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Approaches to a Simplified Yield-per-Recruit Model for Crustacea, With Particular Reference to the American Lobster, *Homarus americanus*

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APPROACHES TO A SIMPLIFIED YIELD-PER-RECRUIT MODEL FOR CRUSTACEA, WITH PARTICULAR REFERENCE TO THE AMERICAN LOBSTER, *HOMARUS AMERICANUS*

by

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ABSTRACT

Caddy, J. F. 1977. Approaches to a simplified yield-per-recruit model for Crustacea, with particular reference to the American lobster, *Homarus americanus*. Fish. Mar. Serv. MS Rep. 1445, 14 p.

        A simplified approach to yield/recruit analysis in crustacean populations is presented based on those information inputs normally collected from crustacean fisheries, namely, moult frequency and increment as functions of size, length-weight relationships, and gear-selection ogives. For long-lived species, size-frequency modes are unlikely to reflect age or even moult groups in the strict sense. However, a mechanism is postulated for generation of size-frequency modes (containing individuals of a mixture of age and moult numbers) in the course of an intensively prosecuted fishery with rigorously enforced size limits. The decline in log numbers per arbitrary moult interval following entry to the legal size range is suggested as an index of overall mortality.

Key words: Yield/recruit analysis, Crustacea, modelling, lobster

RÉSUMÉ

Caddy, J. F. 1977. Approaches to a simplified yield-per recruit model for Crustacea, with particular reference to the American lobster, *Homarus americanus*. Fish. Mar. Serv. MS Rep. 1445, 14 p.

        On présente une approche simplifiée à l'analyse de rendement par recrue pour les populations de crustacés, utilisant les informations suivantes (normalement recueillies sur les pêcheries de crustacés): la fréquence de mue et l'accroissement de taille à la mue en fonction de la taille, la relation taille-poids, et l'ogive de selectivité de l'engin de pêche. Il est douteux que des modes dans les fréquences de taille d'espèces à croissance longue représentent d'authentiques groupes d'age ou même de mue. Par contre, on décrit un méchanisme susceptible de générer des modes (formés d'individus de divers groupes d'age et de mue) dans les fréquences de taille pour les cas de pêche intensive où une limite de taille est strictement respectée. Considérée pour les tailles au-delà d'une limite légale, la diminution des logarithmes de nombre d'individus selon des intervalles de mue arbitrairement choisis pourrait fournir un indice de mortalité totale.

INTRODUCTION

The conventional approach to yield-per-recruit analysis, pioneered by Beverton and Holt (1957) principally for finfish species, assumes that the mean size attained by a cohort is a continuous function of time, most conveniently expressed for many species by the von Bertalanffy growth equation. Yield-per-recruit analyses have proven utility for obtaining a first approximation of the effect of fishing, but are less reliable at higher fishing intensities for two main reasons:

(a) The effects of overfishing on recruitment are not considered.

(b) Even for many fish species, growth is seasonal and, at high fishing intensities, errors can arise if the time of application of fishing effort is not considered in relation to the annual growth period.

Errors of both the above kinds apply to crustacea. Those of type (a) are beyond the scope of this study, and reflect properly on the utility of yield-per-recruit analyses when used out of their proper biological context. Type (b) errors are aggravated for crustacea by:

1) the high exploitation rates and short fishing seasons typical of many high value crustacean stocks;

2) the discontinuous growth form resulting from periodic exuviation or ecdysis, which may be exaggerated if moulting is seasonal as for most homarid stocks described;

3) the difficulty of obtaining an average growth function for many crustacea;

4) the fact that a discrete type of growth coupled with a limited growing season may result in marked departures from the assumption of normality of size distribution at age usually adopted for species showing continuous growth.

The problem may be formulated more precisely as one of reconciling an annual time frame with a physiological time frame, often expressed in terms of the number of moults since hatching; or more conveniently, in this author's opinion, in terms of the arbitrary number of moults completed between recruitment and capture.

GROWTH MODELS AND METHODS OF GROWTH ESTIMATION IN *HOMARUS*

As noted by several authors (e.g. Kurata 1962, Mauchline 1977), crustacean growth can be expressed most realistically in terms of two components: moult increment and moult frequency. These two factors may be influenced differentially by environmental variables and are most easily estimated separately. Moult increment has been measured either from tag and recapture (Ennis 1972), or from tank experiments (Hughes and Mathiessen 1962). Moult frequency has been variously estimated from tag returns either by the anniversary method of Hancock and Edwards (1967) which determines mean annual growth at a particular pre-ecdysal length as a product of the proportion of moulters in the tag returns, and their mean increment in size 1 yr later. Conan and Gundersen (1976) extended this approach to consider tag returns over short intervals of time in order to identify multiple moults among the tag returns, increment in size and moult frequency being then synthesized in attempting to fit a von Bertalanffy growth curve to the data. A similar approach has been adopted in Morrissey (1976) which employs modes in the size frequency, and an assumption of once-annual moulting to fit parameters of the von Bertalanffy equation to various New England lobster stocks. However, the above authors stress some of the limitations of such a von Bertalanffy fitting procedure for a species showing discrete growth. These limitations may be described briefly as follows:

1) It is assumed that, given K and L_∞, the future of an individual can be predicted from its present size, without any knowledge of its age.

2) Size increment per unit time, ΔT, is homogenous over time. This is evidently not the case since growth is seasonal. This makes consideration of growth increments obtained over other than annual periods very subject to bias.

3) Because in highly exploited fisheries (such as most lobster stocks) data on the larger size groups are hard to obtain from the fishery (and even for those relatively few larger lobsters tagged, moult frequency is too low to provide reliable estimates in most cases). As a result, the extrapolated growth rates tend to be too high, and L_∞ is poorly estimated.

