique est estimée à 1 300 tonnes en 1990 et à 1 100 tonnes en 1991. Par ailleurs, la quantité de crevettes consommées par les sébastes a été évaluée à 33 600 tonnes en 1990 et 8 700 tonnes en 1991. Enfin, la prise nominale de crevettes s'est élevée approximativement à 52 000 tonnes en 1990 et à 58 000 tonnes en 1991.

On a tenté d'intégrer les effets de la prédation dans les modèles utilisés en halieutique. Des applications relatives à des évaluations de stocks monospécifiques prennent en considération le cannibalisme et ses répercussions sur la taille des stocks, le recrutement, la production et les stratégies d'aménagement. Il est en outre possible d'étendre les applications des modèles monospécifiques à des pêcheries plurispécifiques simples. L'étude des interactions entre la langoustine et la morue, deux espèces de haute valeur commerciale de la mer d'Irlande, montre que la morue est responsable d'environ 88 % de la prédation vis à vis de la langoustine et que l'exploitation de la morue devrait être maintenue à son niveau maximal (tout en veillant à préserver le recrutement), afin de restreindre la prédation et d'augmenter le rendement de la pêche à la langoustine.

D'autres modèles multispécifiques sont plus complexes. Le Conseil international pour l'exploration de la mer (CIEM) a mis au point deux modèles. Le premier, baptisé MSVPA ("Multi-Species Virtual Population Analysis" - Analyse des populations virtuelles plurispécifique), sert à estimer a posteriori les effets des stocks, les coefficients de mortalité par prédation ainsi que les paramètres permettant de les calculer et les coefficients de mortalité par pêche. Ses principales données d'entrée consistent dans le nombre total de prises par groupe d'âge effectuées par l'ensemble des flottes de pêche, le taux de consommation alimentaire et les proies préférées des poissons prédateurs et le poids individuel par âge des individus de chacune des espèces. Le second modèle, baptisé MSFOR ("Multi-Species Forecast" - modèle de prédiction multispécifique), sert à prévoir les rendements, les effets et la biomasse des stocks et le coefficient de mortalité par prédation en se fondant sur les résultats fournis par le modèle MSVPA (effets des stocks, prédation et autres paramètres définis), le recrutement estimé, le recrutement, et la mortalité par pêche supposés.

Deux études de cas concernant l'application des modèles sont présentées. S'agissant des stocks de merlu et d'anchois dans le nord-ouest de la Méditerranée, l'étude a abouti à la conclusion que l'aménagement devrait favoriser la production maximale chez le prédateur, le merlu.

Cette stratégie s'explique dans une large mesure par la forte valeur marchande de cette espèce. De plus, la prise en compte, dans l'évaluation, de l'interaction prédateur-proie n'a pas donné de meilleurs résultats que ceux issus de modèles monospécifiques. En fait, l'essentiel des résultats a été fourni par l'analyse de populations virtuelles (VPA) appliquée au merlu, notamment en ce qui concerne la quantification des bénéfices obtenus avec un âge à la première capture de 4 ans (correspondant à une longueur de 40 cm environ).

Vu la complexité des écosystèmes multispécifiques, il convient de ne pas trop simplifier les stratégies d'exploitation. L'opinion selon laquelle on peut augmenter la production totale d'un système en intensifiant la pêche des prédateurs et en récoltant ensuite de plus grandes quantités de proies situées plus bas dans le réseau trophique ne semble pas se vérifier dans la pratique. Lorsqu'on pêche davantage de prédateurs apicaux, leur rôle en tant que facteurs de régulation des populations d'espèces situées plus bas dans le réseau trophique est repris, au moins en partie, par les prédateurs immédiatement situés à un niveau trophique inférieur, et notamment par les individus âgés qui sont en mesure d'évoluer vers un niveau plus élevé. Cette évolution est facilitée lorsqu'il existe plusieurs types de prédateurs concurrents pour le même groupe de proies. De plus, dans la mesure où les prédateurs sont des agents de régulation naturelle des populations de proies, leur élimination sélective sur une grande échelle a un effet déstabilisant, illustré par la variation accrue de l'abondance des proies. En revanche, l'élimination sélective de ces dernières est préjudiciable aux prédateurs, bien que cet effet soit moins prononcé s'il existe d'autres sortes de proies.

Il est également indispensable d'évaluer les aspects économiques de l'exploitation des systèmes proie-prédateur. Flaaten (1989) a combiné dans un modèle biologique simple, un système à un seul prédateur et à une seule proie élaboré par May *et al.* (1979) avec des secteurs d'exploitation économiquement indépendants, à raison d'un secteur pour chacune des deux espèces. Comme prévu, dans ce cas très simple, l'auteur a constaté que l'exploitation du prédateur avait pour effet d'accroître le stock de proies exploitable et l'exploitation de la proie, de réduire le stock de prédateurs exploitable. En supposant que l'on peut capturer à moindre coût une proie de valeur marchande et que le prédateur est un poisson de faible valeur avec un coût de capture élevé, l'auteur parvient à la conclusion qu'il peut être économiquement justifié de subventionner l'exploitation du prédateur. A l'inverse, lorsque le prédateur peut être capturé à moindre coût et qu'il a une certaine valeur marchande alors que la proie est un poisson de faible valeur avec un coût de capture élevé, l'accroissement du stock de proies exploitable résultant de l'exploitation du prédateur peut justifier, au plan économique, la récolte de la proie, alors que ce n'était pas le cas précédemment. Cela s'effectuerait toutefois au détriment de la pêche du prédateur.

L'article cite des exemples d'intégration d'effets de la prédation dans les avis en matière d'aménagement des pêches maritimes. Dans l'Atlantique Nord-Est et Nord-Ouest, on a limité les prises de capelan de sorte qu'il en reste suffisamment de proies pour la morue, d'une plus grande valeur marchande.

A l'inverse, l'anchois et le pilchard sont toujours exploités de façon intensive dans l'Atlantique Sud-Est, même si ce sont des espèces proies pour le merlu et d'autres prédateurs de plus grande valeur marchande. Au nombre des autres exemples figurent l'exploitation des phoques à fourrure d'Afrique du Sud et l'abatage des phoques gris en Ecosse.

Il convient d'examiner les implications institutionnelles et sur les lignes de conduite en matière de gestion des ressources plurispécifiques. Trois problèmes, en particulier, sont abordés : la situation défavorable des pêcheurs autorisés (par les permis de pêche) à n'exploiter que certaines espèces; les ressources halieutiques sont souvent partagées avec d'autres prédateurs apicaux (baleines, phoques et oiseaux); et les difficultés institutionnelles qui surgissent lorsque les espèces tombent sous la juridiction de plusieurs organismes indépendants.

Toutefois, il apparaît manifestement qu'on a de plus en plus tendance à étudier et à gérer les stocks halieutiques sur une base multispécifique et, dans certains cas, à gérer les écosystèmes dont relèvent ces stocks. Dans les pêcheries multispécifiques, la viabilité économique continuera à jouer un rôle prépondérant dans les stratégies d'exploitation des stocks de prédateurs et de proies. Lorsque le prix par unité du prédateur est beaucoup plus élevé que celui de la proie, comme c'est généralement le cas, les stratégies de récolte seront surtout axées sur une exploitation durable des prédateurs et accorderont moins d'importance aux rendements que procurent les stocks de proies.

En conclusion, s'il est nécessaire de poursuivre les recherches en appui à l'aménagement des pêcheries multispécifiques, cela ne concerne pas indifféremment toutes les pêcheries. Ce travail de recherche dépendra de la connaissance des interactions entre espèces, de son efficacité en ce qui concerne les écosystèmes complexes et de sa pertinence dans les cas où des évaluations monospécifiques pourraient suffire. Quelle que soit l'importance accordée à la recherche, il sera indispensable de modéliser les interactions et leurs impacts en tenant pleinement compte du contexte bio-économique. Il faudra au moins disposer d'un minimum de connaissances sur les interactions entre espèces et les facteurs abiotiques. Au nombre de ces connaissances devraient figurer une meilleure compréhension des relations entre proies et prédateurs, des phénomènes climatiques naturels, des réponses écologiques et des effets de l'exploitation et de l'aménagement des ressources halieutiques.

EFFECTOS DE LAS RELACIONES DEPREDADOR-PRESA EN LAS ESTRATEGIAS DE EXPLOTACION Y LA ORDENACION DE LA PESCA

RESUMEN OPERATIVO

Los principales depredadores de los peces (incluidas las especies no comerciales) son los peces mismos. La depredación por parte del hombre es sustancialmente menor, aproximadamente del mismo nivel que de otros mamíferos. La depredación es un proceso importante para la regulación de las poblaciones de peces; sin embargo, las interacciones entre depredadores y presas y sus efectos sobre los recursos pesqueros son sumamente variados y complejos, por lo que es necesario estudiarlos en profundidad. El cuadro se complica más aún por la inestabilidad que caracteriza tanto al medio ambiente local como al ecosistema en que tienen lugar la depredación y la competencia. En realidad, las pesquerías del mundo están dirigidas tanto a las concentraciones de depredadores como de presas. Para lograr aprovechamiento más ventajoso es necesario conocer las interacciones, los efectos en el ecosistema, así como elaborar modelos bioeconómicos en un contexto multiespecífico. Este documento examina las interacciones depredador-presa como componente de la regulación de los recursos pesqueros. En él se hacen observaciones sobre el impacto y el alcance de la depredación en los ecosistemas marinos y de aguas dulces, se formulan propuestas para incluir los efectos de la depredación en la elaboración de modelos matemáticos sobre pesquerías de una sola especie y multiespecíficos, y se proporcionan ejemplos de cómo se han incorporado estos efectos al asesoramiento en materia de gestión y a las estrategias de explotación.

La depredación puede tener efectos significativos en los ecosistemas marinos y de agua dulce. La disminución del número de grandes ballenas mysticetes en el Antártico ocasionó en poco tiempo una mayor abundancia de krill, al reducirse en esta especie la mortalidad por depredación. A continuación crecieron las poblaciones de las ballenas mysticetes restantes, focas, aves marinas y sepias. Efectos similares pueden observarse en los ecosistemas de agua dulce, en la depredación de organismos marinos por las focas, y en la depredación de huevos y larvas. Cuando se introducen especies en lagos de agua dulce se observan algunos de los más espectaculares efectos de la depredación en las comunidades; un ejemplo de ello es la destrucción de los cíclidos de la especie *Haplocromis* en el Lago Victoria, tras la introducción de la perca del Nilo.

La explotación de mamíferos marinos constituye un caso particular, por las limitaciones de índole estética y moral que impone la opinión pública. Sin embargo, la continua recuperación de la mayor parte de las poblaciones de estas especies ha planteado el dilema de si debe mantenerse la prohibición casi total de explotarlas o se ha de permitir una explotación limitada, en condiciones cuidadosamente controladas. Se necesitan muchos más estudios para llegar a comprender cuáles serían las consecuencias de cada una de estas alternativas para el mantenimiento de ecosistemas equilibrados.

