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Abstract

Pacific salmon sport-fishing data without time trends in the catchability coefficient q or in fish abundance N show that q is larger at lower N. This phenomenon causes serious management problems because it creates critical thresholds in population size and fishing effort that can lead to stock extinction. The inverse relation between q and N directly parallels the analogous relation shown by some predators in natural ecosystems.

Our purpose in this paper is to determine if catchability of sport-caught salmon varies in some predictable manner with changes in fish abundance.

Variability in the catchability coefficient q is of interest to biologists and managers. Usually, q is assumed to be a constant that represents the proportion of a fish population caught by each unit of nominal effort:

$$C/N = qf; \qquad (1)$$

where C = catch, N = fish abundance, and f = nominal fishing effort (boat-days, hours fished, et cetera). A rearrangement of Equation (1),

$$C/f = qN, \qquad (2)$$

means that the catch per effort is linearly related to fish abundance, with a slope q. This relation frequently is used to estimate fish abundance. However, q actually may vary with N as well as with other variables such as changes in fishing power or area swept by fishing gear, alterations in fish distribution relative to vessel distribution, or variations in fish vulnerability to gear (behavioral shifts) (Gulland 1964). If the catchability coefficient varies with fish abundance, then this must be taken into account to permit proper estimation of fish abundance and effective management.

In our analysis, we apply concepts derived from natural predator-prey interactions to sport-fishing data on chinook salmon *Oncorhynchus tshawytscha*. Relatively good, independent estimates can be obtained for salmon abundance and catch per unit effort, so these data are well-suited for assessments of the relationship between q and N.

Previous Studies

A model by Paloheimo and Dickie (1964) predicted that the catchability coefficient usually would vary inversely with fish density or abundance because as fish abundance decreases, the area searched by each unit of nominal fishing effort should represent a larger portion of the area occupied by the clumped fish population. This model could not be tested at the time because most abundance estimates were derived from the relation shown by Equation (2), which assumes a constant q. Cohort analysis (Pope 1972; Doubleday 1976), based on Ricker's (1948) iterative solution to the catch equation, removed this problem; it allows independent estimates of abundance and catch per unit effort. This technique enabled several authors to show empirically that catchability varies inversely with population abundance (Fox 1974 and MacCall 1976 for Pacific sardine *Sardinops sagax caerulea*; Schaaf 1975 for Atlantic menhaden *Brevoortia tyrannus*; Pope and Garrod 1975 and Garrod 1977 for North Atlantic cod *Gadus morhua*; Ulltang 1976 for Atlanto-Scandian herring *Clupea harengus*). Rothschild et al. (1970) implied a similar trend for one stock of Alaskan king crab *Paralithodes camtschatica*, but they used a rather indirect measure of abundance of legal-sized crabs. However, in all but the herring study there were time-series trends that confounded the interpretation of the functional relation between q and N; abundance generally decreased over time and q increased. An increase in q is a common result of improved fishing technology. Furthermore, the cohort analyses required major assumptions about the age-specific natural
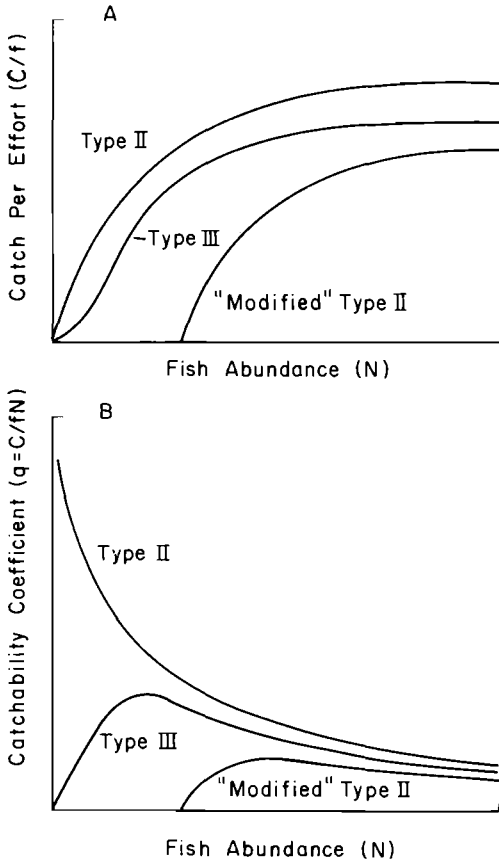
FIGURE 1.—*Functional responses typically shown by natural predators (after Holling 1959a). Dependent variates are described in fisheries terms instead of Holling's original predator terminology: (A) catch per unit of nominal effort instead of catch per predator per unit time; (B) catchability coefficient instead of proportion of prey caught per predator per unit time.*

mortality rate (see Ricker 1977 and Gulland 1977a for reviews). As we will show, the salmon sport-fishing data do not show time trends in q or N and estimates of N do not require the gross assumptions necessary for cohort analysis.

