CM 2001/R:06

Environmental effects of bottom trawling:
a benthic overfishing model

David A. Somerton
National Marine Fisheries Service
Alaska Fisheries Science Center
7600 Sand Point Way NE
Seattle, WA 98115

Tel: +1 206 526 4116
E-mail: David.Somerton@noaa.gov

Abstract

In pursuit of various target species, the use of bottom trawls and dredges can result in the unintended catch and death of a variety of invertebrate species comprising the benthic community. Although the populations of these species can sustain some level of trawl induced mortality, it is not clear what level should be considered as overfishing. In this paper I develop a simple model of the response of a population to fishing mortality based on the Schaefer production model modified to account for the spatial distribution of fishing effort, the change in fishing mortality rate associated with changes in mean body size and the multispecies composition of the benthic community. Parameters of the model are intended to be estimated using field experiments to estimate initial density, fraction of the animals within the swept area killed with one pass of the fishing gear, rate of recovery after trawling and a coefficient controlling the size dependency of the mortality rate. Three overfishing definitions are considered; one based on the maximum production of the entire community, one based on the maximum production of the community when all species are weighted equally and one based on the maximum production of the least productive species in the community (an indicator species). For a specified combination of species, the three measures are arranged from the least conservative (i.e., overfishing occurs at a higher level of effort) to most conservative. The model implicitly includes two control variables to minimize the likelihood of reaching an overfished condition without requiring a reduction in nominal fishing effort. First, fishing mortality per unit of effort may be reduced by utilizing some form of technical modification to the fishing gear that either allows the benthic species to escape or suffer less trauma. Second, fishing effort may be artificially aggregated by the use of closed areas.

Introduction

Although commercial bottom trawling and dredging are conducted with the intent of capturing target species with minimal impact on the marine environment, in practice the use of such towed fishing gears often results in three distinct types of disturbance to the non-target species comprising the benthic community. First, the use of towed fishing gears can alter the geological structure of the bottom by breaking or moving hard structures, by smoothing irregularities in sediments caused by oceanographic or biological processes and by creating furrows and other artificial sedimentary structures (Caddy, 1973; Currie and Parry, 1996; Lindeboom and de Groot, 1998). Second, the use of towed fishing gears can directly kill benthic species by exposing them to dessication after removal from the sea, by crushing from the downward force of the footrope, bridles and doors and by excavation and increased exposure to predators (Bergman and van Santbrink, 2000; Kaiser and Spencer, 1995). Third, the use of towed fishing gears can indirectly alter the species composition of the benthic community by removing the predators of these species or by augmenting the food supply of benthic scavengers (Fonds and Groenewold, 2000; Kaiser and Spencer 1994). The effects of these forms of disturbance on the benthic community will vary among habitats depending upon the degree of exposure of the habitat to natural forms of disturbance and the biological capacity of the community to recover after being subjected to disturbance (Collie et al., 2000). Thus, some habitats have been shown to return to the pre-fished condition within a year of trawl or dredge fishing (Currie and Parry, 1996) while others remain in a recognizably disturbed state after twenty years (Sainsbury et al., 1997).

Most habitats can sustain some level of trawl or dredge disturbance, but what level should be considered as excessive, or, expressed differently, how should benthic overfishing be defined? Reviews of this issue indicate that there are a variety of perspectives and certainly no consensus among scientists let alone managers, fishers, environmentalists and other stakeholders (Murawski, 2000). Consider the following three approaches: MacDonald et al.(1996) developed an index of sensitivity of benthic species to fishing disturbance based on subjective measures of the fragility of the species, intensity of fishing effort and the ability of the species to recover. Although not associated with any threshold value, the index was considered useful for identifying species or habits of concern. Daan (1991) evaluated the potential for benthic overfishing by comparing estimates of fishing mortality rate, based on commercial swept area considerations, to estimates of natural mortality, based on production to biomass arguments. Pope et al.(2000) estimated fishing mortality rates with length cohort analysis of non-commercial benthic fish species and compared these values to threshold levels based on the fishing mortality rate needed to reduce the biomass of the spawning stock to a specified proportion of its unfished state. Although different, the common theme found in these and most other approaches is the balance between the disturbance caused by towed fishing gear and the capacity of the benthic community to recover from this disturbance.