4) The last, and perhaps the most serious objection to the von Bertalanffy model in crustaceans, is that it does not allow extension of the model into real time, to take into account differential environmental and physiological conditions on the two-component growth processes described earlier, and on the interaction between growth and reproduction (Aiken and Waddy 1976).

ENVIRONMENTAL EFFECTS ON GROWTH

There is a considerable body of literature demonstrating the important effects of temperature on growth in lobsters (e.g. McLeese and Wilder 1958, Dow 1969, Flowers and Saila 1972); and a reasonable working hypothesis to explain latitudinal variation in growth for different stocks is that a certain number of degree-days is required to complete the moult cycle. This number of degree-days may be modulated by size or sexual maturity, but must be taken into

account in comparing, for example, lobster growth in Rhode Island (Hughes and Mathiessen 1962), and in Newfoundland (Templeman 1936, 1948). Variations in growth from year to year may also occur due to climatic fluctuations; particularly for the females also, ovarian and somatic cycles may come into conflict under temperature-limited conditions.

APPROACHES TO MEASUREMENT OF LOBSTER GROWTH

Moult increment is undoubtedly the most difficult growth parameter to estimate, particularly for larger lobsters. For reasons of cost and effort, tagging does not seem the most promising approach to estimating growth in this case. Stages in the moult cycle may be recognized from integumental samples (Aiken 1973) and provide an indirect method of measuring moult frequency, in that the frequency of occurrence of post-ecdysal lobsters may be estimated as a function of size in a catch sample. The decline in population of immediately post-ecdysal (soft or buckle-shell) lobsters with size appears to offer an indirect approach to estimating the decline in moulting frequency with size. For females (assuming that mating occurs after each moult for large individuals, and that sperm storage between successive moults does not occur), the percentage of berried females as a function of size may also provide an indirect index of moult frequency. Both of these methods remain to be fully tested but appear to offer some promise. Another approach to moult frequency estimation is shown in the Appendix.

SIZE-FREQUENCY ANALYSIS

Modal analysis of size frequencies is a technique that has been used with success for many small, rapidly growing species, and a variety of techniques (e.g. Cassie 1954; Bhattacharya 1967) have been developed. One may note from *a priori* considerations that, for a species existing in a markedly seasonal temperature regime, any variance in the number of moults per season will be quantal. Consequently, it seems unlikely that after several years have elapsed, individual age (or even moult) groups will follow a normal distribution, even without individual variation in increment per moult. It has generally been postulated (Herrick 1896, 1909; Templeman 1940; Hughes and Mathiessen 1962) that 4 to 7 yr and up to 20 moult stages may occur before the American lobster enters the fishable population. Postulating either a differential physiological response between members of the same cohort to temperature, or individual temperature regimes within a population, it is easy to see with discontinuous growth how members of the same cohort over 4 to 7 yr may readily come to demonstrate discontinuous size distributions, which would give spurious size frequency modes (if at all) by the time that size at recruitment had been reached.

A SIMPLE ILLUSTRATION OF THE EFFECTS OF A FIXED TEMPERATURE SUM BETWEEN SUCCESSIVE MOULTS ON SIZE FREQUENCY IN A SEASONALLY FLUCTUATING TEMPERATURE REGIME

A demonstration of the above contention is provided by a simple simulation for a group of individuals with initially a normal size distribution (μ, σ^2), each individual being assigned a random starting point (t) in the year between early May and the end of August (120-240 days after Jan. 1):

$$t = 120 + 120 \times (u.r.n)$$

where u.r.n. is a uniform random number between 0 and 1. Each individual is subject to a seasonal temperature cycle described by

$$T_t^\circ = a + b \sin \frac{2\pi(56t-c)}{365}$$

(this provides a good approximation to the seasonal temperature cycle at St. Andrews, if a = 6.7, b = 5.9, and c = 1645.0). The individual temperature sum ($Tcum_t$) is accumulated daily from date of last moult by $Tcum_t = Tcum_{t-1} + T_t^\circ$ until a specified temperature sum (Tsum) for moulting is attained, at which time moult increment occurs according to the protocol in Table 1, and $Tcum_t$ is reset at zero (Fig. 1) (i.e. if $Tcum_t > Tsum$, $(CL)_{m+1} = a^1 + b^1 (CL)_m$). At the end of the year, the size frequency is totalled for 500 individuals. Fig. 1 and 2 illustrate that, although size frequency is normal initially, it soon begins to show signs of polymodality (even without variance in individual moult frequency, temperature sum, and season-to-season variation in temperature). The seasonality of moulting acts to differentiate an initially unimodal size group into a polymodal, or at least, widely diffused size group, even after only 4 yr have elapsed (and on average, only two moults per year completed). Since, of course, there are roughly 20 moults in the period between settlement and recruitment, attenuation of any initial modal group, and overlapping with preceding and succeeding cohorts, will be further accentuated.

This suggests that if normal components can be picked out of a crustacean size composition, they are only likely to correspond to age groups for very short-lived, fast-growing species, and may even then be more likely to represent moult classes than age classes in the strict sense of the word.