De todos modos es preciso informar mejor a la opinión pública sobre la medida real de la recuperación de estas poblaciones y sobre sus consecuencias para el ecosistema, a fin de permitir un examen más razonado de los costos y beneficios (estéticos, sociales y económicos) que comporta cada uno de estos enfoques alternativos.

En el documento se indica la amplitud de la depredación de las siguientes especies: bacalao, atún, colín de Alaska, mamíferos, cefalópodos y aves. Se presenta, a título de ejemplo, la magnitud de la depredación de los camarones en las aguas de Groenlandia: el consumo anual de camarón norteño por parte del halibut del Pacífico se estimó en 1 300 toneladas para 1990 y 1 100 toneladas para 1991, mientras que el consumo de camarones por las gallinetas se calculó en 33 600 toneladas en 1990 y en 8 700 toneladas en 1991. En esos dos años la captura nominal de camarones fue, respectivamente, de unas 52 000 toneladas y 58 000 toneladas.

Se han hecho intentos de incorporar los efectos de la depredación a los modelos de las pesquerías. Para su ampliación a evaluaciones de una especie se han tomado en cuenta los efectos del cambalismo y las repercusiones en el tamaño de las poblaciones, el reclutamiento, los rendimientos y las estrategias de ordenación. A su vez, los modelos elaborados para una especie también pueden ampliarse a modelos sencillos para especies múltiples. En un ejemplo referente a las interacciones entre la cigala y el bacalao en el mar de Irlanda, donde son éstas las dos especies más valiosas y se estima que el bacalao es responsable del 88 por ciento de la depredación total de la cigala, se llegó a la conclusión de que la explotación del bacalao se debía mantener al nivel más alto posible (aunque cuidando de evitar que disminuyera el reclutamiento), a fin de reducir la depredación de la cigala y obtener un mayor rendimiento de ésta.

Otros modelos de especies múltiples presentan mayor complejidad. El enfoque del CIBM consta de dos modelos. El primero es el MSVPA (análisis de una población virtual de especies múltiples), que se utiliza para efectuar estimaciones de la magnitud de las poblaciones en el pasado, de los coeficientes pasados de mortalidad por depredación y de los parámetros necesarios para calcularlos, así como de los coeficientes de mortalidad por pesca en el pasado. Utiliza como información primaria las cantidades totales de ejemplares de cada grupo de edades capturados por todas las flotas pesqueras, las tasas de consumo de alimentos y las presas preferidas por el pez depredador en cuestión, así como el peso individual por edad de todas las especies. El segundo modelo es el MSFOR (pronóstico para especies múltiples), que se utiliza para prever los rendimientos futuros, la magnitud de las poblaciones y la biomasa, así como para calcular los coeficientes futuros de mortalidad por depredación. Las informaciones de base de este modelo son los resultados del MSVPA (número de individuos de las poblaciones, depredación, y otros parámetros fijos), el reclutamiento estimado o supuesto y las hipótesis sobre la futura mortalidades por pesca.

En el documento se presentan dos estudios monográficos sobre la aplicación de modelos de especies múltiples. En el ejemplo de las poblaciones de merluza y anchovas del Mediterráneo nordoccidental, la conclusión es favorable a una ordenación que potencie al máximo los rendimientos del depredador, en este caso la merluza. El motivo principal de ello es que el precio de esta especie es más alto.

Por lo demás, la incorporación de una interacción depredador-presa en la evaluación no proporcionó ninguna otra información adicional con respecto a las evaluaciones para especies individuales. Los resultados más importantes se obtuvieron del análisis de la población virtual de una especie única aplicado a la merluza, especialmente en relación con la cuantificación del beneficio potencial que se obtendría si en la primera captura los peces tenían cuatro años de edad (es decir, una longitud de 40 cm aproximadamente).

Dada la complejidad de los ecosistemas de especies múltiples, las estrategias de explotación no deben simplificarse excesivamente. La idea de que se puede aumentar la producción total de un sistema reduciendo mediante la pesca la presencia de los depredadores, para luego explotar la abundancia mayor de presas de niveles inferiores de la cadena trófica, no parece corresponder a lo que ocurre en la práctica. Cuando la pesca del depredador principal se intensifica, su función de agente regulador de la abundancia de las especies inferiores de la cadena trófica es asumida, al menos en parte, por la especie depredadora que le sigue en la cadena; en efecto, en tal situación los individuos de más edad de ésta última se encuentran en condiciones de ascender a un nivel trófico más alto. Este fenómeno se acentúa aún más cuando existen muchos depredadores que compiten por el mismo grupo de presas. Además, puesto que el efecto natural de los depredadores es regular la abundancia de la presa, su eliminación sustancial y selectiva resultará desestabilizadora, reflejándose en una mayor variabilidad de la abundancia de la presa. Por otra parte, la eliminación selectiva de la presa irá en perjuicio de los depredadores, aunque este efecto se atenuará si existen otras presas disponibles.

También es necesario evaluar la economía de la explotación de depredadores y presas. Flaaten (1989) combinó un modelo biológico sencillo elaborado por May et al. (1979), que tomaba en consideración un solo depredador y una sola presa, con sectores pesqueros económicamente independientes, uno para cada una de las dos especies. Tal como se preveía, en esta situación sumamente simple la explotación del depredador llevaba a un aumento de la población explotable de la presa, y la explotación de la presa reducía la población explotable del depredador.

Las conclusiones de Flaaten fueron que si la presa era valiosa y su captura resultaba económica, y el depredador inservible y de captura costosa, podía existir una justificación económica para subvencionar la explotación del depredador. Si, en cambio, el depredador era valioso y de captura poco costosa, y la presa inservible y de captura poco económica, el aumento de la población explotable de ésta última que derivaría de la explotación del depredador podía hacer que la explotación de la presa, antes no conveniente, se volviera económicamente rentable. Sin embargo, esto ocurriría a expensas de la pesquería del depredador. Si ambas especies eran inservibles y de captura costosa, podría no haber explotación pesquera de ninguna de ellas.

En el documento se presentan ejemplos de incorporación de los efectos de la depredación al asesoramiento en materia de ordenación de las pesquerías marinas. En el Atlántico nordoriental y nordoccidental se limita la captura del capelán, a fin de que queden suficientes ejemplares como para alimentar al bacalao, especie de mayor valor.

En contraposición a ello, en el Atlántico sudoriental la anchoa y la sardina se siguen explotando intensamente a pesar de que estos peces constituyen un alimento precioso para especies de depredadores de mayor valor, como la merluza y otras. Otros ejemplos se refieren a la explotación del lobo marino de dos pelos en Sudáfrica y a la matanza sistemática de la foca gris en Escocia.

Es necesario examinar las repercusiones de una ordenación de especies múltiples tanto en el plano institucional como normativo. En el documento se destacan, en particular, tres cuestiones: la posibilidad de que resulten desfavorecidos los pescadores cuya actividad se limita (por ejemplo, mediante la concesión de licencias) a la explotación de determinadas especies; el hecho de que los recursos pesqueros a menudo se comparan con otros depredadores apicales (ballenas, focas y aves); y los problemas institucionales que surgen cuando una especie pertenece simultáneamente a las esferas de competencia de varios organismos independientes.

No obstante, no cabe duda de que se tiende cada vez más a adoptar un contexto de especies múltiples para el estudio y la ordenación de las poblaciones de peces, y también, en algunos casos, a aplicar la ordenación al ecosistema al que tales especies pertenecen. En las pesquerías de especies múltiples, la búsqueda de la viabilidad económica seguirá siendo el factor que más influirá en las estrategias adoptadas para la explotación de poblaciones de depredadores y presas. Cuando, como ocurre habitualmente, el precio por unidad del depredador es muy superior al de la presa, las estrategias de explotación asignarán la preferencia a la explotación sostenible del primero, y se considerarán menos importantes los rendimientos de las poblaciones de la presa.

La conclusión es que, si bien existe la necesidad de realizar investigaciones de apoyo para una ordenación de especies múltiples, estas no serán igualmente pertinentes para todas las pesquerías. Los estudios necesarios dependerán de cuán afirmadas estén las interacciones entre especies, de su eficacia con respecto a los costos en el marco de ecosistemas complejos, y de su idoneidad en casos en que podría ser suficiente efectuar evaluaciones para especies individuales. Por otra parte, cualquiera que sea la importancia que se acuerde a la investigación, es indispensable que los modelos de los efectos se elaboren tomando en cuenta el contexto bioeconómico en su totalidad. Será necesario adquirir por lo menos un conocimiento mínimo de las interacciones entre especies, así como de los factores abióticos. Este ha de incluir, según proceda, una comprensión más cabal de las relaciones entre depredador y presa, los procesos climáticos naturales, las respuestas ecológicas, y los efectos de la explotación y la ordenación.

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1. INTRODUCTION

This thematic paper on predator-prey relationships was prepared as background material to the International Conference on Sustainable Contribution of Fisheries to Food Security being held in Kyoto, Japan, in December 1995.

Worldwide, there are numerous examples of marine ecosystems which have experienced major shifts in species composition and stock abundance. The causes and mechanisms of these shifts are most often poorly understood. Some are no doubt the consequence of natural changes in the ecosystem. Others are clearly the result of interference by man, as through environmental degradation, and as the consequence of harvesting strategies.

This paper examines predator-prey interactions as a component of the regulation of fisheries resources. It includes observations on the magnitude and impact of predation in marine and freshwater ecosystems, the approaches to incorporating predation effects in the mathematical modelling of fisheries, and examples of how these effects have been included in the advice provided to the managers of fisheries. The paper is a review of a selection of existing works provided to the author.

2. PREDATION AS A COMPONENT OF POPULATION REGULATION

Predation is but one of the processes in population regulation in aquatic systems. While knowledge about the magnitude of predation is important, in order to fully appreciate the role of predation it is necessary to understand how predator and prey interact at different life history stages, and how this interaction is influenced through competition and associations with other species. Accepted theories of how populations and communities are regulated, including whether or not an equilibrium or underlying steady state exists (within a chosen context of time and space), will affect this understanding.

There are three principal theories for community regulation. Deterministic (or equilibrium theory) suggests that communities are regulated at an equilibrium or moving towards an equilibrium and that density dependent processes including predation and competition structure these communities (Hutchinson, 1959; Paine, 1974). Stochastic (or non-equilibrium) theory maintains that density independent, abiotic factors exert the overwhelming influence on population regulation (Andrewartha and Birch, 1954).

The more recent competitive crunch theory is somewhat intermediate, where populations are mostly unrestrained in a benign environment, but are subject to intense competitive pressure during occasional periods of severe conditions (Wiens, 1977). Competitive crunch theory implies that mechanisms of population regulation defined at one point of time may not be valid over longer periods.