In this study, I examine another approach to define benthic overfishing based on a model that extends the classic Schaefer (1954) production model to explicitly account for the spatial distribution of fishing effort, the change in fishing mortality rate associated with changes in mean body size and the multispecies composition of the benthic community. The model attempts to describe the biomass production of each species' population, without regard to its sex and age structure, in response to the application of a fishing mortality rate. The overfishing criterion used in production models of this form is typically defined as the fishing effort that, if maintained until population equilibrium, maximizes the production rate of the population ($F_{msy;}$; Schaefer 1954). Although the use of F_{msy} has been considered inappropriate for managing the catch of non-commercial species where maximizing production is not an issue (Pope et al., 2000) and has been often superceded for fisheries management by more conservative measures based on spawning stock biomass (F_{35}; Clark, 1991), it is an objective measure that is derived from a model with modest data requirements. This is an important consideration for benthic invertebrates because few species have been studied in sufficient detail to provide the vital parameters needed for more elaborate models.

Development of a single-species model

Consider a specific benthic habitat encompassing an area, *A*, which includes the total populations of *n* benthic species. The biomass dynamics of one of these species can be described algebraically by the equation:

$$\frac{dB}{dt} = rB\left(1 - \frac{B}{K}\right) - mfB \qquad \textbf{(1)}$$

Where:
B = biomass of the population at any time
K = biomass before fishing starts
r = intrinsic rate of growth
f = fishing effort
m = fishing mortality coefficient

This equation is identical to the Schaefer production model (Schaefer, 1954; Hilborn and Walters, 1992) except that the catchability coefficient of the Schaefer model (*q*) is replaced by *m* because the mortality rate experienced by benthic species may be substantially different from the catch rate. The mortality coefficient, or the proportion of the population biomass killed by the application of one unit of effort, is for later convenience best expressed as:

$$m = \frac{a}{A} M \qquad \textbf{(2)}$$

Where:
a = a unit of area swept by trawls (i.e., one hectare)
A = total area of the habitat
M = proportion of the biomass within the swept area killed by a single pass of the trawl

With this formulation, fishing effort (*f*) is then expressed in terms of total area swept by trawls per unit of time.

The traditional approach to determining an overfishing level of *f* is to consider the response of the population if *f* was held constant for a sufficiently long time interval to allow the population to reach equilibrium. At equilibrium, the change in biomass is zero, therefore Equation 1 can be rewritten as:

$$rB\left(1 - \frac{B}{K}\right) = mfB \qquad \textbf{(3)}$$

The term on the left side of the equality represents the rate of biomass production by the stock and the term on the right side represents the rate of biomass mortality imposed on the population by the action of the trawl fishery.

In this formulation the model is based on the assumption that the mortality rate per unit of biomass (*mf*) is independent of biomass. This means that the first unit of effort experienced by a population will kill the same proportion of the population as the same unit of effort applied when the population has been reduced by the fishery to low levels. However, trawls are size selective because smaller individuals more easily pass under the footrope (Somerton and Otto, 1999) or through the meshes (DeAlteris and Reifsteck, 1993). Since mean body size will decrease, at equilibrium, as the fishing mortality increases, it follows that the mortality coefficient must decrease with a decrease in equilibrium biomass. One functional relationship that is sufficiently flexible and analytically convenient is:

$$m = m_0\left(\frac{B}{K}\right)^{\alpha} \qquad \textbf{(4)}$$

Where: m_0 = mortality coefficient when fishing is initiated

α = parameter controlling the biomass dependency of the mortality coefficient.

Justification for this function form for biomass dependent mortality rate is provided in Appendix

1.

Substituting Equation 4 into Equation 3 produces an equilibrium production model with a biomass-dependent *m*,:

$$r\left(1-\frac{B}{K}\right)=m_0\left(\frac{B}{K}\right)^{\alpha}f \qquad \textbf{(5)}$$

The fishing effort producing the maximum production rate (f_{max}) is obtained by substituting the value of the equilibrium biomass at the maximum production rate ($B = K/2$; Schaefer, 1954) into Equation 5 and solving for *f*. This relationship is:

$$f_{\max}=\frac{r}{m_0 2^{(1-\alpha)}} \qquad \textbf{(6)}$$

This indicates that f_{max} for a species increases as its intrinsic rate of population growth increases and as the mortality produced per unit of effort declines. Compared to the value of f_{max} when *m* is biomass independent ($f = r / (2q)$; Schaefer, 1954), f_{max} in the biomass dependent case is less conservative in the sense that maximum production will always occur at a greater level of fishing effort (unless α=0).