Beginning in 1959, C. S. Holling developed the theory and empirical basis for what Solomon (1949) called the numerical and functional responses of predators to prey abundance. A numerical response occurs if predator numbers increase in response to higher prey abundance, due to aggregation, immigration, or higher fecundity. There are obvious analogies in sport and commercial fisheries.

Functional responses, our main concern

here, occur if prey abundance affects catch per predator per unit of time. Holling (1959a) showed that there should be four major types of functional responses, based on the components of predator behavior. His type-II, type-III, and modified type-II functional responses apply to our analysis (Fig. 1). All these responses reach an asymptote because predators have finite gut capacities, search areas, and times available for seeking and handling prey. In modified type-II functional responses, there is no predation loss below a certain threshold abundance of prey because all prey can hide or prey are so rare that predators do not detect them. Again, commercial and sport fishermen show analogous responses; indeed there is a strong similarity between Holling's (1959b) type-II functional response and Paloheimo and Dickie's (1964) relationship in their Fig. 2 (incorrectly printed as their Fig. 1).

Functional responses measured in terms of catch per effort can be transformed into catchability coefficients merely by calculating the proportion of the prey population caught per predator per unit time at each level of prey abundance (Fig. 1). Thus, based on Holling's work, we predict that q varies with fish abundance in a way that depends on the particular type of fishing process.

These general predation principles were applied to natural predators of juvenile salmon and to native Indian food fishermen who harvest adult salmon (Peterman and Gatto 1978; Peterman 1980). The latter study showed that some good predictions of harvest could be made with a functional-response framework and that q does vary inversely with fish abundance. The present study extends this work to sport fishing for chinook salmon.

Methods

Data Sources

Pacific salmon populations can be enumerated fairly accurately because they are anadromous. Except where sport and commercial fishermen harvest a stock congruently, or where immature "feeder" fish are present, one simply assumes that the sport (and any Indian) catch is removed from a single population, that all remaining fish escape upstream to the spawning grounds that year, and that no mortality occurs before spawning fish are counted. Therefore,

$$N = C_S + C_I + E,$$

where N = total fish available annually, C_S = annual sport catch, C_I = annual native Indian food catch, and E = annual escapement.

These assumptions and restrictions were met by two chinook salmon sport fisheries in British Columbia and one in Oregon. Rivers Inlet is a 3-km-wide fjord that extends about 30 km inland from Wadhams, British Columbia. Chinook salmon spawn in the Wannock River, which empties into the head of this inlet. The sport fishery occurs in a 3 by 10 km permit area that is closed to commercial fishing and up the inlet from it. Permits are issued each year at the Kilbella Bay dock and fishermen are obliged to report their catch there. Effort is measured as permits issued per year. The daily limit was two chinook salmon per day, or four during the permit-area season, but few fishermen approached these limits. Schutz (1975) summarized these catch and effort statistics since 1956. Escapement data for the Wannock River were provided by the Canada Department of Fisheries and Oceans, Vancouver. Three years of data were added (D. Schutz, personal communication, Canada Department of Fisheries and Oceans, Vancouver), so our information spans 1956–1977.

Similar data on the Gold River sport permit fishery for 1957–1975 were provided by D. Schutz (personal communication). This fishery occurs in Muchalat Inlet, off Nootka Sound on the west coast of Vancouver Island. The permit area is at the head of the inlet and covers about 12 km². Annual permits are issued and sport catch is closely monitored at docking facilities. Commercial fishing only occurs seaward of the permit area. Chinook salmon spawn in the Gold and Burman rivers, which empty into the head of Muchalat Inlet, and there is no Indian fishery on chinook salmon in this region. The daily bag limit was four fish, which very few fishermen ever reached.

