The Relationship Between Catch Per Unit Effort and Stock Abundance

by

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Abstract

In recent years, there has been discussion about catch per unit effort, CPUE, of the form CPUE = AN^p where N is abundance and $p < 1$. In this paper, it is first shown that, if one ignores stock depletion, then CPUE can be independent of abundance, proportional to abundance or of the approximate form AN^p with $p < 1$. The same is true when depletion of the stock is considered. A method for determining the regime (CPUE independent of abundance, proportional to abundance, or of the form AN^p) based on search time data is presented.

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Introduction

The relationship between fishing effort, stock abundance, and catch rates is of extreme importance to the management of commercial fisheries. A commonly used heuristic is a linear assumption between catch or harvest rate H, effort E and abundance N. That is,

$$H = qEN \tag{1}$$

where q is the catchability coefficient. If the relationship (1) is valid, then catch per unit effort, CPUE, defined by CPUE = H/E is proportional to N. Consequantly, by tracking the time behavior of CPUE, one has a proxy for the behavior of the abundance of the population. The theoretical underpinnings of (1) will not be discussed here at this point. They have received considerable attention, dating at least to work of Ricker (1940), De Lury (1947, 51), Neyman (1949), Paloheimo and Dickie (1964), Paloheimo (1971), Rothschild (1977), and Clark and Mangel (1979).

There is mounting empirical evidence, however, that (1) is not always valid Some examples are discussed by MacCall (1976), Murphy (1977), Beddington (1978), Ulltang (1980), and Cooke (1985a). The evidence points to a relationship of the form

$$H = AN^p \tag{2}$$

where A is a constant, possibly directly proportional to effort but possibly not, and p is a fixed constant with $0 < p \leq 1$. If (2) is valid then catch per unit effort CPUE = AN^p/E is no longer proportional to stock abundance, but to a fractional power of abundance. If (2) is indeed the valid harvest-abundance relationship, it has many implications such as:

i) If a time series of CPUE shows a decline, the true population has declined even more.

ii) If a time series of CPUE oscillates, then the amplitude of the oscillations of the true population is even greater.

iii) If (2) is valid, but one assumes a relationship of the form (1), then the catchability coefficient q is a function of abundance N. In particular one finds that

$$q = \frac{A}{E} N^{p-1}$$

which can be rewritten, for constant effort, and $b = 1 - p$ as

$$q = kN^{-b},$$

These equations (the latter equation being empirically verified by Ulltang (1980, pg 490)) show that an increase in "catchability coefficient" q occurs as population abundance decreases. Empirical evidence for California sardine (MacCall, 1976) for example, shows $b \approx .6$.

The natural question then arises: under what operational circumstances would one obtain a relationship of the form (2)? Previous work on this subject includes Ricker (1940), De Lury (1947, 51), Neyman (1949), Paloheimo and Dickie (1964), Rothschild (1977), Beddington (1979), Clark and Mangel (1979), Zahl (1982, 83), and Cooke (1985a,b). A number of these authors demonstrated a relationship of the form

$$CPUE = \frac{qN}{\alpha + \beta N} \quad (3)$$

where q, α and β are constants. Cooke (1985a,b) has provided one model that, over a wide range of operational parameters, leads to a catch-abundance relationship similar to (2). His model is based on catch that is locally Poisson with parameter proportional to q, a fixed harvest time per catch, and a log-normal distribution on q. (An alternate derivation of Cooke's model is presented in the next section, so further details are delayed until then.)

In order to use a model such as (3), one needs to have an explicit operational interpretation of α and β. Mangel (1982, 1985) provides such an explicit model in which search and harvest for identical schools of fish are the only components of the fishing process. By using renewal theory and ignoring stock depletion, one can show that the average catch rate is

$$E\{CPUE\} \approx \frac{H(\tau)}{\frac{1}{\lambda} + \tau} \tag{4}$$

where τ is the set time, $H(\tau)$ is the average catch from a set of length τ and $1/\lambda$ is the mean time between detections of schools. If one ignores depletion, then it is reasonable to assume that $\lambda = \epsilon N$ where ϵ is a constant (usually unknown). With this assumption, (4) becomes

$$E\{CPUE\} \approx \frac{H(\tau)\epsilon N}{\epsilon N\tau + 1} . \tag{5}$$

Equation (5) is similar to (3), except that ϵ and τ have clear operational interpretations as the search effectiveness and set time. There are three "regimes" associated with (5). These are:

1. If $N\epsilon\tau \ll 1$, then $E\{CPUE\} \approx H(\tau)\epsilon N$ and catch per unit effort is proportional to population abundance.

2. If $N\epsilon\tau \gg 1$, then $E\{CPUE\} \approx H(\tau)/\tau$ and catch per unit effort is independent of abuncance.

It is perhaps easiest to think of the first case as low abundance, so that finding a school of fish is a rare event and the second case a high abundance, so that one easily finds schools and is essentially fishing all the time.

3. If $N\epsilon\tau \approx 1$, then one is dealing with the "curved" part of (5), rather than the "linear" or "flat" portions (see Figure 1).