Extension to multi-species

If the benthic community comprised only a single species then overfishing could be defined as when fishing effort exceeded f_{max}, essentially the same as Schaefer's(1954) use of F_{msy}. However, when considering many species that are simultaneously exposed to the same effort, a variety of optimality conditions are possible, depending on how the relative contribution of each species is weighted. In the following I consider three potential measures of overfishing for a multi-species benthic community. To examine the relative performance of these measures, consider a hypothetical community comprised of four species having the vital parameters (r, K) and fishing parameters (m_0, α) shown in Table 1.

The first measure considers that a community is overfished when the fishing effort exceeds the minimum f_{max} of all species. This will be referred to as $f_{max,i}$ (f_{max} individual). Since f_{max} is a function of r and m_0 , $f_{max,i}$ will be determined primary by the species that are either very vulnerable to trawling (high m_0) or are especially slow growing (low r). For the hypothetical community, $f_{max,i}$ is 141.2, 56.6, 42.4, 28.3 effort units for species 1 to 4. Overfishing for this community would occur at $f > 28.3$ units of effort.

The second measure considers that a community is overfished when fishing effort exceeds the effort resulting in the maximum production combined over all species. This measure will be referred to as $f_{max,c}$ (f_{max} combined). Although there is no analytical formula for $f_{max,c}$, it can be calculated as follows. Starting with a trial value of $f_{max,c}$ iteratively solve the following equation to estimate equilibrium biomass for each of n species:

$$r_i\left(1 - \frac{B_i}{K_i}\right) = m_{0,i}\left(\frac{B_i}{K_i}\right)^{\alpha_i} f_{\max,c} \qquad \mathbf{(7)}$$

where i indicates species number. Note that each species is characterized by its own unique set of parameters, but all species experience the same $f_{max,c}$. Once equilibrium biomass is determined for each species, the total community production at that level of fishing effort is then determined by substituting into:

$$P = \sum_{i=1}^{n} r_i B_i (1 - \frac{B_i}{K_i}) \qquad \mathbf{(8)}$$

This process is repeated and the value of $f_{max,c}$ varied until the value of $f_{max,c}$ is found that maximizes P. For the model community, $f_{max,c} = 85.0$ effort units.

The third measure also considers that a community is overfished when fishing effort exceeds the effort resulting in the maximum production combined over all species. However, in the previous case combined community production could be driven by a few species that were especially large or highly productive. For the third measure, which will be referred to as $f_{max,e}$ (f_{max} equal), the production from each species is scaled by its maximum production rate in an attempt to equalize the contribution for all species. The methodology for finding $f_{max,e}$ is the same as for $f_{max,c}$ except the production for each species (Equation 8) is divided by the maximum production for that species (*rK/4;* Schaefer, 1954). The resulting production function is:

$$P = \sum_{i=1}^{n} \frac{4B_i(1-\frac{B_i}{K_i})}{K_i} \tag{9}$$

In the case of the hypothetical community, $f_{max,e}$ = 50.0 effort units.

Redefinition of nominal effort

In all three of the above cases, overfishing would occur when the observed effort within the habitat exceeds the appropriate measure of f_{max}. One problem with this rule is that it does not take into consideration the spatial distribution of effort, which is typically quite aggregated (Rijnsdorp et al., 1998). Such effort aggregation is ignored for fish and other highly mobile organisms because individuals removed from the swept area are rapidly replaced by individuals from the surrounding area, which has the affect of randomizing effort over the population. When considering sessile or slow moving benthic organisms, however, the individuals removed or killed by the trawl may not be rapidly replaced. This means that subsequent trawl hauls will have a lesser impact on the entire population than the first haul to sweep an area, because less biomass is removed. Therefore the effect on the population of a given amount of effort will be a function of the spatial distribution of that effort.