The lower Willamette River sport fishery on the spring chinook salmon run in Oregon provides the longest time series of data (1946–1978) on sport effort, catch, and escapements (Hasselman and Stout 1964; Collins 1978, 1979). Collins estimated, in the same way as defined above, the abundance of fish potentially available for harvest by sport fishermen in the lower Willamette River. Run size is composed of the sport catch in the lower Willamette and Clackamas rivers, escapements in the Clackamas River and counts upstream at the Willamette Falls fishway. "Lower Willamette River" refers to the 60 km of river downstream from these falls. Effort and catch data were estimated from extensive aerial surveys and creel censuses. Effort statistics here are angler-days of boat fishing only; bank fishing effort has only been enumerated since 1974. Catch figures include both bank and boat fisheries because the two were not tabulated separately until 1965. However, Collins' (1979) data show that the bank catch averages only 1–2% of the total, and should not bias the analysis seriously. Regulations on the lower Willamette chinook fishery have been fairly constant, with a single 19-day closure in 1964, and a very late closure in 1976. The daily bag limit varied between two and three fish, but the data show total catch per boat has never exceeded 0.2.

Effort data are lacking on the chinook salmon sport fishery on the Naknek River, Alaska (van Hulle and Gwartney 1976), but we can apply Holling's type of analysis to total catches to predict effects of regulations.

Analysis

Catchability coefficients calculated for each year from catch, effort, and total-run data were plotted against fish abundance. These curves are of the type-II form, which can be described by the Michaelis-Menten equation from enzyme kinetics:

$$C/f = (aN)/(b + N). \qquad (3)$$

Here, C = annual catch in numbers;

f = annual nominal effort in angler-days or permits issued;

N = annual abundance of fish (total run size to the location where the fishery starts);

a = maximum proportion of the population that can be caught per unit effort;

b = total run size that yields a catch per effort of $a/2$.

By rearranging Equation (3) we obtain an equation for the catchability coefficient:

$$q = C/fN = a/(b + N). \qquad (4)$$

Equation (4) was fit to the data by a nonlinear,

least-squares method that included a quasi-Newton parameter search. When parameters a and b are positive, q is density-dependent, that is, it varies inversely with run size. For predictive relations we prefer to use Equation (4) instead of Equation (6), introduced below, because of the simple biological interpretations of the parameters a and b.

To understand the true underlying functional relation between q and N, we used an equation that allowed parameters to be estimated by linear functional regression (Ricker 1973). This equation describes potential density dependence in catchability (Fox 1974; MacCall 1976; Gulland 1977b; Radovich 1979):

$$C/f = \alpha N^{\beta+1}. \tag{5}$$

Dividing through by N, we obtain:

$$q = C/fN = \alpha N^{\beta}, \quad \text{or} \tag{6}$$

$$\log_e q = \log_e \alpha + \beta \log_e N. \tag{7}$$

The parameters α and β then were estimated from a functional regression of $\log_e q$ on $\log_e N$. This approach accounts for the bias of unknown measurement error and natural variability and gives the best estimate of the true underlying relation (Ricker 1973). When $\beta = 0$, q is a constant, and when $\beta < 0$, q decreases as N increases. Equation (6) formed only one component of Fox's (1974) nonlinear fisheries model and he fit β by trial and error. The only other authors who empirically estimated β are MacCall (1976), who used a functional regression, and Ulltang (1976), who used a standard least squares regression.

To determine if there is significant curvature in the relation between catch per effort and fish abundance, we used this same functional-regression approach on the logarithmic transform of Equation (5). Empirically estimated β values then were compared with the null hypothesis, $\beta = 0$ (C/f linearly related to N). Such statistical comparisons cannot be applied to Equation (7) because the two variates, q and N, are not mutually independent.