This contention does not of course mean that there may not be other possible explanations for the appearance of modal groups in crustacean size frequencies. One mechanism for this type of phenomenon has been invoked in the case of an extremely heavily exploited lobster population (Robinson, personal communication) in the
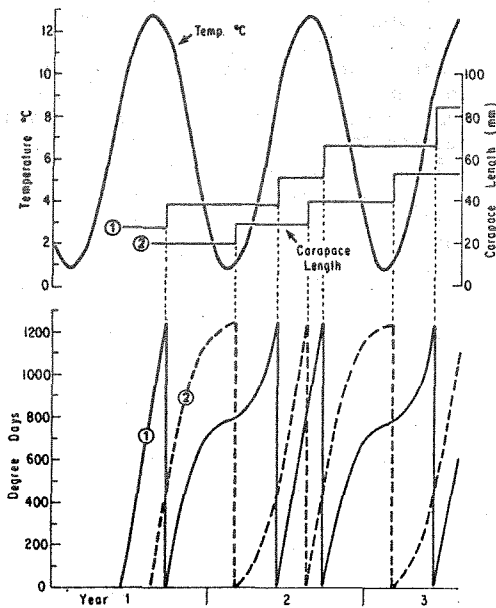
Fig. 1. Diagrammatic representation of seasonal
modulation of growth by means of the
number of degree-days accumulated per
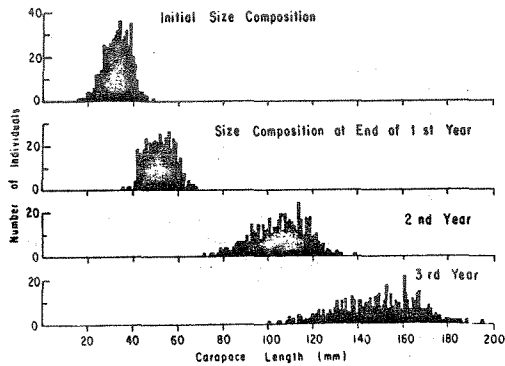individual crustacean between adjacent
moults.

Fig. 2. Initially normal size frequency simu-
lated for 500 individuals under the
seasonal temperature regime shown in
Fig. 1, assuming roughly two moults per
year, and showing size frequencies pre-
dicted at yearly intervals for the next
3 yr.

southern Gulf of St. Lawrence. This hypothesis
assumes that the size distribution in the sub-
legal (and at present, unsamplable prerecruit
population) is continuous without perceptible
normal components. Even in the limiting case
where no obvious size modes existed before entry
to the fishery, it is possible to demonstrate,
assuming roughly synchronous moulting of pre-
recruits, combined with a knife-edge selection
at legal size, that modal size groups can be
generated in the catch size frequency which
represents moult groups of unknown (and probably
mixed) year-classes.

A POSTULATED MECHANISM FOR GENERATION OF SIZE
FREQUENCY MODES FROM A CONTINUOUS SIZE
DISTRIBUTION

If we assume that the legal size limit in
effect for many lobster populations is rigorously
enforced (i.e. knife-edged), an alternative
hypothesis for the appearance of modes in the
catch size frequencies may be illustrated in
Fig. 3 if exploitation rate is fairly high, which
does not require that moult or age groups dis-
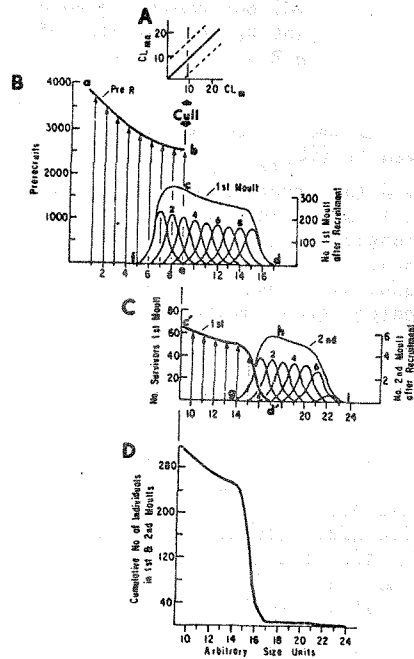tinctly different in size existed before entering
the fishery.

Fig. 3(a-d). Hypothesized mechanism to explain
appearance of size-frequency modes in
commercial catch of lobsters from some
heavily exploited stocks in Canadian
waters. (Note scales are different for
two moult components in B+C, but common
to both for combined plot D, and log
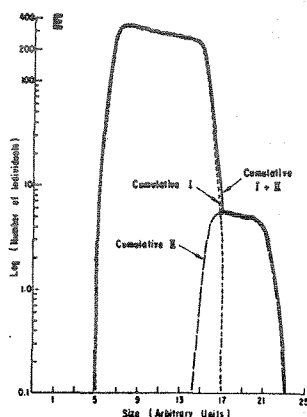plot of combined data in E.)

Fig. 3e. Hypothesized mechanism to explain appearance of size-frequency modes in the commercial catch of lobsters from some heavily exploited stocks in Canadian waters. (Note scales are different for two moult components in B+C, but common to both for combined plot D, and log plot of combined data in E.)

Assume 1) an increment in size at moult given by $(CL)_{m+1} = a + b(CL)_m \pm \epsilon$ (Fig. 3a), where the error term is normally distributed, and 2) a continuous size frequency of prerecruits composed of initial size groups 1-9 given by a-b-e. On moulting, each of these limited size groups will result in one of a series of overlapping normal distributions, whose variance is a function of ϵ. These normal components, on accumulation, will result in a continuous postmoult size frequency f-c-d, of which c-d will be of legal size. Even if a-b and c-d in the illustration might be expected to be continuous if the arbitrary variance around the regression line in Fig. 3a were smaller than chosen, this would not be the case after exploitation with knife-edge selection at sizes larger than CULL (in this illustration, down to 20% of the numbers of moulters initially present before fishing), so that a-b would certainly not be continuous with c^1-d^1 in Fig. 3c. If a second moult of survivors were to result in size groups g-h-i in Fig. 3c, once again composed of overlapping normal components, at the same time a second group of new recruits will have entered the fishery. For convenience (under the usual steady-state recruitment conditions adopted for yield/recruit calculations), we may assume that this recreates size group c-d, and that the combined size frequency for the two moult groups (to the same scale) is given by 3D, and when plotted on a log scale, in 3E. This process could, of course, be extended for successive moult groups. As can be readily predicted, each