Consider a value of N for which $N\epsilon\tau \approx 1$. Suppose that one tries to fit $CPUE = AN^p$ to (5). Taking logarithms gives

$$\log A + p \log N = \log H(\tau) + \log \epsilon + \log N - \log(\epsilon N\tau+1). \tag{6}$$

Thus, one can identify A and $p = p(N)$ by

$$\log A = \log H(\tau) + \log \epsilon$$

$$p(N) = \frac{1}{\log N}\{\log N - \log(\epsilon N\tau + 1)\}. \tag{7}$$

Table 1 shows values of $p(N)$ for a number of choices of ϵ and τ. Clearly, this model can give rise to values of p less than 1. Note from (7) that $p(N)$ can be written as

$$p(N) = 1 - \frac{\log(\epsilon N\tau + 1)}{\log N}$$

so that one clearly sees the importance of the product $\epsilon N\tau$ in determining the value of $p(N)$.

Table 1

Values of p(N) from (7), for the formula

$$E\{CPUE\} = AN^{p}$$

e	T	N	p(N)	e	T	N	p(N)
.01	1	49	.90	.001	1	499	.93
		149	.82			1499	.87
		249	.77			2499	.84
		349	.74			3499	.82
		449	.72			4499	.80
.01	4	12	.84	.001	5	99	.91
		42	.74			299	.84
		72	.68			499	.80
		87	.66			699	.77
		117	.64			899	.75
.005	5	19	.87				
		59	.78				
		99	.73				
		139	.70				
		179	.67				

Two key questions remain. The first is: what happens when stock depletion is taken into account. That is, can one still see a region in which CPUE = AN^p with $p < 1$? The second question is: How does one recognize the magnitude of $N\epsilon\tau$, when both N and ϵ are unknown?

The first question is one that mainly involves modeling. It is answered in the next section. There are three major components to this discussion. These are local catchability based on a search model, handling time, and the possibility of globally varying catchability. Two kinds of search models are used. These are the random search, with and without depletion (Koopman, 1980; Mangel, 1984; Mangel and Beder, 1985) and exhaustive search (Neyman, 1949; Mangel, 1985). The models cover the gamut of possibilities.

The second question is one of statistical estimation and is discussed in the third section. A method that can be used to identify the regime when one has search time data available is described and illustrated using data on Pacific ocean perch from Rennell Sound, British Columbia.

Models with Depletion Can Give $p < 1$.

The objective of this section is to show how to generate the relationship between CPUE and abundance when depletion of the stock is important. For completeness, and pedagogical ease, the first models discussed are ones without depletion.

1. Random Search Models: Fixed Catch

It is instructive to first provide a derivation of the search models, since the concepts involved appear in every sub-section. Imagine a large region of area A containing N "schools" (schools of fish, pods of whales, generic aggregations). Also imagine that in operating time t an area wt is searched. Assuming that the schools are randomly distributed, one has

$$\Pr\{k \text{ schools encountered}\} = \binom{N}{k}\left(\frac{\omega t}{A}\right)^k\left(1 - \frac{\omega t}{A}\right)^{N-k} \tag{8}$$

In the limit of large A, N with $\frac{\omega}{A}$ defined to be q, the binomial distribution (8) is approximated by the Poisson distribution

$$\Pr\{k \text{ schools encountered}\} = \frac{e^{-qNt}(qNt)^k}{k!} . \tag{9}$$

Equation (9) corresponds to random search (see, e.g. Koopman (1980), Mangel (1984)).

Now suppose that one specifies that the catch is C. The time T required to achieve this catch is a random variable with

$$T = T_s + Ch \tag{10}$$

where T_s is the search time and h is the handling time per school. Consider the CPUE, given by CPUE = C/T. It also is a random variable with expectation approximated by a Taylor's expansion around $T = E\{T\}$ as follows

$$\begin{aligned} E\{C/T\} = CE\{1/T\} = CE\{&1/\bar{T} - 1/\bar{T}^2(T-\bar{T}) \\ &+ 2/\bar{T}^3(T-\bar{T})^2 + O(1/\bar{T}^4)\}, \end{aligned} \tag{11}$$

where $O(x)$ means a term that behaves like a constant times x. Taking the expectation in (11) gives

$$E\{C/T\} = C\{1/\bar{T} + 2/\bar{T}^3 \operatorname{Var}\{T\} + O(1/\bar{T}^4)\}. \tag{12}$$

The mean and variance of $T = T_s + Ch$ are computed as follows. Since search corresponds to a Poisson process with parameter qN, the time for the first C encounters follows a gamma distribution with parameters C and qN. (Ross, 1980). Thus

$$E\{T\} = \bar{T} = C/qN + Ch = C\left(\frac{1+qhN}{qN}\right)$$
$$\mathrm{Var}\{T\} = C/(qN)^2 \qquad (13)$$

when (13) is substituted back into (12), the following equation is obtained

$$E\{C/T\} = \frac{qN}{1+qhN} + \frac{2qN}{C(1+qhN)^3} + O(1/\bar{T}^4) \qquad (14)$$

The first term in this expansion was derived by Paloheimo and Dickie (1964), Beddington (1979), Clark and Mangel (1979), and Cooke (1985a,b) in different ways, for differing assumptions. One could, without difficulty, derive more terms (e.g. explicitly compute the coefficient of the $O(1/\bar{T}^4)$ term).

