Modelling capture processes in individual traps: entry, escapement and soak time

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Stationary fishing gear is employed in a diverse array of fisheries including those for many high unit-value species. The mode of operation of these gear types (traps, long-lines, gillnets, etc.) requires special consideration in the development of abundance indices because of gear saturation effects. Specifically, factors affecting the probability of capture and of escapement or other sources of loss must be addressed. Here, we describe two models of capture processes in traps that include existing models as special cases. Deterministic models are first developed to illustrate the basic principles. Stochastic analogues of two well-known models are then described using the theory of birth–death stochastic processes. It is shown that the mean of the stochastic models is identical to the deterministic case for models where closed form solutions are possible. The stochastic models provide additional diagnostic information in terms of the variance and the probability distribution of catch levels. Illustrations of this approach are provided for experimental observations on ingress and catch for the American lobster (*Homarus americanus*).

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Introduction

Fisheries for many high value species, including decapod crustaceans (Krouse, 1989; Miller, 1990), tropical (Munro, 1983) and boreo-temperate fish (von Brandt, 1984), and gastropod and cephalopod molluscs (Hancock and Simpson, 1962), are prosecuted using traps of various designs. Traps can be highly size- and species-selective and are both efficient and cost-effective (Miller, 1990). These devices share with other forms of stationary gear (e.g. long-lines and gillnets) a passive mode of capture in which the behavior of the species sought plays a dominant and critical role. Stationary fishing gears are typically set at fixed locations and retrieved after variable immersion (soak) intervals. Immersion times can vary greatly in these fisheries and catch is typically not a linear function of the soak interval. These characteristics must be considered in the development of relative abundance indices based on standardized catch and effort series.

The problem of gear saturation has long been recognized (Hile and Duden, 1933; Kennedy, 1951) and a number of models have been developed to describe this process following the seminal studies of Gulland (1955) and Beverton and Holt (1957). The fundamental similarities in the deployment and operation of various forms of stationary gear have led to a convergence in modelling approaches. Indeed, the most commonly cited model for trap fisheries (Munro, 1974) is generally expressed in a form identical to the long-line/gillnet model of Gulland (1955) and Beverton and Holt (1957). However, the Munro model is based on fundamentally different assumptions regarding the roles of entry and escapement in traps.

Our objective is to clarify these differences and to provide extensions of both models. This discrimination is essential if these models are to be used in the development of standardized measures of abundance. We also provide contrasts between stochastic forms of these models to highlight these distinctions and to provide

additional diagnostic information. We begin by reviewing the underlying assumptions and derivations of the Gulland–Beverton–Holt model and Munro's model to set the stage for these further developments.

Background

Gulland (1955, pp. 34–36) derived a model for an individual long-line under the assumption of a linear decline in the catch rate with an increase in catch. Escapement or other sources of loss (e.g. removal by predators) were not considered. The model can be written:

$$C_t = C_\infty (1 - e^{-At}) \tag{1}$$

where C_∞ is the maximum catch level, and A is the rate at which the maximum catch is approached. The maximum catch is defined for long-line fisheries by the number of hooks in the set. Gulland derived an expression for the mean effective effort of an individual long-line as a function of soak time and demonstrated that the catch per unit effort is equal to the rate at which the asymptotic catch is reached. Gulland proposed the parameter A as an index of abundance. Murphy (1960) subsequently refined this approach with explicit consideration of the individual processes of capture, escapement, and other sources of loss for long-lines (see also Sinoda, 1981). Beverton and Holt (1957, pp. 94–95) applied a model in the form of Equation (1) above to gillnet catches. For gillnet fisheries, C_∞ could, in principle, be defined as the number of mesh openings; however, this undoubtedly represents an unrealistically high level for the maximum catch (Beverton and Holt, 1957).

Sinoda and Kobayasi (1969) provided an early application of the Gulland–Beverton–Holt model to a trap fishery. Munro (1974) subsequently proposed a model for unbaited Antillean fish traps assuming a constant rate of entry and escapement of a constant proportion of the catch per unit time. Munro began by specifying a model identical in form to Equation (1) but further defined a model which can be written:

$$C_t = (C_{t-1} + E) - p(C_{t-1} + E) \tag{2}$$

where E is the daily rate of ingress (entry) into the trap and p is the daily probability of escapement. The change in catch is therefore equal to the balance between the number entering (a constant) and the fraction escaping per day. Note that the escapement coefficient is applied to the sum of the catch from the previous day and the new entrants. Munro's recursion formula can be written:

$$C_t = \frac{rE}{p}(1 - e^{-Rt}) \tag{3}$$

where R is an instantaneous rate of escapement, $r = \exp(-R)$ and $p = (1 - r)$ (see Equation 6 of Munro, 1974). The asymptotic catch is equal to rE/p in this specification (i.e. the limiting catch is a function of rate of entry and the probability of escapement). Munro proposed the entry rate E as an index of abundance. The interpretation of the factors affecting the asymptotic catch is therefore entirely different in this model relative to the Gulland–Beverton–Holt model. Further, the role of the coefficient in the exponents of the two models differs substantially, representing a capture rate in the Gulland–Beverton–Holt model and an escapement rate in the Munro model.