Of particular interest in the context of this paper is the extent by which aquatic ecosystems are stable, the influence of predation on stability, and whether alterations to predation levels (as through fishing) are reversible. Both observation and ecological modelling have provided a multiplicity of answers to these matters, promoting essential debate while failing to be convincing in detail. Simple models lose credibility when the real systems are known to be complex, while the answers from more extensive analyses of multiple food webs have been determined more by the scale (temporal and spatial) of the available data than the system from which they were collected (Paine, 1988; Underwood and Fairweather, 1992; Warren, 1994).

The effects of predation are intertwined with those of food availability. Starvation can lead to an increased susceptibility to predation (Bailey, 1984; Purcell *et al.*, 1987; Rice *et al.*, 1987).

Predation that changes the habitat occupancy and foraging success of individual fish can lead to decreased individual growth rates (Werner *et al.*, 1983; Werner and Hall, 1988; Tonn *et al.*, 1992), decreased over winter survival (Post and Evans, 1989; Tonn *et al.*, 1992), and an increased period of susceptibility to size dependent predation. Freshwater and marine fish larvae often respond to the threat of predation by staying in the habitat and exhibiting other behavioural traits where the risk of mortality is minimised (Gilliam, 1982; Gilliam and Fraser, 1987; Gotceitas and Brown, 1993).

Predation can influence reproductive development in prey species, delaying the age and size at first sexual maturity until the threat of predation is withdrawn (Belk and Hales, 1993). Longer-term responses to the relative dangers of starvation and predation may be associated with trade off between egg size and egg number in species which have early and late spawning events (Hempel, 1965; Soin, 1971).

The size selective nature of predation can lead to change population growth rates; while selection for species can lead to changed community structure (Vanni, 1987; He and Wright, 1992; Hixon and Beets, 1993). Predation that removes the slower growing fish increases the population growth rate (Hanson and Chouinard, 1992; Sparholt, 1993). Predation that decreases the abundance of a prey, can cause the growth rates of the remaining individuals to increase if food becomes more available to the remaining population (Forsythe and Wren, 1979; Tonn *et al.*, 1992). This in turn can lead to a net increase in recruitment in the event that starvation had been limiting recruitment in the absence of predation (Jones, 1981).

Similarly, predation on the dominant competitor in a community can reduce competition, leading to increased growth rates for the subdominant species (Paine, 1974). The schooling of fish is considered a protective mechanism against predation (Brock and Riffenburgh, 1960). These authors suggested that the frequency of detection of a prey by a predator is an inverse function of the number of schooled or grouped prey; moreover, the larger the school, beyond the quantity of prey that the predators can consume at a single encounter, the lower the frequency of an individual prey being encountered by a predator.

There has been much consideration given to whether the processes of predation (top-down) or competition (bottom-up) control the dynamics of aquatic ecosystems (Hunter and Price, 1992; Power, 1992; Sherman, 1992; Polis, 1994).

Theoretical studies suggest that top-down processes control the upper trophic levels; while bottom-up processes control the lower trophic levels, the productivity of the system itself, and the number of trophic levels (Leibold, 1989).

In an evaluation of fishery ecosystems in enclosed and semi-enclosed seas, Caddy (1993) concluded that nutrient enrichment (bottom-up) and fishing (top-down) acted in synchrony to produce the observed changes in the trophic structure.

3. DISTINCTION BETWEEN SYMMETRICAL AND ASYMMETRICAL INTERACTIONS

Beverton (1985) draws a distinction between what he terms symmetrical and asymmetrical interactions with reference to fishery systems where man is competing with a marine mammal predator.

In symmetrical interactions, a reduction in the exploitation exerted by either top predator is beneficial to the other. This occurs when the commercial fishery and the predator exploit the same species; as in the Gulf of St Lawrence where cod feeds on capelin and both are eaten by harp seals and fished commercially; and in South Africa where snoek feed on anchovy and both are eaten by the Cape fur seal and fished commercially. Where there is this symmetry, at least the direction of impact from a reduced or enhanced marine mammal predation can be assessed with relatively simple mathematical models, even if the final balance between the two species cannot be assessed.

In asymmetric interactions a reduction in the abundance of one of the top predators may not necessarily be beneficial to the other. Examples include sea lions at a Pacific west coast river feeding on both salmon and lamprey, while only the salmon is fished commercially; the Cape fur seal which eats both Cape hake and squid, with the latter being only lightly fished; and Antarctic fisheries targeted at krill, with sperm whales feeding on the squid (an intermediate predator of krill).

In these, reducing the abundance of the marine mammal will tend to increase the presence of its prey.

Unless there is detailed understanding of the interactions between the prey species, there is no way of knowing whether this reduction in numbers of mammals would increase or decrease the abundance of the fished species, and hence the benefit to the fishery. In respect to all examples, reducing the fishing effort could be expected to benefit the marine mammals.

4. OBSERVATIONS ON THE IMPACT OF PREDATION

4.1 Marine Ecosystem Effects

Duggins (1988) combined an experimental removal of sea urchins in controlled areas with an examination of the ecological role of the sea otter. When sea urchins were removed, a kelp association of high biomass and diversity developed in one year, and within two years a high kelp biomass association dominated by one species. Similarly, when sea otters were transplanted into an area in which they had previously been absent for some years, there was a rapid increase in the biomass of kelp species, and a subsequent progression towards domination by a single species. The sea otter is characterized by Duggins (1988) and Simenstad *et al.* (1978) as being a vital predator in near shore communities. They suggest that the extinction of otters along the 6 000 km of Alaskan coastline and the accompanying loss of kelp must have caused major disruption to primary productivity, habitat and nursery areas, with subsequent negative consequences to certain fisheries.

Beddington and May (1982) refer to the reduction of the large baleen whales in the Antarctic (to one-sixth of their previous numbers) as providing an historic opportunity to observe the effects of predation (and competition) at the ecosystem level.

They refer to a reduction in the age at first sexual maturity for a number of the baleen whales, and increases in the pregnancy rates (i.e., probability of becoming pregnant in a given year), and attribute both to the decreased numbers of whales. According to these authors and Basson (1989) the short-term effect observed in 1928-1935 was an increase in krill abundance through reduced mortalities from predation (although the growth rates of krill also declined). Subsequently there was population growth among the remaining baleen whales (particularly the minke), seals, seabirds and squid with much (if not all) of the previous predation levels being established despite the greatly reduced numbers of the large whales. As the whale populations continue to recover, the extent to which the ecosystem reverts back to its earlier structure is sure to attract substantial interest amongst scientists.

Predation and competition obviously act together to determine population structures and inter-relationships. Anderson and Ursin (1977) modelled the gadoid outburst which occurred from 1962 to 1974, in which there were seven-year classes of cod, four-year classes of haddock and four-year classes of whiting that were stronger than any previously recorded. At the same time the abundance of two of the three North Sea herring stocks were at one-twentieth and one-thirtieth of previous peak abundances, and the mackerel stock was at a similar low level.

These small pelagics are known to be predators and competitors for food with larval and juvenile gadoids; thus the above authors concluded that the reduced abundance of herring and mackerel had directly benefited the gadoid stocks. In a later review of the data, Cushing (1980) came to no firm conclusion on the matter, although he favoured wide-scale climatic events as the cause.

Murawski (1983) showed that intensive fishing in the US Northeast continental shelf ecosystem in the late 1960s and early 1970s was accompanied by an approximately fifty percent decline in the biomass of economically important fish (eg. cod, haddock, flounders, herring and mackerel). This decline was subsequently followed by an increase in the biomass of lower value species (eg. sandlance, dogfish and skates) which resulted in changes to consumption and predation throughout the ecosystem (Overholtz and Nicholas, 1979; Powers and Brown, 1987; and Payne *et al.*, 1990).

Herring and mackerel are undergoing a recovery after earlier exploitation levels were reduced; however, the demersal resources remain depleted, with dogfish and skates constituting 74 of the combined stocks biomass on the Georges Bank compared with 24 in 1963.

4.2 Freshwater Ecosystems

The suggestion that top-down and bottom-up effects do not occur in isolation from one another and can alter primary production is well demonstrated in freshwater ecosystems. Bronmark *et al.* (1992) studied a mesotrophic lake and concluded that predation by the top-level predator (pumpkin seed sunfish) decreased the abundance of the second trophic level (snails), which led to an increased biomass of the periphyton at the third trophic level.

Vanni *et al.* (1990) describe a freshwater lake which experienced a massive fish mortality (reduction of cisco biomass from 239 kg/hectare to 13 kg/hectare) in an unusually warm summer. This reduced predation on larger zooplankters, led to an increased abundance of larger daphnia and a decreased abundance of phytoplankton. Physical factors and the concentrations of limiting nutrients were unchanged over the same period, indicating that the apical predation had been important in maintaining phytoplankton levels.

Tonn *et al.* (1992) describe a complex interaction between fish-eating Eurasian carp and crucian carp. The young-of-the-year crucian carp were reduced directly to 10% of control levels by direct predation, and then experienced reduced growth rates (increasing the duration of susceptibility to predation) due to habitat restriction, before finally growing to a larger individual size than control populations due to reduced intra-specific competition. This provides a good example of the direct and indirect effects of predation, the latter mediated through habitat restriction and reduced competition.

A more complex stage-structured interaction occurs when species compete at one life-stage but are predator-prey at another (Werner and Gilliam, 1983; Polis *et al.*, 1989). Largemouth bass are the top predators in many Michigan lakes and almost exclusively piscivorous at larger sizes. Like the bluegill sunfish on which it predate, bass go through an early stage in which they feed on soft-bodied littoral invertebrates.

The transition from competitor to predator occurs in the bass's first year, after which they feed extensively on young-of-the-year bluegill.

Recent experimental work shows that the pattern of bass growth and density is consistent with these stage specific interactions. A strong positive correlation was found between the growth rates of large bass and the density of small bluegill, while the growth of young bass (in the invertebrate feeding stage) was negatively correlated with the density of juvenile bluegill (Mittelbach, 1993).

4.3 Predation by Marine Mammals

The study of fish communities in a Quebec freshwater lake subject to predation by seals, compared with those in adjacent seal-free lakes reported in Power and Gregoire (1978), provided the only convincing case of mammal populations reducing exploited fish abundance in a review of marine mammal predation (Beverton, 1985).

In the lake where seals were present, there was a different impact on two species of trout. Lake trout, which aggregate during spawning and hence increases its vulnerability to predators, showed an absence of larger size classes, increased growth rates, increased fecundity and reduced age at maturity when subjected to predation. The brook trout, which is less vulnerable because they spawn in scattered locations, were relatively more abundant in the lake where seals were present.