One approach to this problem is to define a value of f that would produce the same effect on the population, if applied randomly, as that of the observed spatially aggregated effort. This quantity I will refer to as f_e (effective effort). One estimate of f_e can be obtained as follows. Consider that the population is spatially partitioned into N equal-sized subareas, with area size chosen to achieve a random within-area distribution of effort (Rijnsdorp et al., 1998). For a single species, equilibrium biomass (B_j) in each subarea j as a function of the observed effort in that area (f_j) can be estimated by iteratively solving:

$$r\left(1-\frac{B_j}{K}\right)=m_0\left(\frac{B_j}{K}\right)^{\alpha}f_j \qquad \textbf{(10)}$$

Once all of the B_j are determined, average equilibrium biomass over all subareas ($\overline{B}$) is then calculated. Finally, the effective effort is calculated as:

$$\hat{f}_e=\frac{r\left(1-\frac{\overline{B}}{K}\right)N}{m_0\left(\frac{\overline{B}}{K}\right)^{\alpha}} \qquad \textbf{(11)}$$

To demonstrate the effect of effort aggregation on f_e, consider the population of a species (for example, species 1 from the hypothetical community defined in Table 1) is distributed among four equal-sized subareas with three levels of effort aggregation (equally distributed, mild aggregation and high aggregation; Table 2) with a combined total effort of 2000 units. It is clear from this example that although the total nominal effort (f total, sum of the swept area of all tows) is constant, the effective effort decreases as the level of aggregation increases. Thus, when effort is equally distributed among areas, f_e is identical to the total observed effort, but in the extremely aggregated case, f_e is less than half of the total effort.

Definition of overfishing

Since the effective effort will depend upon the vital parameters of each species, f_e is inherently species specific. This means the use of f_e will differ somewhat between the three measures of overfishing previously defined. For $f_{max,i}$, overfishing would occur when $f_e > f_{max,i}$ for any of the species under consideration. This form of an overfishing definition is consistent with the concept of an indicator species (MacDonald et al., 1996), in that overfishing would be determined by the member of the benthic community that is most sensitive to the effects of trawling. For the combined production measures, overfishing would occur when $\overline{f}_e > f_{max,c}$ or $\overline{f}_e > f_{max,e}$, where $\overline{f}_e$ is the average over all n species. These two forms of an overfishing definition are consistent with the concept of a community response to fishing, with $f_{max,e}$ being the more conservative (i.e., overfishing will be defined at lower levels of effort) of the two because it provides more weight for the less productive species.

Discussion

Parameter estimation

For fisheries applications, the parameters of production models are traditionally estimated by fitting the model to commercial catch and effort data (Schaefer, 1954; Hilborn and Walters, 1992). This approach is not appropriate for use with the collection of species comprising the benthic community because accurate records of the catches of these species are rarely collected and because the mortality imposed on their populations may far exceed that due to the catch alone. From its initial conception, use of the proposed benthic overfishing model was predicated on obtaining estimates of the vital parameters for each species *(r, K)* and the parameters describing the vulnerability of each species to the fishing gear (m_0, α) using data from a field experiment similar to those described in Currie and Parry (1996), Bergman and van Sandbrink

(2000), Hall-Spencer and Moore(2000) and Lindeboom and de Groot (1998). The intended sampling protocol includes the following components: 1) benthic sampling of an experimental plot before the application of fishing effort to estimate initial density, 2) application of fishing effort using a gear and technique mimicking the commercial fishery, 3) post-capture holding experiments to estimate handling mortality of captured individuals, 4) a short-term re-sampling of the post-fished area for density estimates used in mortality calculations and 5) a long-term re-sampling of the post-fished area to estimate recovery rate. One necessary feature of the proposed experiment which distinguishes it from most of those described in the literature is that it must be conducted in an area that has never experienced fishing or has been protected from fishing long enough to have developed a benthic community reasonably close in species composition and individual body sizes to the unfished state. In the following I will detail an experimental protocol to allow estimation of the four parameters.

The virgin population biomass (K) of each species can be estimated from values of density obtained from the unfished experimental plot using a device with an estimable sampling efficiency and a measurable sampling area. Once average density within the experimental plot is determined, virgin population biomass of each species is then estimated by multiplying the density estimates by the total area of the habitat (i.e. A in Equation 2, not the area of the experimental plot).

The mortality rate of the trawl at the initiation of fishing (m_0) is equal to the proportion of the habitat swept by one unit of trawl effort (a/A; Equation 2) multiplied by the proportion of the individuals within the swept area that are killed by the application of the first unit of effort (M). The mortality includes two components, that is, the individuals that die as the result of being caught then subsequently discarded and the individuals that die because they are either injured by a trawl component or are temporarily made more available to predators. Bergman and van Santbrink (2000) described an effective way of estimating M, which, with some algebraic modification, can be expressed as :