successive moult group will gradually approach a normal size distribution. There is a close similarity between the resulting size frequency and some of those observed in the southern Gulf of St. Lawrence (Fig. 4), in which a series of plateaux are apparent in the log size-frequencies. Whether this mechanism could operate in a year-round fishery (e.g. as off New England), as opposed to a short, very intensive fishery in which size regulations are rigorously enforced, is questionable. In this particular case, the similarity is made more clearly evident by comparison of log-frequency plots of the simulated data (catch curves in the original sense of Baranov 1918) with similar plots of size frequency from the southern Gulf (Robinson, personal communication).
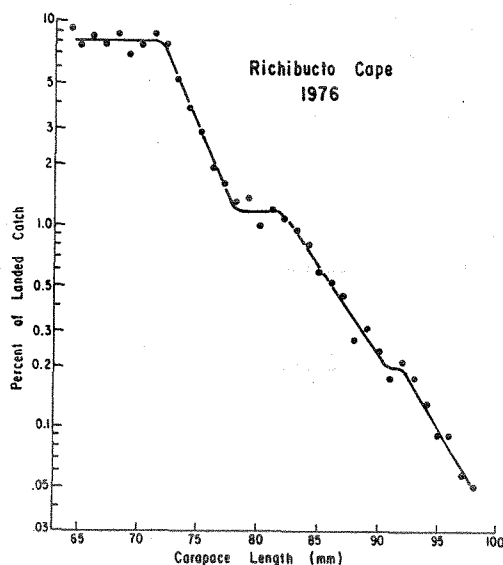

Fig. 4. Log-frequency of commercial catch of lobsters at Richibucto Cape 1976, showing modes in size frequency (Robinson, pers. comm.).

CHANGES OF MOULT INCREMENT AND MOULT FREQUENCY WITH SIZE AND AGE

The literature on reptant decapods of commercial significance generally supports the hypothesis that increment per moult can be fairly accurately defined under a given set of environmental conditions, and is less liable to variation than moult frequency, which declines with size, moult number, and age. For many decapods, as noted by Kurata (1962) and Mauchline (1977), moult frequency (or more conveniently, its inverse, intermoult period) can be expressed as

a logarithmic function of size (CL) and moult number (MN). Using Templeman's transformed data for *Homarus americanus*, Mauchline (1977) obtained:

Male

log (intermoult period) = 1.129 + 0.013 (CL)
                        = 0.93 + 0.051(MN)-
                                          (days)

Although the parameter values given above are based on small individuals (CL = 4-35 mm) and appear to generate too rapid a decline in moult frequency (as will be the case for other growth formulations when extrapolated beyond the range of observed values), the first formulation offers the advantage that it uses data directly obtainable from sampling the commercial catch, as opposed to the von Bertalanffy formulation, which requires estimates of size-at-age which are not always readily available for crustacea.

ESTIMATION OF MORTALITY RATES PER MOULT GROUP

The above phenomenon, if it has any reality in crustacean fisheries, suggests an approach to estimating mortality rates by means of arbitrary moult groups in which catch size frequencies are split up into arbitrary moult groups, using a Hiatt diagram.

This was attempted in Morrissey (1976) on the assumption of Gulland (1969) that, if growth is approximately linear, and it takes approximately 1 yr to grow through the size grouping employed, the relative number per group is a measure of Z. A similar methodology, but one which makes fewer restrictive assumptions, is as follows:

Assuming a deterministic formulation for moult increment beginning at an arbitrary starting point CULL,

$$L_1 = \alpha + \beta \text{ (CULL)}.$$

This can be generalized to give:

$$L_m = \alpha + \alpha\beta + \alpha\beta^2 \ldots \alpha\beta^m \text{ (CULL)}$$

after m moults.

The successive values of L_m are assumed to provide boundaries to arbitrary moult classes. The successive areas subtended under them in a histogram of numbers against size may then be taken to measure the rate of decline in numbers in successive moult classes following the point of full size retention (assuming that gear retention is constant from legal size onwards, and that behavioural considerations do not bias availability with size).

Hence, $\dfrac{N_{m+1}}{N_m} = e^{-Z'_m}$, where Z'_m is the total mortality rate over the mth intermoult period. This may be related to the corresponding exponential mortality rate expressed on an annual basis by

$$Z^1_m = Z\Delta t_m$$

where Δt_m is the mean intermoult duration at the mean size for that arbitrary moult class (which must be estimated independently). The mortality rates per moult obtained by this procedure may be estimated directly by subtraction of the log numbers within successive segments of the catch curve, i.e. $Z^1_m = \log N_m - \log N_{m+1}$. This has been attempted in the Appendix figure for several examples of lobster catch curves.