The local impact of marine mammal predation can depend on the degree of feeding specialization. Grey whales, which feed by sucking sediment into their mouths and extracting food items, cause pits which may cover more than 30% of the seabed in places. Dense mats of amphipod crustaceans are destroyed in this feeding process and replaced by other scavenging invertebrates (Oliver and Statter, 1985). Similarly, high walrus abundance in Alaskan waters are associated with low bivalve mollusc densities (Fay *et al.*, 1977). In contrast, grey seals in the North Sea that feed on a variety of mobile fish species were not considered to be a major factor in influencing community dynamics, because the mortality caused by seals was one or two orders of magnitude less than that caused by fishing, and spread over more prey species (Harwood and Croxall, 1988).

Hauke *et al.* (1995) studied the diets of minke whale in Norwegian and adjacent waters during the spring, summer and autumn of 1993 and 1994. Gadoid fish dominated the spring diet. In summer and autumn the diet in the northernmost areas (Spitsbergen and Bear Island) was primarily krill, and to a lesser extent capelin. This was consistent with an increase in the abundance of krill and a severe decrease for capelin, compared with previous years. In the coastal waters of northern Norway, herring was the most important food item for the whales in both summer and autumn. Statistical analysis suggested that herring and capelin were the preferred diet, ahead of krill and gadoid species.

There have been and continue to be proposals to reduce marine mammal populations, especially seals, so as to decrease the competition for fish between marine mammals and commercial fishermen (Wickens, 1995).

In instances where seals damage fishing nets, scare fish away from nets, and predate on fish approaching or in the nets, there are obvious short-term benefits to the fishermen in reducing their interactions with the seals. In other instances where the aim of reducing a seal population is to achieve an increase in the abundance of the commercial fish stocks (eg. Northwest and Southeast Atlantic), the benefits are far less certain. According to Northridge and Beddington (1992), there are many instances, especially where seals are concerned, in which the diets of marine mammals are too varied and flexible and the inter-relationships between the fish too complex, to enable the results of decreased predation by marine mammals on fish stocks to be predicted. The Royal Commission on seals and sealing in Canada (Anon., 1986) concluded that although there was strong evidence that seals could affect the abundance of fish stocks, it was "not aware of any instance in which known and measured change in the abundance of seals has had a measurable effect on fish catches".

Butterworth *et al.* (1988), investigating the scientific basis for reducing the South African seal population, could find no "proven link between seal population reduction and a consequential increase in yield to any fishery worldwide". Similarly, Bowen (1985) concluded from a review of the interactions between seals and fisheries in the Northwest Atlantic that "we simply cannot say what effect an increase or decrease in the harp seal populations will have on fish catches over the long term", as there is likely to be associated increases in the mortalities caused by other predators (eg. whales, seabirds and cod).

4.4 Predation on Eggs and Larvae

The significance of predation on eggs and larvae is illustrated by the reproductive patterns that have evolved to minimize its effects. Dragesund and Nakken (1973) for example concluded that successful spawning of Norwegian spring spawned herring requires widespread distribution of the larvae, a long duration for the spawning period, and rapid dispersion of the larvae from the spawning grounds to minimize the predation by haddock and saithe that are thought to consume up to 40% of the eggs.

In other species, larvae emerge from the eggs at the same time as those of more abundant species including capelin (Frank and Leggett, 1983) and pink salmon (Parker, 1971) that will bear the brunt of the high predation at this vulnerable stage. Reproductive strategies adopted by cohorts of the same species spawning at different times of the year can include tradeoffs between large numbers of eggs that will satiate predators and fewer eggs of a larger size to prolong survival during poor feeding conditions (Hempel, 1965 and Soin, 1971).

Lambert and Ware (1984) suggested "all at once" egg release for the fast-growing Atlantic mackerel and the batch release of eggs or "bet hedging" by the slow-growing herring, were both directed towards minimizing predation mortality.

Although difficult to establish, the sheer magnitude of predation on eggs and larvae is likely to affect the number of recruits subsequently entering the fisheries for many species.

Van der Veer (1985/1986/1987) concluded that predation by coelenterates in the coastal zone of the western Wadden Sea determined the order of magnitude for the abundance of larval plaice prior to settlement, with the final regulation of year class strength being from the predation of post-settlement larvae by brown shrimp.

Purcell *et al.* (1987) reports on a positive feedback loop for the impact of jellyfish predators on herring, in which the jellyfish affects the herring larvae through direct predation, competes with the larvae for food, and prolongs the latter's vulnerability to predation in the event that the reduced food supply causes slower growth of the larvae.

4.5 Introduced Species

Some of the more dramatic effects of predation at the community level have been observed with respect to introductions into freshwater lakes. The destruction of the haplochromine cichlids of Lake Victoria following the increased abundance of Nile perch in the 1980s, more than twenty years after its introduction, is a well publicised example (Witte *et al.*, 1992). Extrapolating from a limited sample, these authors suggest that possibly two-thirds of the 300+ endemic haplochromine species are now extinct or threatened. The food web in the lake has changed dramatically. Ironically, the fishery yield has increased three to four times, although it is unknown whether such higher catches can be maintained. Estimates of biomass, catches and predation loss for each of the Nile perch, catfish, tilapia and the haplochromines given below from Moreau *et al.* (1993) reflect the net effect of the species interactions and other factors including exploitation (Table 1). Both Nile perch and catfish are predators on the other two species groups, with tilapia appearing to benefit from the Nile perch introduction and the haplochromines an obvious casualty.

Table 1: Biomass, catches and predation loss in the Kenyan sector of Lake Victoria.

Species Group	Biomass (t/km ²)		Catches (t/km ² /yr)		Predation loss (t/km ² /yr)	
	'71 - '72	'85 - '86	'71 - '72	'85 - '86	'71 - '72	'85 - '86
Nile perch	0.0	17.3	0.0	10.0	0.0	5.3
Catfish	2.8	1.7	0.8	0.2	1.3	1.2
Tilapia	2.5	13.0	0.7	2.0	1.7	9.3
Haplochromines	8.4	0.6	1.1	0.0	15.8	1.5
All Fish	27.0	43.4	3.3	16.5	33.3	30.8

4.6 Discard Mortalities and Predation

The incidental kills of dolphins in the eastern tropical Pacific Ocean tuna fishery provide a high profile example of man-induced impacts on the balance of predators. Alversen *et al.* (1994) assessed the magnitude of dolphin mortality. It appears that annual mortalities were between 200 000 and 500 000 dolphins, from the beginning of the fishery in 1959 until the early 1970s. The subsequent decline in dolphin mortality was from technological improvements in gear handling, arising from industry and government concern. The problem re-emerged in the mid-1980s. The subsequent public response favoured producers able to guarantee that their tuna products were caught without any associated mortality of dolphin. Discard mortalities in this fishery have declined markedly since 1989.

Energy flow modelling of the Gulf of Mexico shrimp fishery demonstrated that the incidental mortalities of discards can influence the groundfish predator-prey interactions (Browder, 1981).

This author speculated that the mortalities of prey species similar in size to shrimp, could induce the predators to seek alternative prey species, leading to increased predation on the shrimp.

Estimates from Kuwait (Pauly and Palomares, 1987) indicate that fish consume three times as much shrimp (in weight) as is landed, even with high discard rates of fish. The implication from this is that reducing the fish by-catch (as through the use of more selective gear) might impact negatively on the size of the shrimp stock and landings. Reducing discards could also impact negatively on shrimp stocks, if shrimp feed on the discards.

Conversely, Sheridan *et al.* (1984) found that only a few species of fish included substantial quantities of shrimp in their diet, and from a modelling exercise concluded that the reduction of discards would have only minimal influence on the abundance of shrimp. Some support is provided by Hill and Wassenberg (1990), who found that sharks, dolphins and birds were the most important scavengers of discards from prawn trawl fisheries in northern Australia, whereas scavenging by invertebrates was negligible. The impact of discarding on shrimp stocks clearly needs to be investigated further.

5. OBSERVATIONS ON THE MAGNITUDES OF PREDATION

5.1 Predation in Marine Ecosystems

The few studies on the magnitude of predation in large marine ecosystems in which there are substantial fisheries have shown that the major predators of fish are the fish themselves. In respect to the six ecosystems examined by Bax (1991), predation by fish was concluded as ranging from 2 to 35 times that from commercial exploitation by man (Table 2).

Furthermore, it was determined that mortality from predation was the major component of the total mortality experienced by fish in these ecosystems. In four of the ecosystems, marine mammal predation was about equal to or greater than that from fishing.

Table 2: Comparison of predation in six large marine ecosystems.

Ecosystem	Fish predation (t/km ² /yr) by			
	Birds	Mammals	Fish	Man
Benguela Current	0.3	2.6	56.5	1.6
Georges Bank	2.0	5.4	42.5	6.1
Balsford	0.0	0.0	14.1	1.5
E. Bering Sea	0.2	1.5	11.0	1.4
North Sea	0.6	0.1	7.0	4.4
Barents Sea	0.0	3.0	5.1	1.8

Somewhat similar results are given in Christensen and Pauly (1992) for biomass flows to predation by fish and fisheries in four continental shelf ecosystems (Table 3). The biomass flow to predation by fish was determined as being between 3 and 25 times as large as the respective commercial catches.

Table 3: Comparison of biomass flows for four continental shelf ecosystems.

Ecosystem	Units of measurement	Biomass flows to predation by	
		Fish	Man
Yucatan, Mexico	g.dw/m ² /yr	2.1	0.1
Gulf of Mexico	g.dw/m ² /yr	8.2	2.4
Venezuela	t/km ² /yr	32.0	5.2
Brunei Darussalam	t/km ² /yr	15.1	0.7

5.2 Predation by Tuna

Olson (1995) examined the role of predation by yellowfin tuna (*Thunnus albacares*) larger than 50 cm. in the eastern Pacific Ocean using a bio-energetics model of growth interfaced with population and diet data.

The estimates for the quantities of prey consumed by yellowfin were compared with catches of the prey groupings during the same period (1970-72) and some 10-20 years later (Table 4).

Many of the same prey are consumed by other apical predators, including other tunas, dolphins, billfish, dolphinfish, and sharks.

The main contributors to the diet of yellowfin were frigate and bullet mackerels (*Auxis* spp.) and flyingfish (Fam. Exocoetidae).

Given the large quantities consumed, it was concluded as likely that predation by yellowfin (and others) is an important regulator of the community structure.

Table 4: Comparison of quantities consumed and caught for prey of yellowfin tuna.