$$M = \frac{D_0 - (D_1 + CS)}{D_0} \qquad \textbf{(12)}$$

where D_0 and D_1 are the density before and after one trawl pass, C is the trawl catch scaled by swept area and S is the post-handling survival of the catch estimated using methodology described in Bergman and van Santbrink (2000) and Kaiser and Spencer (1995). Several difficulties in the experimental design must be surmounted. First, post-fishing samples must be collected from within the area swept by the trawl, a requirement that poses an increasing formidable sampling problem as the water depth increases. However, use of acoustic transponders on both the trawl and the sampling device, coupled with the use of a navigation plotter, can allow the sampling device to be positioned quite accurately within in the trawl path (Mckeown and Gordon, 1997). An alternate technique is to accurately position the trawl so that the adjacent trawl paths join (i.e. like mowing a field) producing an even trawl coverage over a sufficient large area (Joll and Penn,1990) that the positioning of the sampling device can be fairly crude. This idea can be extended without precise positioning of the trawling so that the trawl effort is on average one pass (Currie and Parry, 1996).

The second problem to overcome is that benthic scavengers are typically attracted to the area disturbed by trawling (Ramsay et al., 1998), temporally increasing the local abundance of these species. Thus, to avoid biased mortality estimates the post-trawling samples must be collected after some lag time has elapsed to allow the scavengers to disperse. Bergman and van Santbrink (2000), however, considered this to be such a severe problem that they chose not to estimate mortality for the highly mobile scavengers. Another potential approach to circumventing the problem posed by the influx of scavengers is to collect all animals in the trawl path, both those caught and those escaping in some way, during the application of the trawl effort by attaching sampling bags to the trawl to collect animals passing either through the mesh (Kaiser and Spencer, 1995) or under the footrope (Somerton and Otto, 1999; Rose, 1999). Individuals collected in the sampling bags could then be subjected to survival experiments similar to those used to estimate the catch survival. However, like the catch survival experiments, this type of escapement survival experiment (i.e. maintenance in holding tanks) includes only the mortality due to trauma and does not include the additional mortality due to the predation the animals would experience if returned to the sea bed.

The intrinsic rate of growth (r) will require resampling of the trawled area after a duration sufficient for some recovery to have occurred. If we consider that B_t and B_{t+1} are the biomass estimates immediately after fishing and after some recovery period, then an estimator for r can be derived from the discrete form of the non-equilibrium Schaefer model (Hilborn and Walters, 1992):

$$B_{t+1} = B_t + rB_t(1 - \frac{B_t}{K}) \qquad \textbf{(13)}$$

Provided that an estimate of K is available from sampling the virgin population, then r can be estimated as:

$$\hat{r} = \frac{B_{t+1} - B_t}{B_t(1 - \frac{B_t}{K})} \qquad \textbf{(14)}$$

If additional post-fishing estimates of biomass are available at increasingly longer time intervals, then r could be estimated using regression techniques with Equation 13. One important consideration is that estimates of B_{t+1} and subsequent samplings include only the growth from the individuals surviving the fishing experiment and recruitment of young individuals. Immigration from surrounding areas, either because of the initial influx of scavengers or because of longer term movement, will result in an overestimate of r. This effect will be reduced by increasing the size of the experimental area, but to be eliminated might require restricting the estimates to only sessile organisms.

The size dependancy of mortality rate (α) can be estimated by repeating the experiment used to calculate m during one or more of the recovery stage resampling events. If m and B are the mortality and biomass estimates at this later period, then an estimator for α can be derived from Equation 3 as:

$$\hat{\alpha} = \frac{\log(\frac{m}{m_0})}{\log(\frac{B}{K})} \tag{15}$$

If additional post-fishing estimates of B and m are available, α could be estimated using non-linear regression techniques with Equation 4.