A SIMPLE YIELD/RECRUIT FORMULATION FOR CRUSTACEA

Assuming the basic discrete formulation for the catch equation, employing annual mortalities F + M

$$C = \frac{N_0 \cdot F \cdot W}{(F+M)} \quad 1 - e^{-(F+M)} \qquad \ldots\ldots 1)$$

where C is the weight of catch from an initial population N with mean weight W, and the number of survivors is given by

$$N_1 = N_0 e^{-(F+M)}. \qquad \ldots\ldots 2)$$

Equation 1 may be modified while retaining the annual mortality rates, but adjusting for the intermoult duration of different moult groups, under two hypotheses:

Hypothesis I. Natural mortality rate is constant with age + number of moults (m) since CULL:

$$C_m = \frac{n_m F_m \cdot W_m}{(F_m+M)} \quad 1 - e^{-(F_m+M)\Delta t_m} \qquad \ldots\ldots 1a)$$

$$n_{m+1} = n_m e^{-(F_m+M)\Delta t_m} \qquad \ldots\ldots 2a)$$

where C_m is catch of moult group m, from an initial cohort of n_m individuals of mean weight W_m. The fishing mortality rate for each moult group F_m may be further defined in terms of the overall fishing mortality rate F by: $F_m = p_m F$, where p_m is the availability of moult group m to the gear, and M is modified to take into account departure of intermoult period Δt_m from

once-annual moulting. The duration of intermoult period Δt_m is expressed as a function of pre-moult carapace length $(CL)_m$ by

$$\Delta t_m = ce^{d(CL)_m}$$

making fishing mortality rate per moult $F_m = pFc.e^{d(CL)_m}$.

The mean weight of individual W_m in a given moult group is specified by the usual power curve for the length-weight relationship

$$W_m = A(CL^*)_m^{B}.$$

Values for A and B used in this illustration for male and female lobsters are given in Table 1 and predicted outputs in Table 2.

The mean carapace length for a given moult group (CL^*) is defined as the mid-point between the premoult carapace length (CL_m) and the post-moult carapace length as related to each other by another power curve:

$$(CL)_{m+1} = r(CL)_m^{S} \qquad \text{(see footnote[1])}$$

Hence,
$$(CL^*)_m = \frac{(CL)_m + r(CL)_m^{S}}{2}$$

or
$$W_m = A.\left[\frac{(CL)_m + r(CL)_m^{S}}{2}\right]^{B}$$

Assuming that all moult groups are in the population at a given time and have an equal chance of being taken by the fishery (i.e. equivalent to the usual dynamic pool assumptions underlying the Beverton and Holt (1957) and Ricker (1958) models), annual yield

$$Y = \sum_{m=1}^{max} C_m \qquad \text{where } m = 1,2....max$$

- the number of moults from entry into the legal size range (m=1), to the maximum number of moults (max) after entry, i.e. equivalent to the largest size attainable in the population.

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[1]A simple linear formulation may be more convenient here, with or without inflexion at maturity, or the formulation of Mauchline (1977): $\log_{10}$ (% increment) $= b'(CL) + a'$. The formulation used here is that employed by Wilder (1963).

Hypothesis II. While Hypothesis I follows that conventionally accepted in most marine fish yield models, namely, constant natural mortality, this assumption may be reasonably questioned, especially for crustacea, which are probably most vulnerable to natural death during and immediately after ecdysis. It may therefore be equally reasonable to postulate an equal probability of natural death during each moult stage, i.e. from equation 1 + 2:

$$C_m = \frac{n_m F_m \Delta t_m}{F\Delta t_m + M^1}\left[1 - e^{-(F\Delta t_m + M^1)}\right] \qquad .....1b)$$

$$n_{m+1} = n\cdot_m e^{-(F\Delta t_m + M^1)} \qquad .....2b)$$

where M^1 = the natural mortality rate during the intermoult period (summation of terms being again over the range of sizes observed for the population).

YIELD-PER-RECRUIT PREDICTIONS USING THE SIMPLIFIED YIELD MODEL

Yield per recruit changes with fishing mortality, using the simplified model, in a similar fashion to that noted in Morrissey (1976) for American lobsters, employing the standard Beverton and Holt (1957) model with von Bertalanffy growth curve input. Rather similar predictions are given by Bennett (1976) for the edible crab *(Cancer pagurus)* in which mean weight-at-age data were used as growth input.

In the above cases (as for the constant annual natural mortality case here (Fig. 5b)), yield per recruit peaks at low values of F (<0.2) for M≈0.1, the fishing mortality rate giving maximum yield per recruit increasing with higher values of M, together with a general flattening of the yield curve (Fig. 5b).

While no attempt is made here to assess the relative validity of the two assumptions with respect to natural mortality, the idea that M declines with age + size is generally well accepted for many marine fish stocks, although it is conventionally assumed that it levels off within the exploited size range. I am suggesting that in Crustacea, it would not be unreasonable to assume as an alternative first hypothesis that the rate of decline in M with age parallels the rate of decline in moult frequency. If this assumption is made, maximum yield per recruit occurs at even lower values of F (mean catch size < 1.5 kg), and slowly declines subsequently. Evidently, this assumption leads to even more conservative estimates of maximum fishing intensity than the conventional one (Fig. 5).

The long plateau shown on the RHS of most lobster yield curves must be regarded with some reservation from the point of view of effect of F on overall population yield (since other

Table 1. Parameter values used in the yield/recruit simulation.

Relationship	Parameter values males	females	Author
moult increment: $(C.L.)_m = a \, (C.L.)^b_{m-1}$	$a = 1.4038$ $b = 0.9555$	$a = 1.4048$ $b = 0.9545$	Wilder (1953)
length weight: $W = \alpha \, (C.L.)^\beta$	$\alpha = 3.307 \times 10^{-4}$ $\beta = 3.2068$	$\alpha = 1.005 \times 10^{-3}$ $\beta = 2.9456$	Wilder (1953)
moult interval: Males $\log_{10} (I_m) = 1.129 + 0.013 \, (C.L.)_m$ or: $I_m = 13.457 \, e^{\, 0.030 \, (C.L.)_m}$			Mauchline (1977)

legal cull size:

(63.5 mm (C.L.) ≡ 2½" in lobster District #8, Northumberland Strait)

Table 2. Test values generated for arbitrary moult classes by the model from input parameters for *Homarus americanus* from Mauchline (1977) (males).