Other Responses

Lower catchability coefficients at high fish abundance could be created by numerical responses and competition among fishing gear. To detect if numerical responses occurred, we plotted scatter diagrams of effort as a function
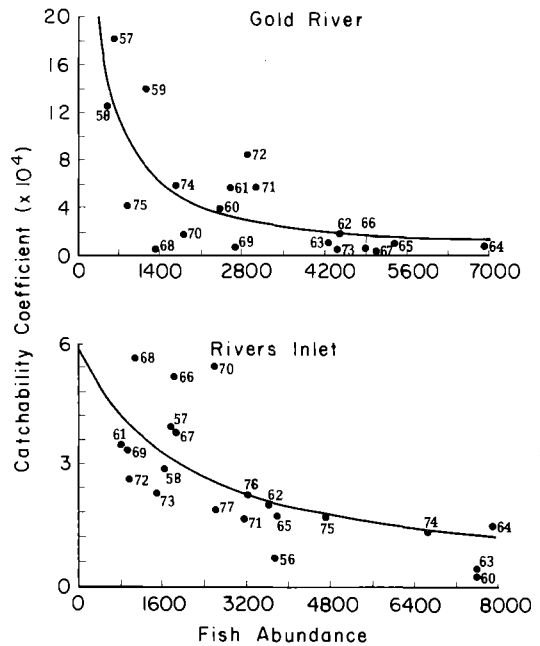

FIGURE 2.—Catchability coefficient q as functions of fish abundance for sport fisheries on the Gold River and Rivers Inlet chinook salmon stocks (q falls in the range 0 to 20 × 10⁻⁴). Numbers beside points are years.

of current run size and last year's run size (the latter accounting for a lagged response), and plotted effort as a function of current year's catch per effort and previous year's catch per effort, which assumed C/f is used as an indicator of fish abundance by fishermen. Any tendency for an increasing linear or nonlinear relation would indicate a numerical response. We looked for competitive and cooperative effects among fishermen by plotting the proportion of fish caught against nominal effort (Rothschild 1977). Any tendency to deviate from a linear relation would indicate cooperation (upward slope) or competition (asymptote at a fixed proportion caught).

Results

Catchability Coefficients

The catchability coefficient increased as fish population size decreased in the Rivers Inlet, Gold River, and lower Willamette River chinook salmon sport fisheries (Figs. 2–4). The q values showed no time trend and the data strongly suggest type-II functional responses for fishermen rather than type-III (see Fig. 1B).
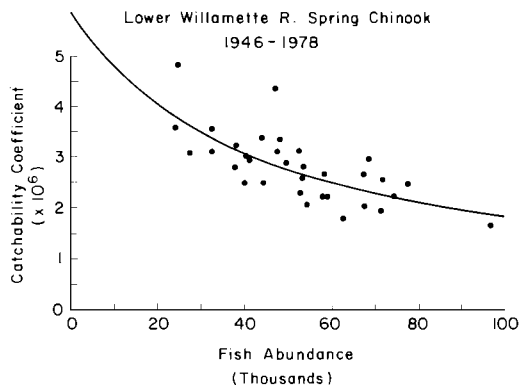
FIGURE 3.—*Catchability coefficient* q *in relation to fish abundance for the lower Willamette River sport fishery on chinook salmon* (q *falls in the range 0 to 5* × 10⁻⁶).

FIGURE 4.—*Time series of catchability coefficients for the lower Willamette River chinook sport fishery.*

Table 1 gives the parameter values for fits of Equations (4) and (6) to these relations. The curves derived from the two equations differ very little in shape. The r^2 values for Equation (6) show over 50% of the variability is accounted for. The β values in Table 1 generally are lower than the ones obtained for California sardines by Fox (-0.3) and MacCall (-0.724), showing that q is more strongly density-dependent in our cases. Ulltang's β for Atlanto-Scandian herring, -1.375, is of the same order as ours, but his estimation method does not account for observation errors and hence it gives too large a negative result.

A strong inverse relation between q and N implies that catch per nominal effort also should be a nonlinear function of fish population size, and this is illustrated by the lower Willamette sport fishery (Fig. 5). The null hypothesis of linearity between C/f and N is rejected ($P < 0.001$) for the lower Willamette fishery but not for Gold River and Rivers Inlet ($P > 0.05$). The latter two fisheries do not show
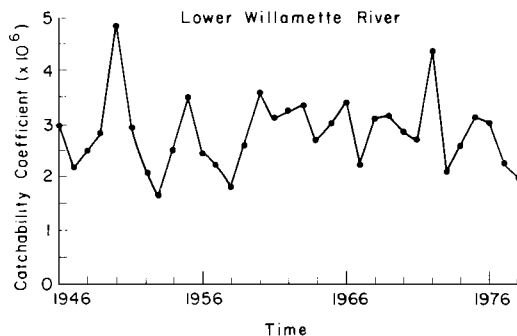
significant curvature in the relation between C/f and N because of the wide scatter in the data when plotted in this form. The asymptotic trend shown in Fig. 5 is similar to the one shown by Rothschild et al. (1970) for one of the stocks of king crab.