Munro's model in the form of Equation (1) has been applied to many crustacean fisheries (see Miller, 1990, for a comprehensive review). However, Munro's more detailed specification of the underlying basis for his model (Equations 2 and 3) has often been overlooked (but see Bennett and Brown, 1979; Robertson, 1989). The Munro model assumes that the entry rate is independent of the number of individuals already in the trap and that the entry and escapement rates are time-invariant. In the following section, we describe a model where these constraints are eliminated and contrast this model with an extension of the Gulland–Beverton–Holt model which includes an escapement component. Somerton and Merritt (1986) described an alternative approach to modifying the Gulland–Beverton–Holt model to include escapement. Our derivation is a direct extension of Gulland's original formulation and leads to a different result. Somerton and Merritt independently derived a model which is nearly identical to a model for long-line fisheries developed by Murphy (1960), again indicating the fundamental similarity of approaches taken in modelling the performance of different forms of stationary gear.

Deterministic models

Models incorporating explicit expressions for trap entry and escapement are described below. Two forms are considered for the entry component to encompass the range of previously published models. For simplicity, only proportional escapement is allowed. The rate of change of the catch (in number) is given by:

$$\frac{dC_t}{dt} = f(C_t) - b_t C_t \tag{4}$$

where C_t is the catch at time t, $f(C_t)$ is a function describing ingress into the trap, and b_t is the instantaneous rate of escapement (which can vary with time). The first form of the entry component considered is a power function model:

$$f_1(C_t) = a_t C_t^m \tag{5}$$

where a_t is a time varying ingress parameter and m is a shape parameter (which we will assume to be time invariant although this constraint can be easily removed). The complete specification for this model is then:

$$\frac{dC_t}{dt} = a_t C_t^m - b_t C_t \qquad (6)$$

where all terms are defined as above. This model is identical in general form to the well known Richards growth function. Notice that the instantaneous escapement rate (b_t) is applied to C_t in this differential equation and therefore differs from the form used by Munro in his difference equation formulation (Equation 2). The parameters a_t and b_t are allowed to vary in time:

$$a_t = \int_0^t a(\tau)d\tau \qquad (7)$$

and

$$b_t = \int_0^t b(T)dT \qquad (8)$$

The solution is given by:

$$C_t = \left\{ \frac{a_t}{b_t} \left[1 - e^{-(1-m)b_t t} \right] \right\}^{1/(1-m)} \qquad (9)$$

for the initial conditions $C_0 = 0$, $t_0 = 0$ (note that m=1 is undefined). For the special case of time-invariant entry and escapement rates, this model describes an asymptotic catch with increasing soak time; the limiting catch is a function of the ratio of the capture and escapement rates. Examples of the relationship between catch and soak time for several levels of the shape parameter m are provided in Figure 1a for the time invariant case. If entry rates decline with time because of decreased local abundance, loss of effectiveness of bait etc., or if escapement rates increase with increasing soak time, the relationship is no longer asymptotic but rather declines with time (see Fig. 1b for an illustration). In trap fisheries where escapement is relatively easy, it is not uncommon to observe catches in baited traps reaching a maximum and subsequently declining with increasing soak time (e.g. Bennett, 1974; Munro, 1974; High and Worlund, 1979; Skud, 1979; Sloan and Robinson, 1985; Somerton and Merritt, 1986; Smith and Jamieson, 1989). Sundberg (1985) developed a model assuming a decaying exponential entry rate due

to loss of effectiveness of the bait (see also Smith and Jamieson, 1989).

For the case m=0 (representing an entry rate which is independent of the number in the trap), we have a variant of Munro's model for unbaited Antillean fish traps:

$$C_t = \frac{a_t}{b_t}(1 - e^{-b_t t}) \qquad (10)$$

where the limiting catch is given by the ratio of the entry and escapement coefficients. For the case m>0, the model is appropriate for certain gregarious species harvested in fish and crustacean traps where conspecifics in the trap attract others (Munro, 1974; Miller, 1990). This effect has been routinely observed and exploited to increase capture rates in spiny lobster and blue crab fisheries (Miller, 1990). Note that in this case, an inflection in the catch at low soak times is predicted (Fig. 1a). For the case m<0, the capture rate declines with increasing catch. This effect has been reported in many crustacean trap fisheries (Miller, 1990) and reflects agonistic encounters and displays and/or chemical signals which reduce entry rates.

For the case of a power function describing the capture process and no escapement or loss (b=0), we obtain a version of Austin's (1977) model:

$$C_t = [a_t(1-m)t]^{1/(1-m)} \qquad (11)$$

In Austin's original notation, $\alpha = [a_t(1-m)]^{1/(1-m)}$, S=t, and $(1-\beta) = 1/(1-m)$ giving $C = \alpha S^{(1-\beta)}$ as the model. Austin's original time-invariant model has been criticized because it leads to a continual increase in catch with increasing soak time (Miller, 1990). However, this objection is removed if the parameter a_t is allowed to decrease with time.