Model assumptions

As in any mathematical model of a biological process considerable simplification is necessary to allow tractable solutions and these simplifications impose assumptions on the model that must be true for valid interpretation of the model results. Some of the more important, and perhaps tenuous, assumptions upon which the benthic overfishing model is based are as follows. First, the model is based on the assumption that there is no interspecific interactions, specifically that the removal of predators of benthic organisms by the fishery and the addition of food for benthic scavangers have no affect and that the members of the benthic community do not compete with each other. Some studies challenge these assumptions (Fonds and Groenewold, 2000). Second, like many of the traditional models used in fish population dynamics, the model proposed here is based on the assumption that, other than reducing the population size, fishing does not alter the ability of a population to reproduce itself. However, trawling can alter the benthic substrate (Caddy, 1973) and it is possible that such alteration could be detrimental to the successful settlement of planktonic recruits. Third, the model is applicable to a uniform habitat encompassing the total populations of all the species comprising the benthic community. However, the sea bed is a mosaic of habitats that grade together, therefore it is difficult, and perhaps somewhat arbitrary, to partition it into discrete units that capture the essence of the ideal model habitat. Fourth, the spatial distribution of fishing effort within the habitat is assumed to be random with respect to the distribution of the various benthic species. This would be reasonable if the distribution of the target species (i.e., a migratory fish) is independent of the distribution of the benthic species. If, however, the benthic species are spatially aggregated in a pattern similar to the distribution of effort then the effective value of m would be higher than the value estimated experimentally. This would be especially problematic in situations where the fishery targets a member of the benthic community (i.e. scallops, clams, *Nephrops*) because the spatial distribution these species is likely dependent on the same physical characteristics of the seabed that are required by the other benthic species. Unless the geographic boundaries of the habitat were carefully chosen (for example, only the combined area of individual scallop beds), such non-random effort would violate the assumptions under which f_e is calculated.

Controlling benthic overfishing

In the proposed model, benthic overfishing is defined as when the current level of effort (f_e), corrected for spatial aggregation, is greater than the effort corresponding to the maximum production of either the least productive species ($f_{max,i}$) or the benthic community as a whole ($f_{max,c}$, $f_{max,e}$). To reduce the likelihood of reaching an overfishing condition, management actions can be taken to increase $f_{max,i}$, $f_{max,c}$ or $f_{max,e}$ or to reduce f_e. The most readily apparent way of doing this is simply to reduce the total nominal effort, but this would engender strong opposition from the fishing community. An alternate strategy is to use one of two control variables implicit in the benthic overfishing model which allow reducing the likelihood of overfishing without requiring a reduction in the overall level of nominal effort. The first way to do this is to reduce m and thereby increase $f_{max,i}$, $f_{max,c}$ or $f_{max,e}$ through gear modifications which reduce the impact of the gear on the bottom community. A variety of studies are in progress or have been completed which consider reducing the contact of various trawl components with the bottom by using field studies (van Marlen, 2000; Fonteyne, 2000) and tank experiments (Richter and Köpnick, 2000). Besides lessening the direct pressure exerted on the bottom, other ways of reducing mortality include the use of escape panels and sorting grids to remove benthic organisms from the trawl before they are brought to the surface (van Marlen, 2000). The crux of using such technical measures, however, is to design them such that they do not significantly reduce the capture efficiency of the gear for the target species. In situations where nominal fishing effort is unregulated, fishers would likely respond to a decrease in capture efficiency by increasing total effort to maintain their catches and this could negate any gains from the technical measure.

The second way of reducing the likelihood of benthic overfishing is to increase the aggregation of effort and thereby decrease f_e. In the absence of any management control, fishing effort is typically aggregated due to the combined factors of availability of a smooth seabed, proximity to port and density of target species (Rijnsdorp et al., 1998). Since an increase in this aggregation results in a decrease in f_e, management can reduce the likelihood of benthic overfishing by artificially increasing effort aggregation. To be effective, however, such management actions must lead to a spatial distribution of effort that is unchanging with time, because the gains from aggregation only accrue under equilibrium conditions. For example, area closures could be used to increase effort aggregation, but if the closed areas vary between years much of the effectiveness of the closures may be lost. To insure stability may require the definition of Marine Protected Areas in which all trawling is prohibited. Establishment of such areas have been proposed by many researchers (Auster, 2001; Lindholm et al., 2001) both to help protect the benthic population and provide an area where the community might return to an unfished state. Similar to the use of technical measures, however, if the imposition of closed areas leads to a decrease in the catch rate of target species, fishers may increase the total effort expended to maintain the same catch. Without effort limitation, the imposition of closed areas to preserve the benthic community will inevitably lead to increased disturbance in the open areas.

References

Auster, P.J., 2001. Defining Thresholds for Precaustionary habitat Management actions in a fisheries context. North American Journal of Fisheries Management 21: 1-9.

Bergman, M. J. N. and J. W. van Santbrink, 2000. Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. ICES Journal of Marine Science 57: 1321-1331.

Caddy, J. F., 1973. Underwater observations on tracks of dredges and trawls and some effects of dredging in a scallop ground. Journal of the Fisheries Research Board of Canada 30: 173-180.