Assume now that qhN is sufficiently large that all terms other than the first in (14) can be ignored. If one makes this assumption, then the expected value of CPUE is

$$E\{CPUE\} \approx \frac{qN}{1+qhN} \,. \qquad (15)$$

Cooke (1985a,b) argues that q in (14) or (15) should be constant only locally. That is, the catchability q may vary on a global scale due to environmental fluctuations, etc. Cooke suggests that q should have a skewed distribution and chooses the log-normal. A different choice of a skewed distribution is the gamma distribution with parameters ν and α, so that

$$\Pr\{\bar{q} \le q \le \bar{q} + d\bar{q}\} = \frac{\alpha^\nu}{\Gamma(\nu)} e^{-\alpha\bar{q}} \bar{q}^{-\nu-1}\, d\bar{q}. \qquad (16)$$

The mean of q is then $E\{q\} = \nu/\alpha$ and the coefficient of variation is $CV\{q\} = 1/\sqrt{\nu}$. The average, over q, of the $E\{CPUE\}$, denoted by $\langle E\{CPUE\}\rangle_q$, is then

$$\langle E\{CPUE\}\rangle_q \approx \int_0^\infty \frac{qN}{1+qhN} \cdot \frac{\alpha^\nu}{\Gamma(\nu)} e^{-\alpha q} q^{\nu-1}\, dq$$

$$= \frac{\alpha^\nu N}{\Gamma(\nu)} \int_0^\infty \frac{e^{-\alpha q} q^\nu}{1+qhN}\, dq$$

$$= \frac{\nu}{h}\left(\frac{\alpha}{hN}\right)^\nu \Gamma(-\nu, \alpha/hN) e^{\alpha/hN} \tag{17}$$

where $\Gamma(a,x)$ is the incomplete gamma function (Erdelyi, 1981) given by

$$\Gamma(a,x) = \int_x^\infty e^{-t} t^{a-1}\, dt. \tag{18}$$

It is worthwhile to study two limits of (17). These are N fixed, $h \to 0$, in which one expects from (15) that the average CPUE will be proportional to N, and the limit h fixed, $N \to \infty$ in which one expects that the average CPUE will be equal to $1/h$, since virtually all the time is spent fishing. The first limit corresponds to $\alpha/hN \to \infty$. Now for large x,

$$\Gamma(a,x) \sim x^{a-1} e^{-x} \quad \text{as } x \to \infty \tag{19}$$

so that (17) becomes

$$\langle E\{CPUE\}\rangle_q \sim \frac{N\nu}{\alpha} \quad \text{as } h \to 0,\ N \text{ fixed.} \tag{20}$$

Observe that since $E\{q\} = \nu/\alpha$, (20) is in accord with intuition.

For the other limit ($N \to \infty$, h fixed) reconsider the integral defining $\langle E\{CPUE\}\rangle_q$. It can be rewritten as

$$\langle E\{CPUE\}\rangle_q = \frac{1}{\Gamma(\nu)h}\int_0^\infty \frac{t^\nu e^{-t}}{t+\frac{\alpha}{hN}}\,dt \tag{21}$$

(to do this, simply set $\alpha q = t$ in the integral in (17) and then divide both numerator and denominator by hN). Letting $N \to \infty$ for h fixed in (19) gives

$$\langle E\{CPUE\}\rangle_q \sim \frac{1}{\Gamma(\nu)h}\int_0^\infty t^{\nu-1}e^{-t}\,dt = \frac{1}{h}\,. \tag{22}$$

Thus, the two limits are verified. What remains is to study the behavior of $\langle\{CPUE\}\rangle_q$ given by (17) for moderate values of the dimensionless variable

$$x = \alpha/hN. \tag{23}$$

To do this, rewrite (17) as

$$\frac{h}{\nu}\langle E\{CPUE\}\rangle_q = x^\nu\Gamma(-\nu,x)e^x \tag{24}$$

so that

$$\log(\frac{h}{\nu}) + \log(\langle E\{CPUE\}\rangle_q) = \nu\log x + x + \log(\Gamma(-\nu,x)). \tag{25}$$

observe that $\log x = \log\alpha - \log h - \log N$. Thus, a slope plot of $\log[\frac{h}{\nu}\langle E\{CPUE\}\rangle_q]$ against $-\log x$ gives the parameter p in the formula $CPUE = AN^p$. In order to construct such a plot, $\Gamma(-\nu,x)$ was integrated numerically, the plot generated and fit by a straight line. Figure 2 is an example of the results of such a procedure. The slope of the line in Figure 2 is about .5. The result derived here is similar to the results obtained by Cooke (1985a,b).

2. Random Search: Fixed Operating Time

An alternate random search model is based on a fixed operating time. It can be described as follows. Let $p(n,t)$ denote the probability that n schools are encountered in search time t. If the operating time is T, each encounter requires a handling time of h, and search or handling are the only two operations, the possible catches are $n = 0,1,2 \cdots \min(M,N)$ whe[re] $M = \mathrm{Int}[T/h]$ schools and $\mathrm{Int}(x)$ is the integer part of x. Strictly speaking, the catch of the last school may require time greater than T, but if $T \gg h$ the error from this approximation should be negligible. (This error is currently being investigated.) Consequently, the expected CPUE is

$$E\{CPUE\} = \frac{\sum_{n=0}^{\min(M,N)} \frac{n}{T}\, p(n,T-nh)}{\sum_{n=0}^{\min(M,N)} p(n,T-nh)} \,. \tag{26}$$

The upper limit for the sum in (26) is either the total number of schools (N) or the maximum possible number of schools that can be caught in $[0,t]$ (M), whichever is smaller. The denominator in (26) is required for purposes of normalization. Once a model for $p(n,t)$ is given, the expected CPUE can be easily calculated. A number of models will be introduced here. These are:

Globally Random Search. For this model, assume that

$$p(n,t) = \frac{e^{-qNt}(qNt)^n}{n!} \,, \tag{27}$$

i.e. a pure Poisson process with parameter $\lambda = qN$.