Prey Species Group	Mean Annual Catch (1970-72) (mt)	Mean Annual Predation (1970-72) (mt)	Mean Annual Catch (1982-91) (mt)
Yellowfin tuna	130 067	250	219 596
Skipjack tuna	62 733	19 556	70 166
Striped tuna	0	416	0
Wahoo	0	83	0
Frigate/bullet tuna	0	383 631	19
Flyingfish	0	106 748	0
Pomfrets	0	41 179	0
Jacks	1 067	16 450	2 220
Triggerfish	0	9 079	203
Dolphinfish	0	3 844	85
Billfish	33	1	1 185
Squid	133	23 754	2 150
Octopus	67	449	603
Craylets	0	28 834	3 969

In a study of the food consumption and diet composition in the southwestern Gulf of St. Lawrence by Waiwood and Majkowski (1984), plaice (*Hippoglossoides platessoides*) and snow crab (*Chionoecetes opilio*) were found to be the principal commercial species in the diet of cod (*Gadus morhua*). They estimated that 6 840 t of plaice had been consumed by cod age groups 3 - 15 yr. during the study period (May - November, 1980). In 1980 the annual catch of plaice for the entire Gulf of St. Lawrence was 7 100 t. Cod consumption of snow crab was estimated to be 8 520 t. The annual catch of these crab in 1979/1980 approached 15 000 t, of which about half would have been caught in the study area.

These two species accounted for 8.5% of the cod food biomass. The contribution of non-commercial species in the food biomass was 88%: comprised of other fish (18%), decapods (22%), molluscs (11%), euphausiids (15%), annelids (8%), and other invertebrates (15%).

According to Mehl (1989) and Bogstad and Mehl (1992), capelin may comprise up to 50% of the annual diet of cod in the Barents Sea. Mehl (1989) estimated that from 1984 to 1986, Barents Sea cod consumed 0.4 to 1.2 times their own biomass of capelin, which included an estimated 85% of the numbers of 3- and 4- group capelin in 1985. These values represent a threefold increase from the preceding years, and were due to an abnormally strong year class of cod reaching a size at which large capelin could be consumed.

The strong 1983 year-class of herring also contributed substantially to the predation on capelin (Hamre, 1988 and 1990). The resulting decline in the abundance of capelin (and herring) stocks in the Barents Sea during the late 1980s, are believed to have resulted in emaciated cod along the Norwegian coast, and possibly the previously mentioned invasion of seals in 1987 (Hamre, 1988). These dramatic events provided much of the impetus towards including predator-prey interactions within the mathematical models used as aids to fisheries management.

While rarely cannibalistic at lengths less than 30 cm, Bogstad *et al.* (1994) found that cod of the Barents Sea and the shelves off Iceland and eastern Newfoundland became increasingly so as they grew older. Most of the prey were found to be smaller than 40 cm in length and younger than three years. Almost all the cannibals were at least twice the length of their prey, and most were more than three times longer. Expressed on a age weight basis, the contribution of young to the diet of cod, was found not to exceed 9% on average, even for the largest predator size group. Cannibalism was most prevalent in the Barents Sea, lowest off Newfoundland, and intermediate off Iceland.

The estimates for the number of cod consumed annually by cod in the Barents Sea were found to have the same order of magnitude as an average 3+ year class (i.e. about 600 million individuals). The frequency of occurrence of cannibalism increased with the abundance of juvenile cod. The results provided little support for the hypothesis that the frequency increased when the abundance of capelin was low.

5.4 Predation by Marine Mammals

Predation by marine mammals on fish also taken by commercial fishermen can be large. A collection of papers in Beddington *et al.* (1985) provides examples where the quantities of commercially caught fish eaten by marine mammals is similar or greater than the quantities caught by fishermen in several areas. These include South Georgia, the Kerguelen Islands, Southern Africa, the Northwest Atlantic, and the Bering Sea.

Other examples are cited, such as the US Pacific Northwest coast and Bristol Bay where the development of commercial fisheries on shellfish is being prevented through localized predation by marine mammals.

The previously mentioned invasion of the Norwegian coast by harp seals in 1987 is a somewhat special case, although previous invasions have been recorded (1902-1903). Ugland *et al.* (1993) estimated the fish consumed by these seals over a three to four month period in 1987 to be about 215 000 tonnes, mostly cod and saithe. They estimated that consumption by seals in 1988 was about 40% of the level in 1987.

Hauksson (1993) gives an account of the consumption of commercially important fish by seals in Icelandic waters. He concluded that without seal predation, yields from commercial fish stocks might have increased by about 300 000 tonnes in 1987, when the total Icelandic catch of fish was about 1.7 million tonnes; and hence the cod quota could have been increased by about a third.

The possible indirect effect from reduced seal predation, such as increased predation on other fish by cod and other piscivores, was not figured into these estimates.

Preliminary analysis of data collected during 1986-89 by the Marine Research Unit in Reykjavik has provided estimates for the consumption by cetaceans in Icelandic and adjacent waters (Vikingsson, 1993).

The estimate of total consumption is 4.6 million tonnes, consisting of about 50% krill, and 25% each of finfish and cephalopods. Fin whales were the principle consumers, taking about a third of the total. The main finfish consumers were the minke whales, pilot whales, and two species of dolphin.

5.5 Predation of Walleye Pollock

Aron (1988) analyzed the quantities of walleye pollock removed annually by predators in the Eastern Bering Sea during the early 1980s. In order of importance by weight consumed, the main predators are the walleye pollock and other fish, man, marine mammals, and marine birds (Table 5).

In a review of predation by seabirds, Furness (1982) found that their consumption was the equivalent of 22 of the fish production off Oregon (USA), 29 within a 45 km radius of a colony in the Shetland Islands (UK), 24 of the mean catch off South Africa, and 17 of the anchovy off Peru (from 1961 to 1965). In Vermeer *et al.* (1987) reference is made to daily consumption by murres being between 10 and 30 of their body weight.

5.7 Predation by Birds

Cephalopods are abundant and widespread predators of fish. They have a high metabolic rate, and are able to rapidly increase population numbers. They are also prey to mammals, seabirds and fish. Longhurst and Pauly (1987) provide estimates for the annual consumption by cephalopods in the Gulf of Thailand of 700 000 t in the early 1960's and 500 000 t in the early 1980's. The annual fisheries harvest in the two periods is given as 200 000 t and 800 000 t respectively. Lipinski (1992) provides estimates for the consumption by cephalopods in the Benguela ecosystem. The diet of one of the five major squid species contains 10 to 50 of commercial fish species, during the sixty of the year when their distribution overlaps with hake and anchovy. Estimated abundance for this squid is 20 000 to 100 000 t and the daily food requirement is 2 to 15 of body weight. This provides estimates for the annual consumption of commercial fish by this taxa from 8 500 to 1 600 000 t.

5.6 Predation by Cephalopods

Source of Removals	Est. Biomass Removed (mt)	%	Est. Number Removed (x10 ⁹)	%
Fishery	1 000 000	18	2.0	0.4
Marine mammals: fur seals	167 000	3	2.5	0.5
sea lions	274 000	5	1.3	0.3
all others	60 000	1	0.1	<0.1
all species	501 000	9	3.9	0.8
Marine birds	272 000	5	68.0	13.8
species	2 696 000	48	416.5	84.4
Marine fish: walleye pollock	1 116 000	20	3.1	0.6
others	3 812 000	68	419.6	85.0
Totals	5 585 000	100	493.5	100

Table 5: Sources and scale of walleye pollock predation

An estimate of 2 675 t/day is given for the consumption by fish-eating alcids in the eastern North Pacific, and 866 t/day as the consumption by other species of birds. The diets include juvenile fish of commercial importance, as well as non-commercial species.

Northern gannets in Newfoundland waters consume the same pelagic prey species as occur in the commercial fishery. According to Montevecchi *et al.* (1988), the estimates for the consumption of mackerel and squid by gannets often exceeds the quantities landed by fishermen.

An important proportion of the diet of seabirds can consist of fish discarded at sea from fishing vessels. An estimated 90 % of the offal and 75 % of the whole fish discarded from commercial vessels around the British Isles is consumed by seabirds according to Furness *et al.* (1988).

These quantities are equivalent to between 5 and 10 % of the landed weight from the associated flatfish and gadoid fisheries. Primarily as the result of the at-sea discard of non-target species and processing wastes, the number of scavenging seabird pairs in the North Sea region has risen from 37 000 in 1990 to 614 000 recently (Furness, 1993; Hudson and Furness, 1988). This increase in birds is presumably reflected by an increase in the predation of live fish.

Predation of seabirds on juvenile fish can be extremely high when juvenile fish are in a restricted area. Mace (1983) found that birds captured 10 to 12 % of a release of chinook salmon within 2 km of their release from a hatchery in British Columbia. Wood (1987) found this to be an exceptional case, however, and cited maximum mortality rates of salmon due to bird predation as generally not exceeding 10 % over the entire seaward migration.

5.8 Predation on Shrimp

The magnitude of the predation on shrimp in the waters of Greenland has been studied by Pedersen (1993). The annual consumption of northern shrimp by Pacific halibut was estimated as 1 300 tonnes for 1990 and 1 100 tonnes for 1991. The consumption of shrimp by redfish was estimated to be 33 600 tonnes in 1990 and 8 700 tonnes in 1991. The nominal catch of shrimp in the two years was about 52 000 tonnes and 58 000 tonnes respectively. The annual consumption of redfish by Greenland halibut was estimated as 2 900 tonnes and 5 100 tonnes in the two years.

5.9 Predation on Eggs and Larvae

Fish eggs and larvae constitute the major component of the diet for many marine species.

These include invertebrates such as medusae, which have been estimated to individually consume the equivalent of 57 herring larvae per day (Arai and Day, 1982), to collectively consume up to 28 and 60 % of larval stocks daily in some locations (Purcell *et al.*, 1987), and between 2 to 5 % daily for the total stock of herring larvae (Moller, 1980). Fortunately these very high rates of consumption are confined to relatively short periods of each year.

Invertebrates are not the only predators of herring eggs. Johannessen (1980) found an average of 15 000 to 20 000 eggs in the stomachs of cod caught near a herring spawning ground in a Norwegian fjord and concluded that predation could remove 40 to 60% of total egg production in years of low egg deposition. Dragesund and Naken (1973) concluded that haddock and saithe eat up to 40% of the eggs of spring spawning herring.

6. APPROACHES TO INCORPORATING PREDATION EFFECTS WITHIN FISHERIES MODELS

6.1 Extensions to Single Species Assessments

An example of the simple extension of single species methods to include predation is the inclusion of cannibalism in a virtual population analysis (VPA) for Cape hake taken off the coast of Namibia (Leonart *et al.*, 1985). Juveniles can constitute over fifty% of the diet of Cape hake over 60 cm, and it was therefore thought that reducing the adult population could lead to an increased survival of the juveniles and hence recruitment to the fishery. In the analysis the natural mortality input was compartmentalised to separate that due to cannibalism from that due to other causes. As the effects of cannibalism are not the same for all year classes this results in a variable natural mortality with age. The overall effect was that the computed numbers at age were different than if the cannibalism effect had not been included, and the management implications from the results were changed, especially in respect to the choice of mesh size in the fishery.