Clark, W., 1991. Groundfish exploitation rates based on life history parameters. Canadian Journal of Fisheries and Aquatic Science 48: 734-750.

Collie, J.S., S. J. Hall, M.J. Kaiser and I.R. Pointer, 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. Journal of Animal Ecology 69:785-798.

Currie, D. R. and G. D. Parry,1996. Effects of scallop dredging on a soft sediment community: A large-scale experimental study. Marine Ecology Progress Series 134: 131-150.

Daan, N., 1991. A theoretical approach to the evaluation of ecosystem effects of fishing in respect of north sea benthos. ICES CM 1991/L:27.

DeAlteris, J.T. and D.M. Reifsteck, 1993. Escapement and survival of fish from the codend of a demersal trawl. ICES Marine Science Symposium 196: 128-131.

Fonds, M. and S. Groenewold, 2000. Food subsidies generated by the beam-trawl fishery in the southern North Sea. Pages 130-150 *in* M.J. Kaiser and S.J. de Groot (eds.). Effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues. Blackwell Science Ltd. Oxford, UK .

Fonteyne, R. 2000. Physical impact of beam trawls on seabed sediments. Pages 15-36 *in* M.J.

Kaiser and S.J. de Groot (eds.). Effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues. Blackwell Science Ltd. Oxford, UK .

Hall-Spencer, J. M. and P. G. Moore, 2000. Impact of scallop dredging on maerl grounds. Pages 105-117 *in* M.J. Kaiser and S.J. de Groot (eds.). Effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues. Blackwell Science Ltd. Oxford, UK

Hilborn, R. and C.J. Walters, 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York.

Joll, L.M. and J.W. Penn, 1990. The application of high resolution navigation systems to Leslie-DeLury depletion experiments for the measurement of trawl efficiency under open-sea conditions. Fisheries Research 9: 41-55.

Kaiser, M.J. and B.E. Spencer, 1994. Fish scavenging behavior in recently trawled areas. Marine Ecology Progress Series 112: 41-49.

Kaiser, M. J. and B. E. Spencer, 1995. Survival of by-catch from a beam trawl. Marine Ecology Progress Series 126, 31-38.

Lindeboom, H. J. and S. J. de Groot (ed.), 1998. Impact II: The Effects of Different Types of Fisheries on the North Sea and Irish Sea Benthic Ecosystems. NIOZ-RAPPORT 1998-1/RIVO-DLO REPORT C003/98. Netherlands Institute for Sea Research. Texel, The Netherlands .

Lindholm, J.B., P.J. Auster, M. Ruth, and L. Kaufman. 2001. Modeling the effects of fishing and implications for the design of marine protected areas: juvenile fish responses to variations in seafloor habitat. Conservation Biology 15:424-437.

MacDonald, D. S., M. Little, N. C. Eno, and K. Hiscock, 1996. Disturbance of benthic species by fishing activities: A sensitivity index. Aquatic Conservation: Marine and Freshwater Ecosystems. 6: 257-268.

McKeown, D. L. and D. C. Gordon Jr,.1997. Grand Banks otter trawling impact experiment: II.

Navigation procedures and results. Canadian Technical Report of Fisheries and Aquatic Sciences 2159, Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, Canada , xi + 79 p.

Murawski, S.A., 2000. Definitions of overfishing from an ecosystem perspective. ICES Journal of Marine Science 57: 649-658.

Pope, J.G., D.S. MacDonald, N. Daan, J.D. Reynolds, and S. Jennings, 2000. Gaging the impact of fishing mortality on non-target species. ICES Journal of Marine Science 57: 689-696.

Ramsay, K., M. J. Kaiser, and R. N. Hughes, 1998. Responses of benthic scavengers to fishing disturbance by towed gears in different habitats. Journal of Experimental Marine Biology and Ecology 224: 73-89.

Richter, U. and W. Köpnick 2000. Measuring methods used in model tests for analyzing the interactions between towed marine structures and the sea bed. Pages 15-32 *in* M.. Paschen,, W. Köpnick, G. Niedzwiedz, U. Richter, and H.-J. Winkel (eds.) Contributions on the Theory of fishing gears and related marine systems. Neuer Hochschulschriftenverlag Dr. Ingo Koch and Co., Rostock.

Rijnsdorp, A. D., A. M. Buys, F. Storbeck, and E. G. Visser,1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. ICES Journal of Marine Science 55: 403-419.