<u>Local Random Search, Globally Varying Catchability</u>. For this model, assume that q in (27) has a distribution. Based on the results of the last section, assume that the distribution of q is a gamma with parameters ν and α. Then

$$p(n,t) = \int_0^\infty \frac{e^{-qNt}(qNt)^n}{n!} \frac{e^{-\alpha q}}{\Gamma(\nu)} q^{\nu-1}\alpha^\nu \, dq$$

$$= \frac{\Gamma(\nu+n)}{\Gamma(\nu)n!} \left(\frac{\alpha}{\alpha+Nt}\right)^\nu \left(\frac{Nt}{\alpha+Nt}\right)^n. \tag{28}$$

The distribution in (28) is a negative binomial distribution (see Feller (1968) for a general discussion or Mangel (1985) for a discussion relevant to fisheries).

These two models (local random search) do not have depletion in them. Thus, the upper limit in (26) should be replaced by M and one should envision that each time a catch occurs, that school is replaced. The inability to include depletion is an inherent fault of models based on the Poisson assumption. The next two models do not suffer from this deficiency.

<u>Global Random Search With Depletion</u>. For this model, assume that catchability q is constant but that stock depletion is important. It can then be shown that (Mangel and Beder, 1985) the appropriate model is

$$p(n,t) = \binom{N}{n}(1 - e^{-qt})^n(e^{-qt})^{N-n}, \tag{29}$$

which is a binomial distribution. Observe that for large N and small qt, this distribution is well approximated by the Poisson with parameter $N(1-e^{-qt}) \approx Nqt$. Thus, the global random search model can be thought of as the "short operating time" limit of the model global random search with depletion.

<u>Local Random Search With Depletion, Globally Varying Catchability.</u> In this model, one wants to assume that q in (29) has a distribution as well. Once again choosing the gamma distribution with parameters ν and α leads to the following result.

$$p(n,t) = \binom{N}{n} \int_0^\infty (1-e^{-qt})^n (e^{-qt})^{N-n} \frac{e^{-\alpha q} q^{\nu-1} \alpha^\nu}{\Gamma(\nu)}\, dq$$

$$= \binom{N}{n} \int_0^\infty \sum_{j=0}^{n} \binom{n}{j} (-1)^j (e^{-qt})^{j+N-n} \frac{e^{-\alpha q} q^{\nu-1} \alpha^\nu}{\Gamma(\nu)}\, dq$$

$$= \binom{N}{n} \sum_{j=0}^{n} \binom{n}{j} (-1)^j \left[\frac{\alpha}{\alpha+t(j+N-n)}\right]^\nu . \tag{30}$$

Although not a standard distribution, (30) is easily computed for a given set of parameter values.

It now remains to compute the expected CPUE given by (26) for each of these models. Each of the models involves a number of parameters. By appropriate scaling, the number of parameters that one has to deal with can be reduced. It is instructive to work through an example, so consider the model of local random search, globally varying catchability. Using (28) in (26) gives

$$E\{CPUE\} = \frac{\displaystyle\sum_{n=0}^{\min(M,N)} \frac{n}{T} \binom{n+\nu-1}{n} \left[\frac{\alpha}{\alpha+N(T-nh)}\right]^\nu \left[\frac{N(T-nh)}{\alpha+N(T-nh)}\right]^n}{\displaystyle\sum_{n=0}^{M} \binom{n+\nu-1}{n} \left[\frac{\alpha}{\alpha+N(T-nh)}\right]^\nu \left[\frac{N(T-nh)}{\alpha+N(T-nh)}\right]^n} . \tag{31}$$

For simplicity assume that $T = Mh$ exactly and introduce the following scaled variables

$$\left.\begin{aligned} M &= T/h \\ \beta &= \alpha/T \\ \lambda &= N/M \end{aligned}\right\} \tag{32}$$

Thus, M is a measure of the maximum number of schools that could be caught in the operating time, β^{-1} is a nondimensional measure of the operating time and λ is a measure of abundance in terms of M. Finally, set $M^* = \min(M,N)$. Using these scaled variables in (31) gives

$$E\{CPUE\} = \frac{\sum_{n=0}^{M^*} \frac{n}{T} \binom{n+\nu-1}{n} \left[\frac{\beta}{\beta+\lambda(M-n)}\right]^{\nu} \left[\frac{\lambda(M-n)}{\beta+\lambda(M-n)}\right]^{n}}{\sum_{n=0}^{M^*} \binom{n+\nu-1}{n} \left[\frac{\beta}{\beta+\lambda(M-n)}\right]^{\nu} \left[\frac{\lambda(M-n)}{\beta+\lambda(M-n)}\right]^{n}} \tag{33}$$

Finally, defining $\hat{\lambda} = \lambda/\beta$ leads to one more simplification, which gives

$$T \cdot E\{CPUE\} = \frac{\sum_{n=0}^{M^*} n \binom{n+\nu-1}{n} \left[\frac{1}{1+\hat{\lambda}(M-n)}\right]^{\nu} \left[\frac{\hat{\lambda}(M-n)}{1+\hat{\lambda}(M-n)}\right]^{n}}{\sum_{n=0}^{M^*} \binom{n+\nu-1}{n} \left[\frac{1}{1+\hat{\lambda}(M-n)}\right]^{\nu} \left[\frac{\hat{\lambda}(M-n)}{1+\hat{\lambda}(M-n)}\right]^{n}} \tag{34}$$

The formulation (31) has as parameters: M, T, ν, α, N, h, but (33) has only three parameters: M, ν, $\hat{\lambda}$. A further simplification occurs if one is willing to considerable uncertainty in the system, say a coefficient of variation of the order of 100% so that $\nu = 1$. Once again, there are two limits that can be easily studied in (34). These are $\lambda \to \infty$ ($N \to \infty$) and $\lambda \to 0$ with M fixed ($N \to 0$). The following behavior is easily verified.

$$T \cdot E\{CPUE\} \sim M \text{ as } \lambda \to \infty. \tag{35}$$

The interpretation of (35) is that for very large abundance all the operating time is spent fishing ((35) is equivalent to $E\{CPUE\} \sim 1/h$).