Arbitrary moult group no. after legal size	Group size range (C.L. mm)	Modal size (C.L. mm)	Modal weight (kg)	Gear select'n factor (p)	Inter-moult duration (yr)	Fishing mort/moult annual (F = 0.1)	Hypothesis 1 Constant natural mort/moult	Hypothesis 2 Constant annual mort. (M = 0.1) natural mort/moult
1	63.5-72.8	68.14	0.250	0.8	0.283	.023	0.1	.028
2	72.8-82.9	77.83	0.384	1.0	0.662	.038	0.1	.038
3	82.9-93.9	88.38	0.577	1.0	1.182	.052	0.1	.052
4	93.9-105.7	99.80	0.852	1.0	1.913	.073	0.1	.073
5	105.7-118.4	112.08	1.236	1.0	2.969	.106	0.1	.106
6	118.4-132.0	125.23	1.764	1.0	4.534	.157	0.1	.157
7	132.0-146.4	139.23	2.477	1.0	6.915	.238	0.1	.238
8	146.4-161.7	154.07	3.428	1.0	10.626	.371	0.1	.371
9	161.7-177.8	169.73	4.675	1.0	16.557	.593	0.1	.593
10	177.8-194.6	186.17	6.289	1.0	26.259	.970	0.1	.970

Mean Weight

```
         ——————  ♂ Mode = 2 ;  M = 0.1
         ————— ♀ Mode = 2 ;  M = 0.1
         ——— —  ♂ Mode = 1 ;  M = 0.3
         ········· ♂ Mode = 2 ;  M = 0.3
```
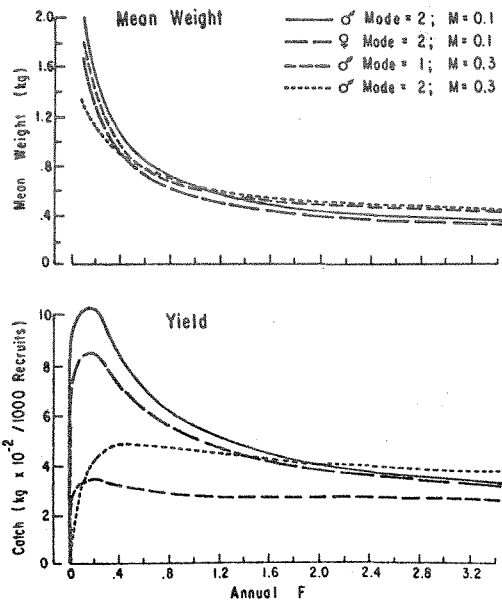
Yield

Annual F

Fig. 5. Variation of predicted mean size of
commercial catch and yield per 1000
recruits with increasing annual fishing
mortality. Input values after Mauchline
(1977), employing two hypotheses of
natural mortality.

factors such as the effect of F on recruitment
enter the picture if mean size falls below size
at maturity). However, the immediate impact on
yield for a fixed recruitment level is not pre-
dicted to be significantly changed by small
decreases in effort, if exploitation level is as
high as we suspect it is for some Canadian
stocks.[2] Some indirect evidence that exploi-
tation rates are high (bearing in mind comments
made earlier about Mauchline's estimates) is
provided by the low mean size of catch in many
areas (less than 0.5 kg in many Canadian inshore
districts) which is predicted to occur at values
of F in excess of 1.3 (annual rate) in Fig. 5.

AGE AT FIRST CAPTURE

Ignoring the possible effects of discard
mortality (which is probably a major factor in
influencing yield for a given gear type),
raising the legal age or size at first capture

_____

[2]This does not mean we should not strongly recom-
mend significant reductions in fishing effort,
just that they may not produce commensurate
increases in yield, even though population
stability may be improved.

has been predicted to produce an initial increase
in yield up to 5 to 10 yr (depending on other
parameter values) before a slow decline begins.
No attempt has been made to extend this analysis
beyond the usual range of sizes considered
practical for size-limit implementation (<100 mm
CL), and it is noted that, up to this size, yield
increases continually with size limit for either
hypothesis. It is felt in conclusion, therefore,
that the case for size-limit increases and con-
siderable overall effort cutbacks has been
supported by this analysis, with the former types
of measures giving more immediate economic
benefits.

SUMMARY AND CONCLUSIONS

1) A yield-per-recruit formulation is pre-
sented employing information inputs of a type
compatible with that normally collected in crus-
tacean fisheries, namely, for each sex, moult
frequency and moult increment as functions of
size; length-weight relationships; and gear
selection ogives. Input values for natural
mortality rate can be considered either constant
per moult or, on a more conventional basis,
considered constant annually, or varied with
moult stage if data are available. Outputs are
given directly in terms of size at first capture,
together with predicted mean weights of crus-
taceans in the catch. This makes it easier to
estimate indirectly the point on the Y/R curve.

2) Although it is demonstrated that the per-
sistence of discrete age-groups in the size
frequency of the commercial catch is unlikely
(given the number of years between settlement
and recruitment for lobsters), a mechanism is
proposed which may account for such modes, if
they occur in a fishery which is relatively
intensively fished, but where size limits are
strictly enforced.

3) The above demonstration allows us to con-
sider catch curves (in the original sense pro-
posed by Baranov (1918), i.e. log size-frequency
plots) as a source of information on mortality
rate per arbitrary moult group. The legal size
limit is suggested as a useful point to begin
specifying arbitrary moult intervals in this
catch curve (as long as this exceeds the point
of full gear retention), the difference between
successive areas under the catch curve then
being a measure of the mortality rate per moult
(under the usual constant recruitment assumptions).