More recently Punt and Hilborn (1994) examined the inclusion of cannibalism within a model of the Cape hake fishery off South Africa. They obtained estimates of stock size and potential yield for given levels of fishing effort from the application of Schaefer-type production models (with and without the inclusion of cannibalism effects) fitted to the observed catch and effort data. The models also allowed for the effect of compensatory changes in the rate of reproduction.

The estimates for stock size and yield were very similar, although there was a tendency for the non-cannibalistic version to overestimate the maximum sustainable yield (MSY). Also the estimated biomass associated with MSY was found to be 30% of the unexploited biomass from the cannibalistic version, compared with 50% from the non-cannibalistic version.

In respect to this application and with simulated data, the implications for the management of the fishery (using an F_{MSY} harvesting strategy) in the short and medium term were found to be very similar. While not discounting the need to include cannibalistic effects within fishery models where appropriate, especially in respect to identifying the appropriate long-term strategies for management, the above authors cautioned against too readily discarding the simpler approaches.

Their point was that before embarking on lengthy and costly stomach sampling programmes and formulating more complex models, the existing models and management strategies should be tested for resilience. In many situations, it was suggested that the cost-effective alternative to explicitly modelling cannibalism (and other predation effects) may be the definition of management strategies that are robust to the expected range of biological interactions for the stock being managed.

6.2 Simple Multi-Species Models

The approach of Shepherd (1988) was for a multi-species extension of the existing age structured yield per recruit models, which incorporates predation mortality coefficients and stock/recruitment relationships. The objective was to achieve greater realism than from the single species models, while avoiding the uncertainties of more complex models. The approach was applied to investigate possible yield scenarios for North Sea gadoids subject to industrial and consumption fishing (Macer and Shepherd, 1987) and to explore the interactions between Norway lobster and cod in the Irish Sea (Brander and Bennett, 1986; and Brander, 1988). Cod and Norway lobster are the two most valuable species landed from the Irish Sea. Cod is the main predator of the lobster, consuming an estimated 88% of the total consumption by all species. They are targeted by separate trawl fisheries, although juvenile cod are a bycatch of the lobster fishery (which employs a smaller mesh size). The conclusion from the multi-species analysis was different to that from the previous single species assessments, in identifying that the exploitation of cod should be kept as high as possible (though not so high as to cause declining recruitment) in order to reduce predation and increase the yield of lobster.

Another extension of single species models are the multi-species adaptations of production models and the models used in theoretical ecology (May *et al.*, 1979; and Kirkwood, 1982). These are idealised in the sense of incorporating simplified predator/prey and competition relationships, and hence suffer from substantial uncertainty about whether they adequately reflect the real situations to which they are applied. They have nevertheless been extensively used to develop an understanding of the possible interaction between species, and hence the aspects requiring further research.

6.3 ICES Multi-Species Models

The ICES multi-species approach principally comprises two models. The first is MSVPA (Multi-Species Virtual Population Analysis), which is used to estimate the past stock numbers, the past predation mortality coefficients and the parameters to compute them, and the past fishing mortality coefficients. It takes as its primary inputs the total numbers caught by age group by all fishing fleets, the food consumption rates and prey preferences of the predatory fish, and individual weights by age for all the species. The second model is MSFOR (Multi-Species Forecast), which is used to predict future yields, stock numbers and biomass, and future predation mortality coefficients. Its inputs are the outputs from the MSVPA (stock numbers, predation and other fixed parameters), estimated or assumed recruitment, and assumed future fishing mortalities.

These models seek to use all the data at the highest level of dis-aggregation. The concept is that each stock is composed of age groups (or cohorts), and that each year there is a new batch of recruits entering the stock (from reproduction). The models follow the cohorts during their life, and account for the number of survivors at the beginning and end of each time interval, and the numbers dying from each of capture, predation, and other natural causes. Mean individual weights are determined for each time interval, which in turn allows catch numbers to be converted to catch weights and stock numbers to biomass. In these aspects, apart from the estimation of predation mortality, the models are the same as single species models of the analytical type.

The first versions of MSVPA were presented in Helgason and Gislason (1979) and Pope (1979). Further developments have occurred largely within the multi-species working groups of ICES. Its predation part is a simplified version of a more comprehensive model developed by Andersen and Ursin (1977). Food preference coefficients (ie, the preference of a predator for a particular prey) estimated within MSVPA are used in conjunction with stock numbers to predict the predation mortality impacts within MSFOR. The preference for a prey by its predators is assumed to remain constant.

ICES attempted to test this assumption in respect to the North Sea fisheries. In 1981, 55 166 stomachs from five species were collected, and in 1991, 92 984 stomachs were collected from ten species (including the previous five). Predicted and observed consumption by species was compared to test whether the diet preference over the ten years had remained constant.

The conclusions from the most recent analyses of these data (Anon, 1994) were that preference had not remained entirely constant over the ten-year period. The MSVPA model was able to explain about fifty of the differences. The unexplained component was suggested as possibly resulting (1) from changes in the spatial overlapping of the species (no spatial structure is included in the North Sea MSVPA), (2) other aspects of predator-prey interactions that have not been modelled, and (3) error arising from sampling and data preparation.

6.4 Multi-Species Models for the Barents Sea

The model for the Barents Sea (MULTSPEC) was initially developed for estimating predation mortalities on mature capelin by cod (Bogstad and Tjelmeland, 1990 and 1992).

Related simpler models have been produced in concert: AGMULT which is an area aggregated version of MULTSPEC for use in connection with bio-economic modelling, and CAPSEX which is used to assist in formulating management specifically for the capelin stock (Tjelmeland and Bogstad, 1993).

In its more recent application the MULTSPEC model was extended to also include herring, harp seal and minke whale interactions (Bogstad *et al.*, 1995). Like MSFOR it enables predictions of future outcomes by simulation.

It is more ambitious in its treatment of migration between geographical sub-areas, and individual growth as a function of predator size, prey size, prey availability and temperature. Within the model the stocks are structured by geographical sub-area, age, length, sex and maturity. The recruitments are estimated from spawning stock biomass.

A shortcoming of the applications so far reported is that the fishing mortalities on capelin, herring and cod are assumed constant and not dependent on stock abundances. The harp seal and minke whale components are presently limited to investigating the effects of mammal predation on the fish stocks.

Future versions are expected to allow examination of the impacts of fluctuating prey abundance on the mammal stocks. The model may also be extended to include nearby waters, to take account of that part of the minke whale stock which remains outside the Barents Sea.

6.5 Management by Field Experimentation

Controlled field experiments (or adaptive management) are being suggested by a number of authors as ways of achieving better management (Walters and Hilborn, 1976; Tyler *et al.*, 1982; Punt and Butterworth, 1991; Polis, 1994).

A promising example is occurring in respect to the demersal multi-species fisheries of the Northwest shelf of Australia. Here sub-areas are being subjected to different levels and types of fishing effort, including complete closure (Sainsbury, 1988).

Changes in stock abundance, structure, biological impacts and fishery performance are being monitored, and the results will be used to compare the observed and predicted changes from multi-species models based on alternative interaction hypotheses.

7. CASE STUDY OF ICES MULTI-SPECIES MODELS APPLIED TO COD, HERRING AND SPRAT STOCKS IN THE BALTIC SEA

7.1 General Description of Stocks and Diets

The Baltic fisheries system is relatively simple with one major predator (cod) and two major prey species (herring and sprat). The impact of predation by marine mammals is relatively minor. Cod are demersal in habit, spawning from 2 - 3 years of age, mostly from May to June.

The eggs are pelagic, concentrated mainly at the salinity gradient of 10 ‰, and requiring about 2 g/m³ of oxygen for development (Bagge *et al.*, 1992; Nissling and Westin, 1991a & 1991b). Egg survival depends significantly on suitable hydrological conditions, as influenced by intermittent water inflows from the North Sea (Matthaus, 1993).

Herring and sprat are pelagic in habit. There are up to sixteen herring populations, including 9 which are spring spawners and 7 which are autumn spawners. Sprat tends less to form separate populations. Spawning by herring occurs in most months of the year, while for sprat it is mainly from March to August.

The relative importance of fish and invertebrates in the diet of cod depends on sizes of the predator and prey (Jensen and Sparholt, 1992).

In the case of cod less than 40 cm (ages 3 and younger), invertebrates constitute about 60 - 80 % of the diet by weight. In the larger cod, the average diets consist of 65 - 90 % fish. Smaller cod tend to eat more sprat than herring. Cod from about 40 cm prey on cod between 5 - 20 cm (0 - 2 yr age groups) and to a lesser extent on cod of 21 - 38 cm (3 - 4 yr age groups). The presence of cod in the stomachs of cod larger than 46 cm is about 5 - 12 %.

7.2 Outputs from MSVPA

In the model, cod were considered as a single stock, herring as two stocks, and sprat as one stock. Outputs are for the period 1977 to 1992 and as described in Sparre and Jensen (1995).

The estimates for cod stock biomass gradually increase up to 1980 and then decline. The factors influencing this were recruitment, fishing, and predation. The estimates for recruitment varied considerably, by a factor of 4 between the periods of highest recruitment (1977 - 1981) and lowest recruitment (1985 - 1990). There was an increasing trend in the fishing mortality and a decreasing trend in the predation mortality in the period considered. Overall, the reduction in recruitment was determined to be the principal factor leading to the decline in cod stocks, with the high fishing mortality (mean $F = 0.89$ for ages 4 - 7 yr in the period 1977 - 1992) being the secondary factor. The predation (cannibalism) was important only in the years when the cod stock was large.

Both recruitment and stock biomass varied less for herring. The biomass for the larger southwest stock varied without trend, while for the northeast stock it approximately doubled during the period.

This result fits with the estimated decline in the cod stock being most apparent in the eastern Baltic, due to less favourable hydrological conditions. The sprat stocks were shown to have increased dramatically from 288 000 t in 1980 to 1 743 000 t in 1992.

Both herring stocks and the sprat stock were only lightly exploited, with mean fishing mortalities around $F = 0.2$ and 0.22 (all ages) for the herring and $F = 0.16$ (all ages) during the period. These values reflect the limited market demand for herring and sprat. Both species obviously benefited from the reduced predation by cod.

The biomass of herring and sprat estimated to be consumed by cod was highest in the interval 1980 - 1984, when the cod biomass was also at its highest level for the period. During this interval the total landings of herring and sprat (about 450 000 t) were much less than the amount eaten by the cod (about 750 000 t).

The predation on herring and sprat declined from around 1982 due to the decline in the cod stock. The cannibalism of cod declined from 1980, when an estimated 70 000 t were consumed, because of the decline in the recruitment of young cod.

7.3 Predictions from MSFOR with Constant Recruitment

The predictions were made in respect to three assumed levels of cod recruitment based on the historical observations. The high level was defined as about 1 000 - 1 400 million individuals annually (as in 1976 - 1981), the medium level as about 500 million individuals (as in 1982 - 1985), and the low level as about 100 - 300 million individuals (as in 1986 - 1991).