For $\lambda \to 0$, it is easily shown from (33) that

$$E\{CPUE\} \sim \frac{\nu}{\beta T} (M-1)\lambda \quad \text{as } \lambda \to 0, \tag{36}$$

i.e. that expected CPUE is proportional to N.

For the intermediate range of λ values, numerical computation of (34) is easily done. Figure 3 shows two plots of $\log\{T \cdot E\{CPUE\}\}$ against $\log \hat{\lambda} = \log N - \log M - \log \alpha + \log T$ for two values of M. The slopes of the lines in Figure 3 are about $p = .5$, giving $E\{CPUE\} \propto N^{.5}$ (assuming that all other parameters are fixed).

Similar calculations were performed using the four different models (27) - (30) in (26). The results of these specific calculations for specific parameter values are summarized in Table 2. The results presented in this table show that all of the four models can give values of p less than 1.

Table 2

Results for Random Search Models with Fixed Operating Time

Model	Depletion	Parameter Values	p
Global Random Search	No	$h = .25 \quad T = 20 \quad q = 1$	.5
Local Random Search Globally Varying Catchability	No	$\nu = \alpha = 1 \quad h = .2$ $T = 10$	.6
Global Random Search with Depletion	Yes	$\nu = \alpha = 1 \quad h = .2$ $T = 3$	.6
Local Random Search with Depletion, Globally Varying Catchability	Yes	$\nu = \alpha = 1 \quad h = .2$ $T = 3$	.6

3. Exhaustive Search: Fixed Operating Time

The alternative to random search is exhaustive search, in which vessels follow straight line tracks and detect with probability 1 everything within a fixed sighting distance of the vessel. This case was studied by Neyman (1949) and again by Mangel (1985). It is once again assumed that the operating time T is fixed and that each discovery of a school leads to a handling time of h hours. In this theory, there are two probabilities of interest:

$$P_f(k,T) = \Pr\{\text{catch is } k \text{ schools and the vessel is fishing at } T\}$$

$$P_s(k,T) = \Pr\{\text{catch is } k \text{ schools and the vessel is searching at } T\} \tag{37}$$

If $Z(t)$ is the number of schools completely or partially fished by time t, a natural choice for the definition of expected CPUE is

$$E\{CPUE\} = \sum_{k=0}^{\min(M,N)} \frac{k}{T} \Pr\{Z(T) = k\} \tag{38}$$

where, as before, $M = \text{Int}(T/h)$. Note that

$$\Pr\{Z(T) = k\} = P_f(k-1,T) + P_s(k,T). \tag{39}$$

Consider a region of area A that contains N schools of fish. Assuming that the area swept per unit time is $2W$, and that all schools within the swept area are discovered, the following results can be demonstrated (Neyman (1949), Mangel (1985)).

If the N schools are randomly distributed in A, so that the chance that an area a has k schools is binomial with parameters N and $p = a/A$, then

$$\left.\begin{aligned}
P_f(M,T) &= 1 - \sum_{m=0}^{M} \binom{N}{m}\left(\frac{2W(T-Mh)}{A}\right)^m\left(1 - \frac{2W(T-Mh)}{A}\right)^{N-m} \\
P_f(k,T) &= \sum_{m=0}^{k} \binom{N}{m}\left(\frac{2W(T-(k+1)h)}{A}\right)^m\left(1 - \frac{2W(T-(k+1)h)}{A}\right)^{N-m} \\
&\quad - \sum_{m=0}^{k} \binom{N}{m}\left(\frac{2W(T-kh)}{A}\right)^m\left(1 - \frac{2W(T-kh)}{A}\right)^{N-m} \\
&\qquad k = 0,1,2,\ldots,M-1 \\
P_s(k,T) &= \binom{N}{k}\left(\frac{2W(T-kh)}{A}\right)^k\left(1 - \frac{2W(T-kh)}{A}\right)^{N-k} \\
&\qquad k = 0,1,2,\cdots
\end{aligned}\right\} \quad (40)$$

If one uses the Poisson limit of the binomial, with $\lambda = N/A$ being the density of schools, then in (40) terms of the form

$$\binom{N}{m}\left(\frac{2W(T-nh)}{A}\right)^m\left(1 - \frac{2W(T-nh)}{A}\right)^{N-m}$$

are replaced by

$$\frac{e^{-\lambda(2W(T-nh))}(2W\lambda(T-nh))^m}{m!}\,.$$

One could imagine that the N schools are not randomly distributed in the region, but have some "clumped" or "contagious" distribution. In such a case, the negative binomial distribution can be used as a model (see e.g. Pielou (1977)). If this model is adopted, terms of the form

$$\binom{N}{m}\left(\frac{2W(T-mh)}{A}\right)^{m}\left(1-\frac{2W(T-mh)}{A}\right)^{N-m}$$

are replaced by

$$\binom{m+\nu-1}{m}\left(\frac{\alpha}{\alpha+2W(T-mh)}\right)^{\nu}\left(\frac{2W(T-mh)}{\alpha+2W(T-mh)}\right)^{m}$$

where ν and α are parameters in the negative binomial distribution. In particular, ν is a measure of the level of aggregation (larger ν implying less aggregation) and $\alpha = \nu A/N$.