4) The type of formulation used here pro-
duces similar predictions to those given by
methods based either on von Bertalanffy growth
inputs, or discrete weight-at-age data, but seems
to offer several advantages not only in ease of
data input but also in terms of future develop-
ment to real-time models. These are as follows:

a) Growth is divided into the components of increment and interval, allowing consideration of effects of environment and maturity on both separately.

b) The existence of both fairly restricted moulting seasons and of fishing seasons in several lobster fisheries means that moult stage since recruitment (or legal size) is the unit of time giving most specified yield predictions (especially if more than one moult is accomplished annually).

c) Ecdysis and reproduction in lobsters are closely scheduled in the animal's life history so that any attempt to extend simulations to consider, for example, effects of size limits on population fecundity, or any other type of real-time model, must express time in terms of moult groups. This preliminary model allows such an extension, which is not the case for the Beverton and Holt (1957) type of model.

ACKNOWLEDGMENTS

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APPENDIX

Approximate estimates of mortality rate per moult can be obtained from log frequency at size plots, examples of which are shown in Appendix Fig. 1a-3, which combine groups of catch samples taken at individual ports around the Canadian Maritimes. Ideally of course, these samples should be combined over a period of years to avoid bias due to recruitment variation, but will serve for illustration of the principle. An arbitrary size following the inflexion point (presumed to occur at the size of full gear retention) is chosen as a starting point and an appropriate equation relating premoult to post-moult carapace length used to step off successive moult increments from that arbitrary starting point. As noted by Gulland (1969), assuming linear growth over the size interval, the slope of the RHS is proportional to the mortality coefficient. Without making the linear growth assumption, but assuming in an analogous fashion that for crustacea the numbers taken in successive moult increments represent the mortality over a moult interval,

$$N_{m+1} = N_m \cdot e^{-Z'm}$$

where $Z'_m = Z\Delta t_m$.

Estimates of Z'_m can be obtained by $\ln(N_m) - \ln(N_{m+1})$, the numbers in successive arbitrary moult intervals (Appendix Tables 1 and 2). The intriguing points about the mortality estimates as given (see Appendix Fig. 2) are:

a) They are high by most normally accepted standards for marine fisheries.

b) The high estimates are supported by the relatively few moult groups in the fishery.

c) The estimates rise with median moult group size.

From c) we may conclude that, if behavioural factors are not responsible for declining catchability (which cannot of course be discounted), and if it can be assumed that all fully recruited individuals suffer the same overall mortality, then the increase in Z'_m with size is a measure of increasing intermoult duration. This appears to provide an indirect method of estimating Δt_m, if the intermoult duration of one size group can be established.
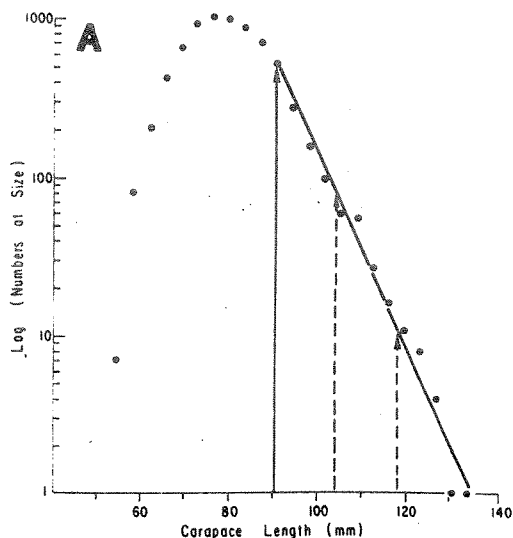