The values in each case refer to all 0+ fish as one-year old on January 1st. In respect to one set of predictions, the fishing mortality of the pelagic fleets is kept constant, whereas the fishing mortality of the cod fleet is varied from zero to twice the reference fishing mortality. In the other set the fishing mortality of the cod fleet is kept constant, and the fishing mortality of the pelagic fleet is varied. In each case the extent of variation is from zero to twice the respective fishing mortality estimated for 1992.

In 4 of the 66 predictions, there was no convergence to equilibrium from the 100 iterations.

This was for the cases of medium to high cod recruitment combined with low cod fishing mortality (with the pelagic fleet mortality kept constant). In these instances, cod biomass was changing cyclically, reflecting the alternating importance of cannibalism and recruitment in determining stock numbers. It can be expected that as the predator stock biomass oscillates, so also will the prey stock oscillate, because of predation. The following discussion of results concerns only those combinations for which equilibrium was achieved.

Concerning the effects of cod recruitment, the higher levels lead generally to a higher cod biomass, higher yields of cod for given levels of fishing mortality, and a decrease in the mean age of the cod stock. The higher cod biomass is associated in turn with higher predation on all stocks. In the case of the herring and sprats this causes a decrease in biomass and yields for given levels of effort and an increase in mean age.

The increase in cannibalism associated with the higher cod recruitment is to some extent counterbalanced by the lower mean age of the cod stock. Increasing the fishing mortality of the cod stock (with the pelagic fleet mortality kept constant) within any recruitment level has the effect of reducing the biomass and mean age of cod, and increasing the biomass and mean age of the other stocks. Yields from all stocks are increased.

7.4 Predictions from MSFOR with Variable Recruitment

In the context of the Baltic Sea stocks, the variation in cod recruitment is believed to be the most important source of uncertainty when forecasting future yields. This was investigated by undertaking additional analyses with MSFOR for each of high, medium and low recruitment levels using values drawn from a random number generator.

The recruitments were assumed to be log-normally distributed around pre-determined means. Only the recruitment for cod was varied, although in reality all stocks are known to have large variations in recruitment.

The predictions were of yield, spawning stock biomass, mean numbers of cod recruits, and stock biomass, with the fishing mortalities for all stocks kept constant at the level estimated for 1992. They were made in respect to each of the nine years from 1993 through 2001, and repeated 100 times.

An interesting result is that the means (from 100 simulations) for the yield, spawning stock biomass, and stock biomass in year 2001 tend towards being the same irrespective of whether the cod recruitment is assumed to be at the high or medium level. The explanation is that as the recruitment levels become higher, the cod stock will consume more of its own young, and hence reduce the consequences of the greater number of recruits. The implication is that above a certain level of recruitment the equilibrium yields and biomass will tend to remain the same (for given levels of fishing mortality).

Increasing the recruitment from low (base year) levels to medium or high levels (which are then maintained) while keeping the fishing mortality constant, leads to increased cod yields and biomass in the early years, after which yields decline, presumably to equilibrium values. The explanation here is that in the initial years, when the cod stock is recovering and the stocks of small pelagics are relatively high, the latter bear much of the burden of predation; later as the herring and sprat stocks are reduced through predation towards new equilibria, more of the burden is shifted to the young cod.

In the purely biological sense, the implication for management is to fish more intensively than might be otherwise thought appropriate in years when cod recruitment is high, to prevent the depletion of the herring and sprat stocks and a subsequent increase in cannibalism. All individual predictions concerning cod for the years from 1997 were found to be extremely variable.

The incorporation of predator/prey interactions in the model appears not to have the desired effect of dampening the impact of variable recruitment. The individual predictions for the herring and sprat stocks are also highly variable, which is surprising in that recruitment levels and fishing mortalities for these were held constant. The variation can only be explained by the variation in cod predation.

7.5 Conclusion

The hope, when using multi-species models, is to identify management strategies more beneficial than those revealed from single species models. This might have been possible if the herring and sprat were more valuable than the cod; in which case the financial benefit from fishing down the cod and reducing predation could be substantial. In the case of the Baltic Sea fishery the predator fetches much higher prices than the prey. Some increased exploitation on cod does have the positive effect of reducing losses to cannibalism. This could be beneficial in the unlikely event of continuous high recruitment levels. Even in this extreme circumstance, the extent of benefit would be offset by the fact that larger cod have a higher market price than small cod. This is because the consequence of increased exploitation is to lower the average size of the fish being caught.

The over-riding determinant of performance in this fishery is the recruitment of cod. The substantial quantities of historical data indicate that this is highly variable, and greatly influenced by oceanographic conditions. The ideal management strategy is likely to be one which enables exploitation levels to be increased following years when the recruitment of cod is high, in a way which does not cause the fishery to collapse when recruitment falls. This would imply that exploitation should be increased through better use of existing vessels and plant (as possible), rather than through additional investments.

8. CASE STUDY OF MULTI-SPECIES MODEL APPLIED TO HAKE AND ANCHOVY STOCKS IN THE NORTHWEST MEDITERRANEAN

8.1 General Description of Stocks and Diets

In the northwest Mediterranean, hake and anchovy are the most important species, in weight and value, contributing to the landings of the benthic and pelagic fisheries respectively.

Since 1975, hake landings have been mostly between 4 000 - 5 500 t. The principal gears used are trawls (~ 900 boats), longlines (~ 60 boats) and gillnets (~ 20 boats). Immature fish (9 - 16 cm) are landed from trawlers, and larger fish (35 - 45 cm) from other vessels.

Anchovy are exploited with purse seiners (246 boats) and pelagic trawlers (24 boats). The fishery is seasonal with highest catches in spring and summer. Recruits from the previous spawning comprise about 45% of the landings. Since 1975, landings have fluctuated about 15 - 25 000 t, except for a period in the mid-1980s when they were between about 10 - 15 000 t. The range of lengths in the landings is about 8 - 16 cm. The market price for anchovy is a bit less than a third of that for hake.

Hake is principally benthic, but also pelagic in habit. It is an opportunistic predator of the anchovy and other species.

During the first months of life, its diet is mainly crustacea. Once it reaches about 10 cm in length it begins to predate on small pelagics, mostly clupeidae; from about 30 cm its diet is mostly gadoid fish. At this time its habit is benthic. Cannibalism does not seem to be prevalent other than during the spawning period, when juveniles are eaten. Its habit is to eat the largest individuals it can ingest whole. Most commonly, stomach contents are a single fish, with the digestion occurring every 24 hours.

Anchovy is the most important prey when the hake are between about 15 and 40 cm. The age of full stomachs which contain anchovy varies considerably. The reported observations are 3.7% (Bozzano *et al.*, 1994), 8.4% (Karlovac, 1959), about 24% (Larraneta, 1970) and 44% (Jukic, 1972). The latter is for hake of 20 - 30 cm when anchovy are abundant.

The most intense predation occurs in autumn and winter when the species are occupying the same general locations, and younger hake, up to 30 cm, make feeding forays throughout all depths in the water column.

8.2 Defining the Model

The description of the model and the findings from its application to the northwest Mediterranean fisheries are taken from Oliver *et al.* (1995). The pseudo cohort data for hake were subjected to a standard single species VPA analysis, from which the outputs include estimates for the fishing mortality coefficients applying to hake and stock numbers. The consumption of anchovy was estimated from these hake stock numbers and the pre-determined consumption matrices. Two consumption matrices were employed based on local studies, to represent high and low levels of predation, (Bozzano *et al.*, 1994; Larraneta, 1970). They are expressed as numbers of anchovy eaten per hake per year, grouped according to the ages of the predator and prey.

The estimated consumptions were then added to the landings data for anchovy to obtain the pseudo cohort numbers to be included in the MSVPA analysis. The output from the MSVPA included estimates for the fishing and predation mortalities for anchovy. Long-term predictions of yields and stock size were then made for both species, under different fishing mortality and size at first capture regimes applying to hake. In this the recruitment levels were kept constant for both species, and the fishing mortality and size at first capture were kept constant for anchovy. In respect to each regime the new level of anchovy consumption was calculated from the predicted hake stocks and the pre-set consumption matrices.

8.3 Predictions from the Model

The predictions of yield for hake are the same as from a single species VPA. The estimated yields are maximized at about 18 000 t (ie. about three times the present yield) from a combination of the contemporary fishing mortality and an age at first capture of 4 years.

As might be expected, yields of anchovy are highest (ie. about twice the present yield) when the exploitation on hake is greatest and the age at first capture for hake is least. The extent of the potential benefit is also higher with the consumption matrix depicting the higher levels of predation. Because of its high price compared to anchovy, the value of the landings from the two species combined is maximized with the regime which maximizes the yield of hake. This coincides with a predicted yield from anchovy of about 20 000 t (ie., the present yield).

8.4 Conclusion

In this rather simple two species assessment, the conclusion is very much in favour of management which maximizes the yields from the predator. The dominant effect that hake has on the outcome arises from its much higher price.

Furthermore, in this case the incorporation of a predator-prey interaction into the assessment did not provide any further insights beyond that available from a single species assessment. The important results were from the single species VPA applied to hake, particularly in respect to quantifying the extent of potential benefit from having an age at first capture of 4 years (equivalent to a length of about 40 cm).

9. ECONOMICS OF PREDATOR-PREY HARVESTING

Inadequate attention has been afforded the bio-economics of predator-prey harvesting. A brief consideration is provided in Flaaten (1989). He combined a simple biological model involving a single predator and a single prey from May et al. (1979), with economically independent harvesting sectors, one for each of the two species. As expected, harvesting the predator in this very simple situation increased the harvestable stock of the prey, and harvesting the prey reduced the harvestable stock of the predator.

In the case where the prey is inexpensive-to-catch and valuable, and the predator is expensive-to-catch and less valuable, he concluded that it may be economically justified to subsidise the harvesting of the predator. In the reverse, when the predator is inexpensive-to-catch and valuable, and the prey is expensive-to-catch and less valuable, the increase in the harvestable stock of the prey resulting from the harvesting of the predator, may make it economic to harvest the prey when previously it was not. This would occur, however, at the expense of the fishery on the predator.

Where both species are expensive-to-catch and of low value, there may be no fishery on either.

Flaaten and Stollery (1994) applied a simple bio-economic model to estimate the likely loss of profit to the fisheries sector, from the minke whale stock of the north-east Atlantic.

Estimating the number of whales at 86 736 in 1989, and an annual food consumption per whale of 26.7 tonnes, they estimated a total food consumption of about 2.3 million tonnes. Diet information was then used to determine the quantities of commercial species consumed (incl. cod, saithe, haddock, capelin and herring). Multiplying these by the average fish prices for 1991 and 1992 provided estimates for the gross value of the losses to whales; which in turn was multiplied by 0.3 to estimate the loss of profit.