It turns out, in fact, that for the parameter values used in the computations reported below all three models gave virtually the same results. For these computations, the values $T = 1$, $h = .1$ and $\nu = 1$ were chosen. The values of p in the formula $CPUE = AN^p$ for three different values of WT/A are shown below:

WT/A	p
.01	~ 1
.1	.8
.3	.6

The decrease in the value of p with increasing values of W/A can be partially understood by a consideration of (40). That is, for extremely small values of WT/A, the chance of finding more than one school is so slight that CPUE roughly grows linearly with N. For larger values of W/A, this is not the case and the effects of handling, saturation, and depletion on CPUE become important.

Identifying the Regime

The results in the previous section show that one can generate formulas of the form CPUE = AN^p with $p < 1$ for virtually any reasonable model. It is now worthwhile to reconsider equation (5), rewritten below

$$E\{CPUE\} \approx \frac{H(\tau)\varepsilon N}{\varepsilon N\tau + 1} . \qquad (41)$$

Recall that the major question associated with this formula is how one estimates N and ε simultaneously. One way to do this involves an extension of the methodology of Mangel and Beder (1985). This extension proceeds as follows.

The underlying stochastic model is the following one. Assume that N schools are initially present and that, given n schools were discovered and fished already,

$$\begin{aligned} &\text{Prob}\{\text{another detection of a school} \\ &\qquad \text{in the next } \Delta t\} \\ &= \varepsilon(N-n)\Delta t + o(\Delta t) \end{aligned} \qquad (42)$$

This assumption leads to the binomial distribution (29), with $q = \varepsilon$. This assumption also means that the time to detect the i^{th} school is an exponential random variable with parameter $\varepsilon(N-(i-1))$.

Imagine now a data set consisting of the times $T_1, \ldots, T_k$ needed to detect the first k schools and the search time S after the detection of the k^{th} school but before the detection of the $(k+1)^{st}$ school. The likelihood of this data set is

$$\mathcal{L} = \left[\prod_{i=0}^{k-1} (N-i)\varepsilon\, e^{-(N-i)\varepsilon T_i}\right] \exp\{-(N-k)\varepsilon S\}. \qquad (43)$$

The maximum likelihood estimates $\hat{N}$ and $\hat{\varepsilon}$ for N and ε satisfy the equations

$$\frac{k}{\epsilon} = \sum_{i=0}^{k-1} (N-i)T_i + (N-k)S$$

$$\epsilon = \frac{k}{(N-k)S + \sum_{i=0}^{k-1} (N-i)T_i} \tag{44}$$

These are easily solved on a desk top microcomputer. One is interested in the product $\hat{N}\hat{\epsilon}$, since the regime will be determined by the product $\hat{N}\hat{\epsilon}\tau$.

As an example, consider the following data on Pacific Ocean perch in Rennell Sound, British Columbia (see Mangel and Beder (1985) for more details):

T_1 = 13.9 hrs	T_7 = 31.5 hrs
T_2 = 4 hrs	T_8 = 22.6 hrs
T_3 = 4.5 hrs	T_9 = 11.1 hrs
T_4 = 5.6 hrs	T_{10} = 16.5 hrs
T_5 = 1.3 hrs	T_{11} = 5 hrs
T_6 = 11.7 hrs	T_{12} = 30.3 hrs
	T_{13} = 23.1 hrs

The value of S was unknown, so it was treated as a parameter in the estimation. Table 3 shows the results of solving (44).

These results show that as the search time without a detection increases, the estimate for N decreases, in accord with intuition.

Table 3

Estimation of $\hat{N}e$

S (hrs)	$\hat{N}$	$\hat{\varepsilon}$	$\hat{\hat{N}}e$
5	386	2.11×10^{-4}	.081
10	199	4.05×10^{-4}	.081
15	137	5.84×10^{-4}	.080
20	106	7.49×10^{-4}	.079
25	87	9.00×10^{-4}	.079
30	75	1.04×10^{-3}	.078
40	60	1.28×10^{-3}	.077
50	51	1.49×10^{-3}	.076
60	45	1.66×10^{-3}	.075
70	41	1.80×10^{-3}	.074

The remarkable aspect, however, is that the product $\hat{N}\hat{\epsilon}$ is very stable (as $\hat{N}$ decreases by about 90%, $\hat{N}\hat{\epsilon}$ decreases by about 9%). This suggests that one may be able to estimate $\hat{N}\hat{\epsilon}$ without knowing the last search time S.

For the data presented here $\tau \approx 1$ hour, so that the results indicate that $\hat{N}\hat{\epsilon}\tau \ll 1$, and CPUE should be proportional to abundance. (There are, however, some other problems with using CPUE to measure abundance. See Mangel and Beder (1985) for details, where abundance estimation based on encounter rates is also discussed.)