Numerical and Other Responses

No linear or nonlinear numerical response existed with either type of abundance data (N or C/f), lagged or not ($P_{r=0} > 0.5$). Thus, variation in effort must be determined mainly by other factors. Proportions of fish caught were linear functions of nominal effort and showed no tendency for either competitive or cooperative effects at greater effort.

If numerical responses are weak or nonexistent over the range of run sizes observed in our data, then effort can be considered a random variate, with some mean, with respect to fish abundance. Thus, we would expect total sport catch as a function of fish abundance to have the same shape as the catch per effort or true functional-response relation. Figure 6 shows one such case where a modified type-II

TABLE 1.—*Parameter values[a] for two equations that describe the catchability coefficient for sport-caught chinook salmon as functions of fish abundance. Proportion of variability accounted for by the second equation is given in the last column.*

	For $q = a/(b + N)$		For $q = \alpha N^\beta$		
	a	b	α	β	r^2
Lower Willamette River	0.26	42,684.0	6.30×10^{-3}	-0.72	0.53
Gold River	0.89	83.5	44.5	-1.56	0.50
Rivers Inlet	1.21	2,064.0	1.23	-1.10	0.56

[a] q = catchability coefficient; N = fish abundance; a, b, β, and α are parameter values.
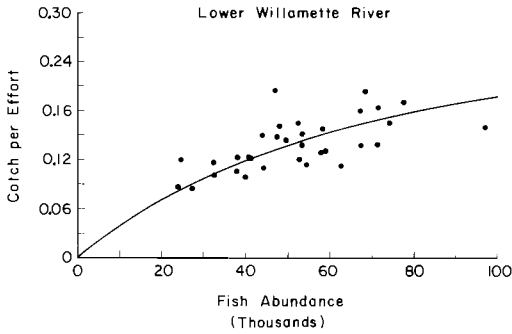
FIGURE 5.—*Sport catch per effort of chinook salmon on the lower Willamette River as a nonlinear function of fish abundance. Equation (3) was fit to the data by nonlinear least squares.*
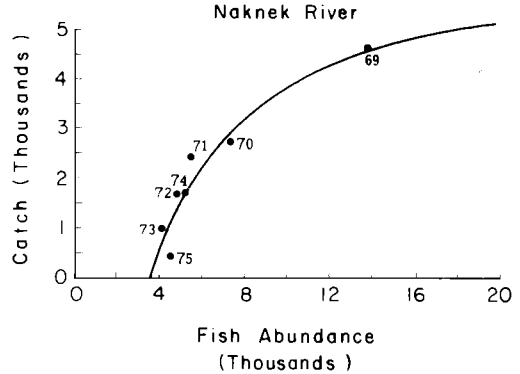

FIGURE 6.—*Total catch as a function of fish abundance for the Naknek River, Alaska chinook salmon sport fishery. Numbers beside points are years.*

functional response best describes the Naknek River sport catch of chinook salmon. The equation fit to this graph by the nonlinear least squares method is a variant of Equation (3):

$$C = a(N - k)/(b + N - 2k) \qquad (8)$$

The parameter k is the value of the non-zero intercept on the fish-abundance axis, or the population size below which no harvest is taken. In this equation, the parameter a represents the maximum total catch.

Discussion

The chinook salmon sport fisheries of the lower Willamette River, Gold River, and Rivers Inlet show a tendency for catchability coefficients to increase as fish abundances decrease. That is, the proportion of fish caught by each unit of effort varies inversely with fish abundance. Our data do not show any time trend in q values, so this inverse relation between q and N is not due to an increase in catching power over time, as might be the case in the studies of Fox (1974), Schaaf (1975), MacCall (1976), and Garrod (1977). The lack of numerical responses or competitive effects in our salmon data means that the catchability coefficient varies with fish abundance for reasons other than changes in effort.