The estimates obtained for the annual loss of profit to fisheries (according to three diet scenarios) ranged from US\$ 155 million to US\$ 182 million; or between US\$ 1 783 and US\$ 2 097 per whale. The conclusion is based on the very doubtful assumption that all of the consumption by whales would be able to be caught (in the absence of the whales), and ignores the possibility of other predators increasing in number in response to the reduced abundance of whales.

10. HARVESTING STRATEGIES FOR MULTI-SPECIES ECOSYSTEMS

The idea that the total production of a system can be increased by fishing down the predators, and then harvesting the more abundant prey lower down in the food web, does not seem to work in practice. As fishing increases on the apex predator, its role as a regulating agent on the abundance of the lower trophic species is replaced, at least in part, either by another apical predator or the next predator down (in the case of older individuals being able to move into a higher trophic level than formerly). The extent to which this happens is increased when there are many competing predators on the same group of prey. Furthermore, as the natural effect of predators is to regulate the abundance of the prey, the substantive and selective removal of predators will be de-stabilizing, as reflected by increased variation in the abundance of the prey. Selective removal of the prey, on the other hand, will be detrimental to the predators, although less so if alternative prey are available.

Clearly, where there are species interactions, it is not possible to maximize the sustainable yield from each species concurrently. Achieving a maximum sustainable yield of an apical predator, for example, would require no harvesting of its prey. For the prey the maximum sustainable yield would be achieved by eliminating all of its predators (and competitors).

It is unlikely, from biological criteria alone, that some optimal sustainable mixture of harvests could be identified. This has nonetheless been attempted by Caddy and Sharp (1986). Their proposal seeks to maintain the trophic balance while achieving close to maximum utilization of the stocks, through a harvesting strategy in which for each species the fishing mortality rate is set between 33% and 100% of the natural mortality rate. As acknowledged by these authors, the strategy takes no account of the importance of economic viability in determining fishing strategies, nor of the aesthetic and ethical constraints (as applying to the harvesting of marine mammals).

11. PREDATION EFFECTS INCORPORATED INTO MANAGEMENT ADVICE FOR MARINE FISHERIES

Predation interactions are considered in fisheries management in the Northeast and Northwest Atlantic, where capelin catches are restricted to leave sufficient food for higher valued cod. In the case of the Barents Sea, the annual catch quota is set to ensure sufficient capelin survive predation by cod and fisheries exploitation, to enable adequate stock replenishment from reproduction.

The lower safeguarding limit chosen by the Atlanto-Scandian Herring and Capelin Working Group of ICES for the size of the spawning stock was 0.4 - 0.5 million tonnes (Tjelmeland and Bogstad, 1993).

It was on the basis of these considerations that the fishery was closed in the period 1987-1990, and then re-opened in 1991. Sandberg (1993) refers to the decision to open the Barents Sea fishery for capelin in 1991, as being a first application of multi-species management. Shelton (1992) contrasts this management approach with that in the Southeast Atlantic, where anchovy and pilchard continue to be heavily exploited, despite their importance as forage fish for the higher value hake and other top predators.

A recent report by the Fisheries Resource Conservation Council (FRCC, 1994), an independent advisory body set up in 1993 to make recommendations to the Canadian Minister of Fisheries and Oceans, endorsed the need for an ecological approach to management. They concluded that: "from an ecological perspective, we believe that recovery of groundfish stocks will only occur when there is an abundance of food and a balance in the predator/prey relationship" and expressed the concern that fishing on prey species including capelin may constrain the rebuilding of groundfish stocks. The Council also commented that early action should be taken to significantly reduce the populations of seals to help groundfish stocks to recover. Controlled harvesting of the South African fur seal has continued throughout the century. Before 1983, the management objective was to maximize the sustainable yield of pups. Following the collapse of the fur market in 1983, harvesting continued with the objective of reducing predation on commercial fish, thereby increasing commercial fish harvests (Wickens *et al.*, 1992). This harvesting was without scientifically-based management until 1988, but since then seal quotas have been set following scientific assessment. Butterworth *et al.* (1988) have questioned the quality of the scientific advice which suggests that harvesting the seals off South Africa will result in increased yields of commercial fish. As mentioned earlier, these authors contend that the existence of squid as a prey of seals and a predator of anchovy, may result in the culling of seals, reducing the catches of anchovy.

Following expressions of concern about competition from grey seals, in the case of the Scottish salmon fishery, and especially gear damage and the scaring of fish from nets, a pup cull commenced in 1962 and reduced stocks by twenty five on the Orkney and Farne Islands (Harwood and Greenwood, 1985).

Despite this cull, seal populations continued to grow and in 1977 a new management programme started requiring a 30% reduction in the seal stocks by 1982, from the culling of both pups and cows.

The analysis was based on a simple calculation of the quantity of commercial fish consumed by the seals, and an assumption about the proportion that might be caught by fishermen after culling. The culling was abandoned in 1978 following vociferous public protest. Apart from aesthetic considerations, the conservation groups successfully argued that there were too many unknown interactions to enable any prediction of the effects of culling.

The ICES approach to multi-species modelling has had an impact on the scientific advice provided to managers. The incorporation of predator-prey interactions into multi-species models has provided a means of getting better estimates of natural mortalities with age. The assumption that juvenile fish suffer the same instantaneous mortality rate as adult fish was known to be incorrect, and could now be avoided.

Since this recognition, more realistic mortality rate schedules have been estimated (as output from MSVPA) and incorporated into the single species assessments for the North Sea fisheries. The incorrect specification of mortality rates can substantially alter the scientific advice provided to managers, for example in respect to the yield per recruit projections and the best choice for the minimum mesh size (Gislason and Helgason, 1985).

ICES scientists have also been requested to investigate the utility of the multi-species forecasting model (MSFOR) in predicting the effects from applying different management options, including transitional and long-term effects of changing the fishing effort and mesh sizes. On this the conclusions so far are that the predictions are too uncertain to be used directly within management plans, although having substantial interest in a qualitative sense (Anon., 1991).

The quantitative outputs from these multi-species assessments have nevertheless tended to underscore the danger that intuition and models with inadequate levels of robustness can mislead when used to predict the outcome from changes to management.

At present it is the results from the single species assessments which most directly influence management of the North Sea fisheries.

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is unusual among international marine resource commissions in that it has statutory obligation to take into consideration ecosystem interactions in the management of marine resources. Ecological relationships must be maintained, for example, between harvested and dependent populations of Antarctic marine living resources, and depleted populations must be managed to restore them to a level at which the greatest net annual increment in biomass occurs.

Concerning krill harvesting, an objective is to keep the abundance of krill stocks greater than might be judged as necessary purely from single species considerations. The Commission deliberately sets Total Allowable Catches (TACs) for exploited species which are conservative, particularly when the scientific advice is uncertain. It seeks to prevent or minimize the risk of changes in the marine ecosystem which are not potentially reversible over two or three decades.

12. POLICY AND INSTITUTIONAL IMPLICATIONS OF MULTI-SPECIES MANAGEMENT

The consideration of predator-prey interactions and multi-species modelling has made it evident that it is not possible to maximise the yield (or profit) from all species simultaneously. The multi-species approach to resolving this problem is to seek increased yields (or profit) from the fisheries collectively. This is difficult to apply in practice, partly for data and modelling reasons, but also because groups of fishermen restricted (as through licensing) to exploiting specific fish species, may become disadvantaged. An example of this was the reduction in the TAC for capelin from the Barents Sea in 1992, on the grounds that capelin is prey for cod. This measure met with heavy criticism from fishermen tied to the capelin fishery by the licensing system (Hoel, 1993).

The realities of sharing fish resources with the other apical predators (eg. whales, seals and birds) add a further layer of difficulty. At one extreme, the increased harvesting of whales and seals continues to be proposed as a means of increasing fishery yields.

At the other extreme, and already in certain geographical areas (eg. the northeast Atlantic), the management regimes have been progressively altered towards total protection for the mammals. There have been changes proposed to the US federal fisheries legislation which would require a designated share of the TAC for particular fish stocks to be allocated for consumption by marine mammals (Hoel, 1993). These principles are shared by the International Whaling Commission (IWC), and the Commission for Conservation of Antarctic Marine Living Resources (CCAMLR). Problems at the institutional level are intensified when the species in question come under the jurisdiction of several independent agencies. This becomes more likely when applying multi-species management, where one is considering the management of fisheries across trophic levels and at the ecosystem rather than the individual fisheries level.

In respect to the North Atlantic, apart from the separate national entities with management responsibilities, there is a proliferation of international and regional entities, including the Northeast and Northwest Atlantic Fisheries Commissions (NEAFC and NWAFC), the North Atlantic Salmon Commission (NASC), the North Atlantic Marine Mammals Commission (NAMMC), and the IWC. Management of a large ecosystem with a single or substantially reduced number of management institutions has been suggested for this region, but not yet been implemented.

13. CONCLUSIONS

The diversity and complexity of predator-prey interactions and their effects on populations are great. Understanding the observed variation of fish stocks and the performance of fisheries is further magnified by the non-equilibrium character of both local and ecosystem environments.

This is reflected in the growing consensus that in most cases it is impossible to predict accurately the consequences on future yields and profits from management strategies which are developed without consideration of species interaction effects and abiotic factors. This is an over-pessimistic response, as applied to many of the world's fisheries. Nevertheless there is certain to be an increasing trend towards the study and management of fish stocks in a multi-species context, and in some cases to the management of the ecosystem in which they belong.

The perceived benefits from multi-species management are increased and less variable yields from fisheries. In purely biological terms, there would seem to be some scope to increase yields by removing predators and fishing more intensively at the lower end of the food chain. The observational and modelling experience, however, have so far led to the conclusion that multi-species management is unlikely to result in any substantial increase in the global yield. The most likely benefits will be reduced variability in the landings and increased fishery profits.

The first will arise from dampening the natural variations in stock abundance, by adjusting harvesting strategies according to the relative abundance of the species, and the nature of the interactions. The second will arise from multi-species/multi-fisheries bio-economic modelling, giving due recognition to the relative prices of the species and the costs of fishing. The present mix will tend to be preserved by the fact that generally the predators command higher market prices than the prey.

Research in support of multi-species management will not be equally relevant across all fisheries. It has most relevance where the species interactions are well established and complex, and the perceived benefits from multi-species management are substantial. If the perceived benefits are not substantial, then the cost-effectiveness of the research would be in doubt. In complex coral reef ecosystems, expensive research in support of multi-species management may not be cost effective (in the strictly fisheries sense).

It may be sufficient to monitor species assemblages (as indices of community health) as a basis for formulating management. There are many fisheries for which research in support of the single species approach will continue to be appropriate.

For large fisheries on small pelagics in major upwelling areas, research on the abiotic determinants of stock abundance may prove to be the more rewarding.

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