Summary and Conclusion

There are three themes to this paper. The first is that, depending on operational parameters when depletion is ignored one can expect CPUE to be proportional to abundance, independent of abundance or of the form AN^p with $p = p(N)$ less than 1. The second theme is that virtually all reasonable models that include depletion also lead to the three regimes and, in particular, to a regime with $p < 1$. The third theme, perhaps the most important one from a management viewpoint, is that it is possible to use encounter rate data to estimate the regime (CPUE proportional to abundance, independent of abundance or CPUE = AN^p). Thus, one is capable of determining the regime, at least at some approximate level. This provides another way of interpreting catch-effort data.

Two aspects of the problem not discussed here are:

1) the behavior of catch per effort searching and 2) the role of school structure in the process of search, handling and harvest.

A number of authors (e.g. Cooke (1985a,b), Zahl (1982,83)) have suggested that CPUE be defined in terms of catch per unit effort of searching (CPUEs).

For the fixed catch model one has (see equations 11 - 13)

$$E\{C/T_s\} \approx C\{1/\bar{T}_s + 2/\bar{T}_s^3 \, Var\{T\}\}$$

$$= qN + \frac{2qN}{C} . \qquad (43)$$

Thus, the simple use of $C/E\{T_s\}$ underestimates the true CPUEs (also noted by Zahl (1982)). More importantly, there is no guarantee that the higher terms in (43) are small -- in fact they may be of the same order or larger as (43) demonstrates. Thus, the validity of an expansion similar to (12) comes into question. Cooke (1985b) has found that for a log-normal distribution on catchability, CPUEs is proportional to N^p with $p < 1$.

The work presented here ignored the effects of school size and structure on CPUE. These effects may occur in many ways. First, the probability of detection in the search process may depend upon school size (see, e.g. Quinn (1979) for a discussion of the effects of school structure on abundance estimates in transect theory). In addition, school size and structure will affect the number of schools and density of stock within schools. Some behavioral rules for schools are:

i) constant density of fish within a school

ii) constant school radius

iii) constant number of fish within a school

Since the search and detection process is one in which schools are detected, the ultimate relationship between CPUE and abundance will depend upon the mechanism of school formation. This problem awaits further investigation.

In the end though, perhaps the most important question is the inferential one: how does one estimate the value of p, at least to be able to say $p \approx 1$, $p \approx 0$ or $p \approx .5$? If search times are known, then the method introduced here works well. If the data just consist of effort and catch, the problem is harder. The kinds of models discussed in this paper may provide guidance in the analysis of such noisy catch-effort data.

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Figure Captions

Figure 1. a) The CPUE curve given by equation (5).

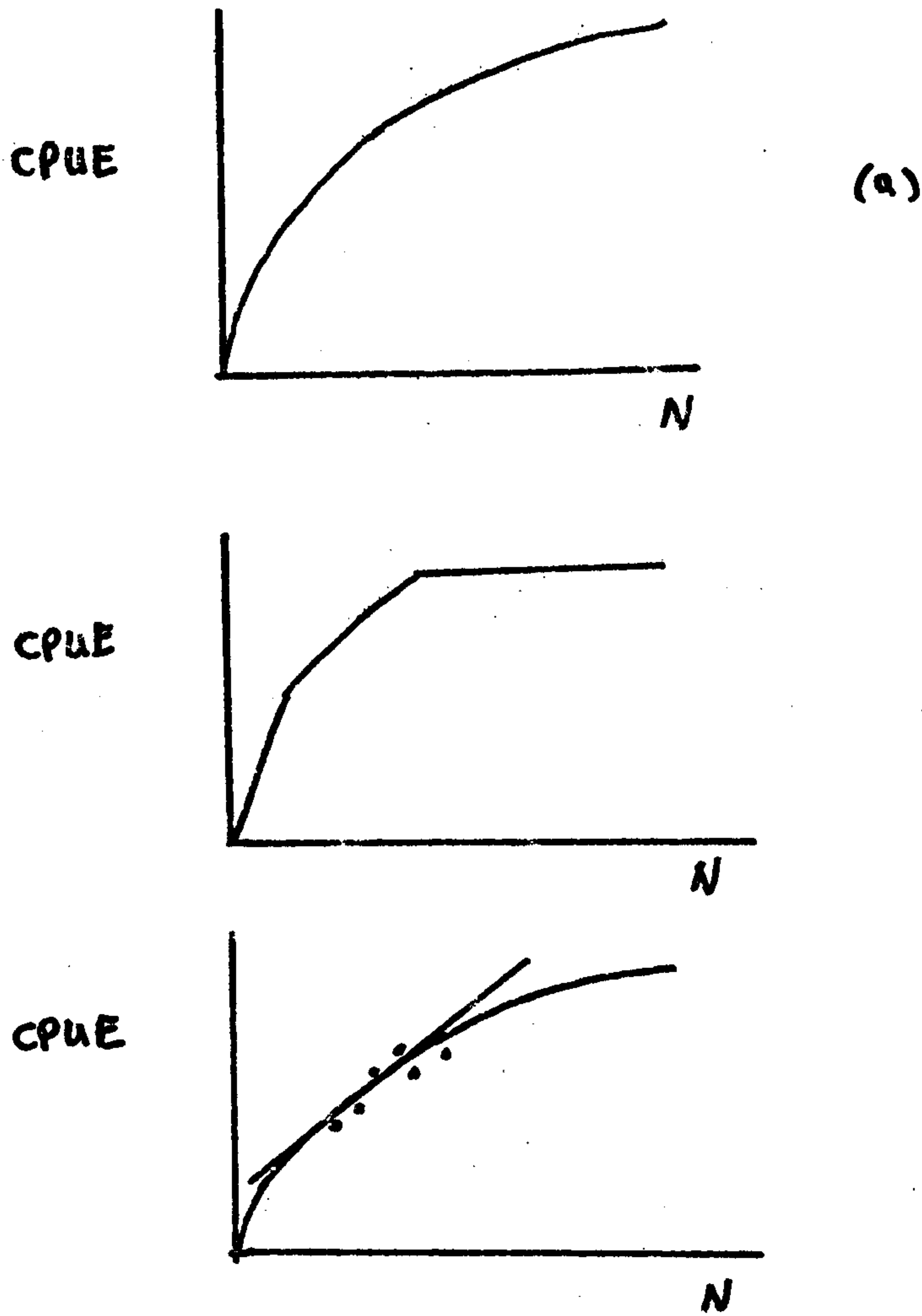
b) A linear approximation to it.