Several authors have postulated that a decrease in q as N increases could arise from gear saturation, limited available searching area and time, schooling or clumping behavior of fish, or a nonrandom search pattern by fishermen (Gulland 1964; Paloheimo and Dickie 1964;

Clark 1974; Garrod 1977; Rothschild 1977). In our situations, there is no evidence for gear saturation. However, the increase in q at low salmon abundance can be attributed to the physically restricted environments for salmon, which can be searched by fishermen fairly effectively. Fishing is concentrated where the fish are located, in part due to communication among fishermen. As fish abundance decreases, this concentrated fishing effort on a spatially localized fish stock will result in higher harvest efficiencies. Alternatively, the water volume "searched" per angler-day has a maximum value, and as fish abundance and total volume occupied by fish increase, the ratio of volume "searched" to volume occupied decreases. Therefore, the proportion of fish caught and the q value should also decrease.

We have documented only type-II functional responses, yet both type-II and type-III functional responses are common among natural predators. So why do not sport fishermen show a type-III relation? As Hassell (1978) points out, a type-III response most likely is generated when some component of the searching rate increases with prey abundance: for example, when learning occurs. This could arise where fish densities are low and the area occupied by fish is very large relative to the searching ability of fishermen, which was not the case in our examples.

There are important management consequences of higher q values at low fish abundance. If there is no numerical response among
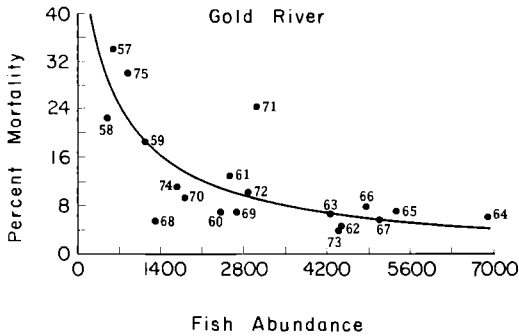
FIGURE 7.—*Percent mortality caused by sport fishermen in relation to fish abundance for Gold River chinook salmon stocks. Numbers beside points are years.*

fishermen, then we would expect the percent mortality caused by all units of effort to also increase at low abundances. Such relations will not be identical to the q versus N curves because effort is variable from year to year. For example, the Gold River case shown in Fig. 7 illustrates the inverse relation between percent fishing mortality and fish abundance. An equation of the same form as Equation (4) [% mortality $= a/(b + N)$] was fit to the data by the nonlinear least squares method mentioned above. The depensatory mortality effect shown in Fig. 7 means management attempts to keep small stocks from going extinct will be made additionally difficult because effort will have to be controlled much more severely than would be the case if q were a constant function of N. This positive feedback of higher percent fishing mortality at low fish abundance also could create the critical-depensation case discussed by Clark (1974), Fox (1974), Gulland (1977b), and Clark and Mangel (1979). There would be a critical threshold population size below which the stock would go to extinction because recruitment to the spawning grounds would not reach replacement levels. A modified type-11 functional response, as in Fig. 6, could prevent the stock from going extinct by establishing a stable, lower equilibrium point, but there would still be a critical threshold population size that separates commercially valuable from "commercially extinct" stocks (see Peterman 1977).

There is another important management implication. An asymptotic relation of C/f with increasing N means that decreases in catch per effort *underestimate* decreases in actual abun-

dance (Gulland 1977b; Radovich 1979). Thus, a manager can be dangerously misled by catch per effort as an abundance estimator.

We do not know the extent to which the density-dependent q values found in salmon sport and Indian food (Peterman 1980) fisheries are applicable to other fisheries, including commercial ones. We suspect the relation is more prevalent than currently believed, because of the highly nonrandom searching behavior of fishermen and the schooling behavior of many fish. An inverse relation between q and N could underlie the time trend in q and N values found in the other studies discussed. The temporal increase in q that coincides with a drop in fish abundance will only be added on top of any true relation between q and N and this will make careful control of the fishery even more important. Because of the extremely large catching power of commercial boats, many commercial fisheries could be operating on the very low, left hand end of a type-II catch-per-effort curve. If this is true, then the assumption of a constant q and a linear relation between C/f and N may not be too misleading. This would be analogous to the low end of Holling's type-I functional response, where C/f rises linearly to a maximum, giving a constant q until the maximum is reached. Many commercial fisheries are managed under this linear assumption, but because of the potentially severe consequences if it is wrong, the assumption should be carefully tested.

Acknowledgments

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