Rose, C.S., 1999. Injury rates of red king crab, *Paralithodes camtschaticus*, passing under bottom-trawl footropes. Marine Fisheries Review 61: 72-76.

Sainsbury, K. J., R. A. Campbell, R. Lindholm, and A. W. Whitelaw,1997. Experimental management of an Australian multispecies fishery: Examining the possibility of trawl-induced habitat modification. Pages 107-112 *in* E.K. Pikitch, D.D. Huppert and M.P. Sissenwine (eds.). Global trends: fisheries management. American Fisheries Society Symposium 20.

Schaefer, M.B., 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Bulletin of the Inter American Tropical Tuna Commission 1: 27-56.

Somerton, D.A. and R.S. Otto, 1999. Net efficiency of a survey trawl for snow crab, *Chionoecetes opilio*, and Tanner crab, *C. bairdi*. Fishery Bulletin 617-625.

Van Marlen, B. 2000. Technical modifications to reduce the by-catches and impacts of bottom-fishing. Pages 253-268 *in* M.J. Kaiser and S.J. de Groot (eds.). Effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues. Blackwell Science Ltd. Oxford, UK.

Table 1. Population parameters for a hypothetical benthic community consisting of four species. The parameters included are: the intrinsic rate of population growth (r), the population biomass before fishing is initiated (K), the mortality rate per unit of swept area at the initiation of fishing (m_0) and a parameter controlling the biomass-dependency of mortality rate (α)

Species	r	K	m_0	α
1	2.0	15	0.01	0.5
2	0.8	20	0.01	0.5
3	0.6	10	0.01	0.5
4	0.4	4	0.01	0.5

Table 2. The effect of effort aggregation on the estimated value of effective effort (f_e) when the total nominal effort (f total, total swept area) is held constant. The values of f_1-f_4 are the nominal effort in each of four subareas. Calculations are based on the vital and fishing parameters for species 1 in Table 1.

f_1	f_2	f_3	f_4	f total	f_e
500	500	500	500	2000	2000
300	700	700	300	2000	1678
100	900	900	100	2000	941

Appendix 1. Development of a biomass dependent fishing mortality rate

Since equilibrium body size decreases as fishing effort increases, the fishing mortality rate (*m*) per unit of effort will decline if the fishing gear is size selective. Although the change in fishing mortality rate with mean size is an inherent part of most age based fishery management models, because they typically include age dependent catchability coefficients, I am not aware of any production models that include this feature. The relationship that I propose (Equation 4) rests on the adequacy of using the quotient of equilibrium biomass to virgin biomass as proxy for mean body size. To demonstrate that the relationship mimics quite well the behavior of average q ($\overline{q}$) in an age based model, consider a simple comparison using age based population consisting of *a* age classes. The biomass of the population is:

$$W = \sum_{k=1}^{a} W_k N_k \tag{16}$$

Where N_k is the number of individuals and W_k is the individual body weight at age k. The survivorship to age k is:

$$\mathrm{N}_k = N_0 \sum_{i=1}^{k-1} e^{-(n+q_i f)} \tag{17}$$

Where n is the natural mortality rate, f is the constant nominal fishing effort, q_i is the catchability at age i, and N_0 is the constant number of recruits at age 0. The weight of the catch is:

$$C = \sum_{k=1}^{a} N_{k-1}(1 - e^{-(n+q_i f)})(\frac{q_k f}{n + q_k f}) \tag{18}$$

From the perspective of a surplus production model, $\overline{q}$ is determined as:

$$\overline{q} = \frac{C}{Wf} \tag{19}$$

To demonstrate how $\overline{q}$ varies with f, Equations 16-19 were repeated evaluated over a range of f using estimates of W_k, q_k, and m for walleye pollock (*Theregra chalcogramma*; Ianelli, 2000; I was not able to find similar data for a benthic species). The values of equilibrium $\overline{q}$ are shown plotted against f in Fig. 1. Also shown are values of q predicted from

$$q = q_0 \left(\frac{W}{K} \right)^{\alpha} \tag{20}$$

Where q_0 and K were estimated as q and W at $f = 0$ (from Equations 16-19) and α was determined by trial and error to be 0.5. For this example the general shape of $\overline{q}$ as a function of f is captured quite well by the approximation.

Figure 1. Average *q* calculated from the age based model as a function of *f* (points) is shown along with the approximating function (solid line).