c) When data fall in the middle region, a linear fit gives $CPUE \approx AN^p$ with $p < 1$.

Figure 2. A plot of $\log[h/\nu \langle CPUE \rangle_q]$ given by (22) against $-\log x$, where $x = \alpha/hN$ for the fixed catch model. The straight line has a slope about 0.5.

Figure 3. A plot of $\log[T \cdot E\{CPUE\}]$ given by (32) against $\log \hat{\lambda}$ where $\hat{\lambda} = NT/\alpha M$ for two values of M, $\beta = \nu = 1$. The straight lines have slope about 0.5.

figure 1



Figw

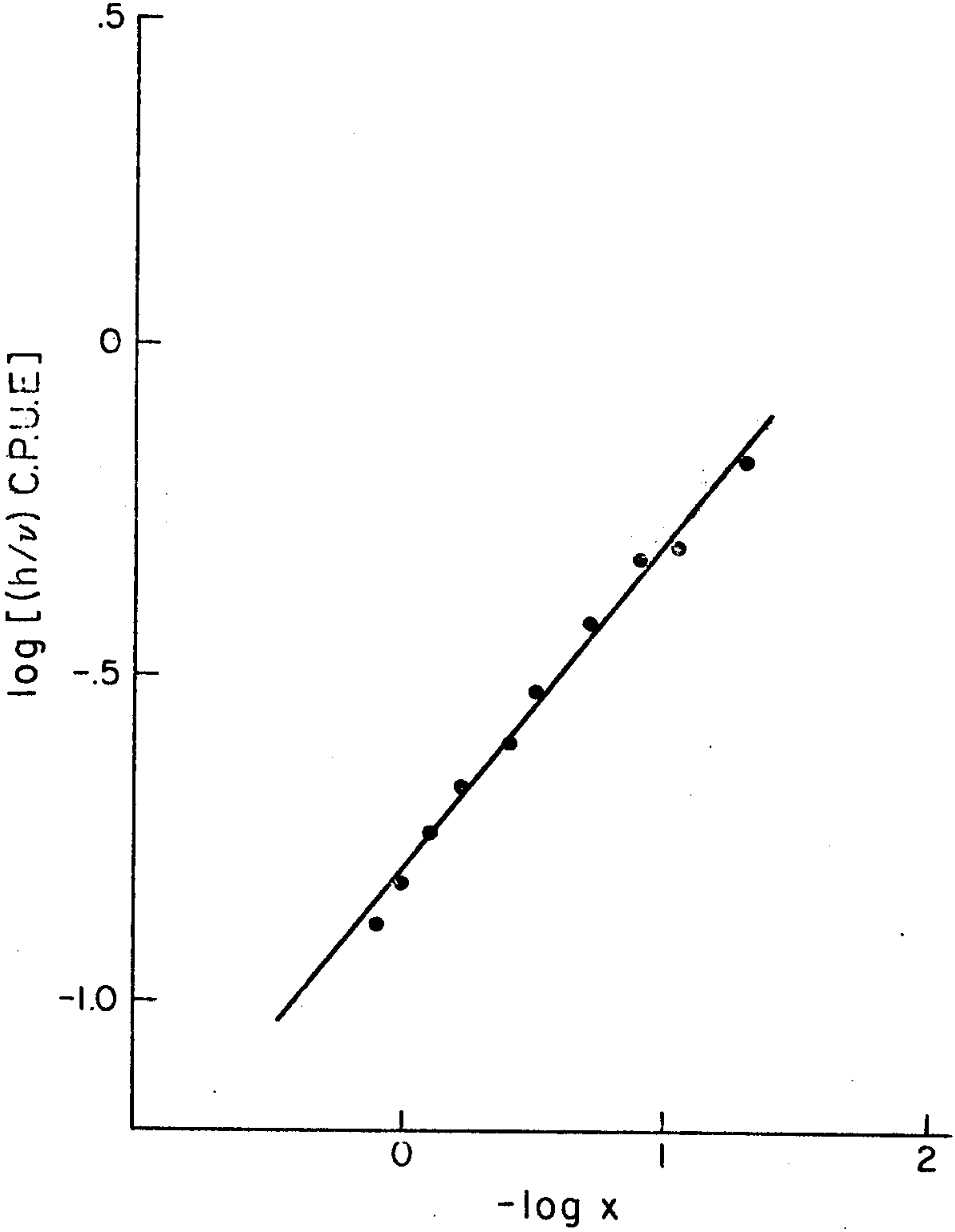


Figure 1