Appendix Fig. 1(a-e). Combined log-frequency plots of commercial catches over a period of 1-2 mo at various ports around the Maritimes of Canada. Regression lines have been calculated from the point of inflexion (or by eye-fit in e), and divided up by the appropriate moult intervals starting at an arbitrary point after the inflexion.
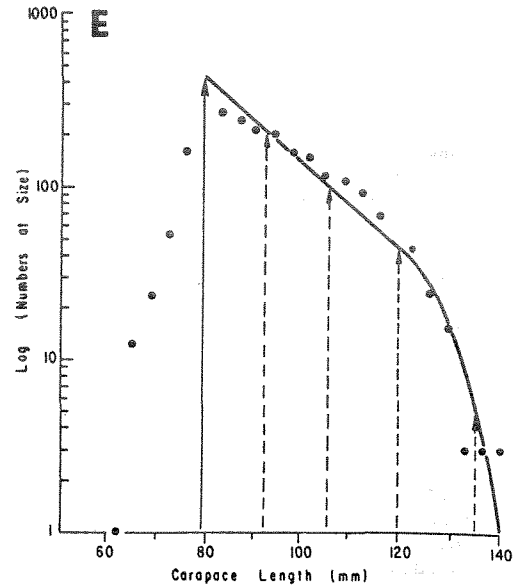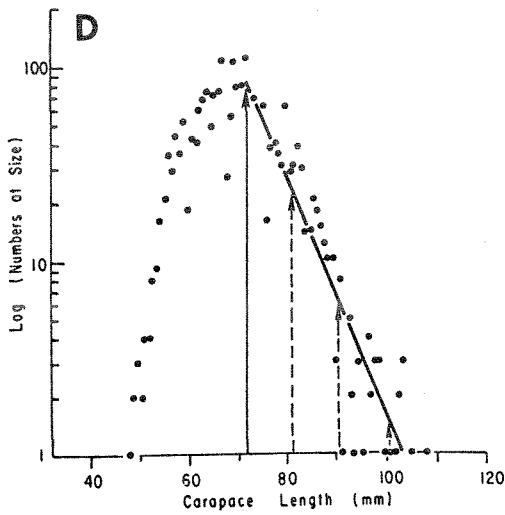
Appendix Fig. 1a. Abbott's Harbour, N.S.
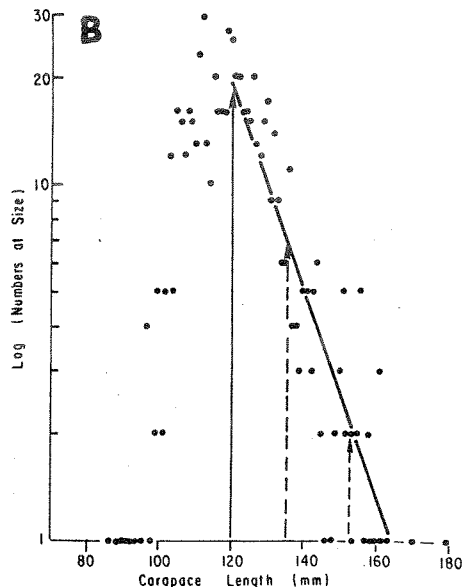
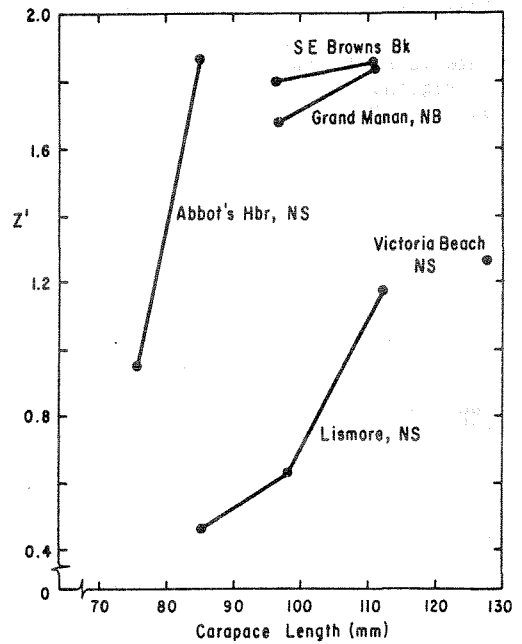Appendix Fig. 1b. S.E. Browns Bank (offshore stock).
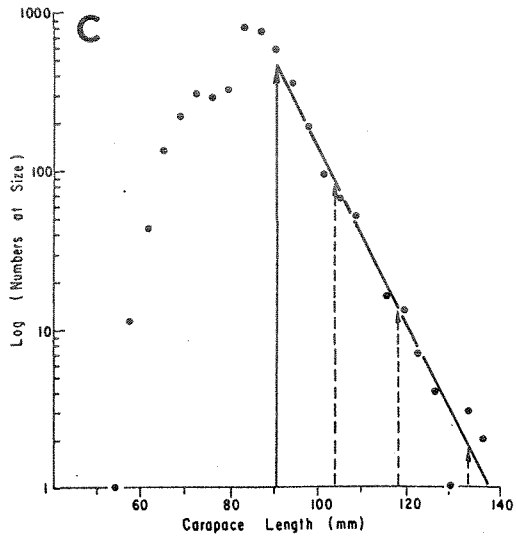
Appendix Fig. 1c. Grand Manan, N.B.

Appendix Fig. 1e. Victoria Beach, N.S.

Appendix Fig. 1d. Lismore, Merigomish, Arisaig,
N.S.

Appendix Fig. 2. Plots of estimated mortality
rate per arbitrary moult group against
size for five different areas.

Appendix Table 1

Lismore, N.S.			Grand Manan, N.B.			Abbotts Harbour, N.S.		
Arbitrary moult group(length in mm)	No./group	$\underline{Z'}$	Arbitrary moult group(length in mm)	No./group	$\underline{Z'}$	Arbitrary moult group(length in mm)	No./group	$\underline{Z'}$
1) Between 71.4 and 80.5	559		1) Between 90.4 and 103.7	929		1) Between 90.4 and 103.7	787	
median size 76.0		$Z'_1 = 0.94$	median size 97.1		$Z'_1 = 1.80$	median size 97.1		$Z'_1 = 1.68$
2) Between 80.5 and 90.2	219		2) Between 103.7 and 118.2	153		2) Between 103.7 and 118.2	147	
median size 85.3		$Z'_2 = 186$	median size 110.9		$Z'_2 = 1.85$	median size 110.9		$Z'_2 = 1.85$
3) Between 90.2 and 100.6	34		3) Between 118.2 and 133.9	24		3) Between 118.2 and 133.9	23	
median size 95.4			median size 126.0			median size 126.0		

Appendix Table 2

S.E. Browns Bank				Victoria Beach, N.S.		
Arbitrary moult group(length in mm)	No./group	$\underline{Z}'$		Arbitrary moult group(length in mm)	No./group	$\underline{Z}'$
1) Between 120 and 135.8	223			1) Between 79.5 and 91.7	945	
median size 127.9		$Z'_1 = 1.31$		median size 85.7		$Z'_1 = 0.46$
2) Between 135.8 and 153.0	60			2) Between 91.7 and 105.0	597	
median size 144.4				median size 98.4		$Z'_2 = 0.62$
				3) Between 105.0 and 119.7	322	
				median size 112.4		$Z'_3 = 1.17$
				4) Between 119.7 and 135.6	100	
				median size 127.6		