We next consider an extension of the Gulland–Beverton–Holt model to explicitly incorporate escapement. The entry function is taken to be:

$$f_2(C_t) = k_t(C^* - C_t) \qquad (12)$$

where C^* is maximum catch (a function of the gear configuration), k_t is the (time varying) rate at which the maximum is approached:

$$k_t = \int_0^t k(\varepsilon)d\varepsilon \qquad (13)$$

This is the form underlying the Gulland–Beverton–Holt model (see Equation 2.9 of Gulland, 1955). It is also identical to the form underlying the von Bertalanffy growth model. The full model can be specified:
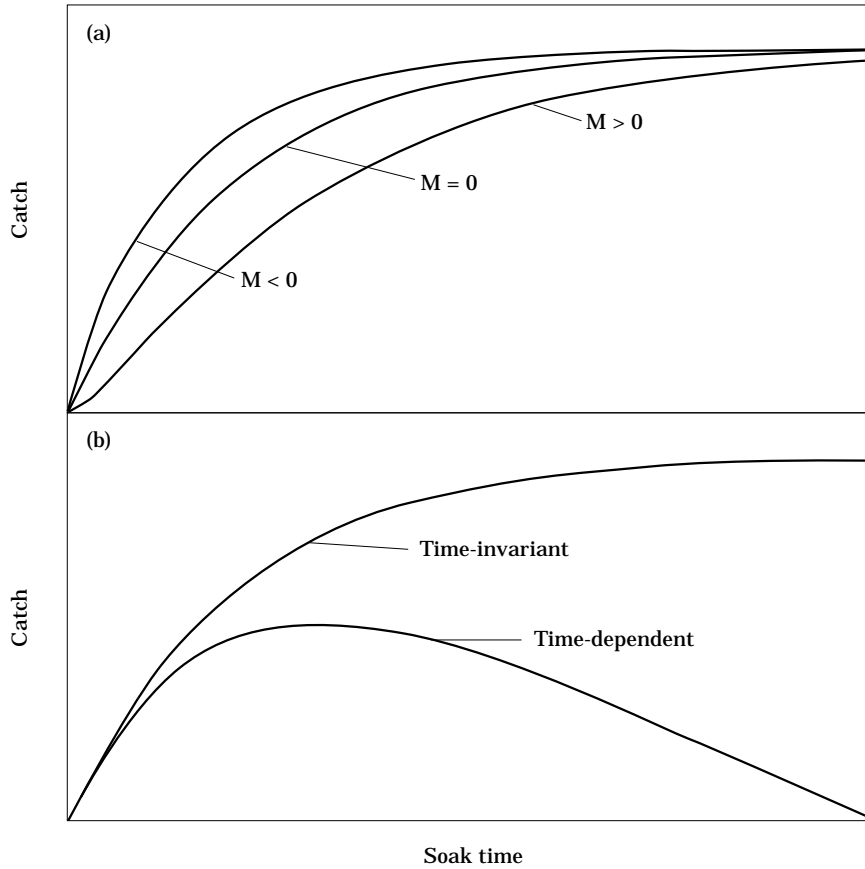
Figure 1. (a) Relationship between catch and soak (immersion) time for the generalized Munro model for three values of the shape parameter (m). (b) Illustration of the effects of time-invariant and time-dependent capture processes for the power function model. The time dependent model is based on a linearly decreasing capture rate with time.

$$\frac{dC_t}{dt} = k_t(C^* - C_t) - b_t C_t \qquad (14)$$

where b_t is the escapement rate as defined above. The solution is given by:

$$C_t = \frac{k_t C^*}{k_t + b_t}(1 - e^{-(k_t + b_t)t}) \qquad (15)$$

Note that when $b > 0$ (i.e. escapement is possible), the asymptotic catch will be below the maximum possible catch. Examples of the relationship between catch and soak time for several escapment levels are provided in Figure 2a for the time invariant case. An illustration of the effect of a linear increase in the escapement rate with time is provided in Figure 2b; again the catch decreases with increasing soak time.

Stochastic models

In this section we describe the development of stochastic analogues of the deterministic models outlined above based on the theory of birth–death processes (see Feller, 1957; Cox and Miller, 1965; Bailey, 1964; Karlin and Taylor, 1975 for overviews). Stochastic models have previously been developed for hook and line fisheries using the theory of Markov processes (Rothschild, 1967) and renewal theory (Deriso and Parma, 1987). Reed (1986) illustrated the development of a stochastic catch model and Sampson (1988) described a catch model based on a pure death stochastic process. These models directly address the issue of variability in catch processes and also provide additional diagnostic information on the probability distribution of the catch and its mean and variance.

The probability of an individual entering a trap during a short interval of time t to t+h can be designated $\alpha_C h + oh$; the probability of escapement during this
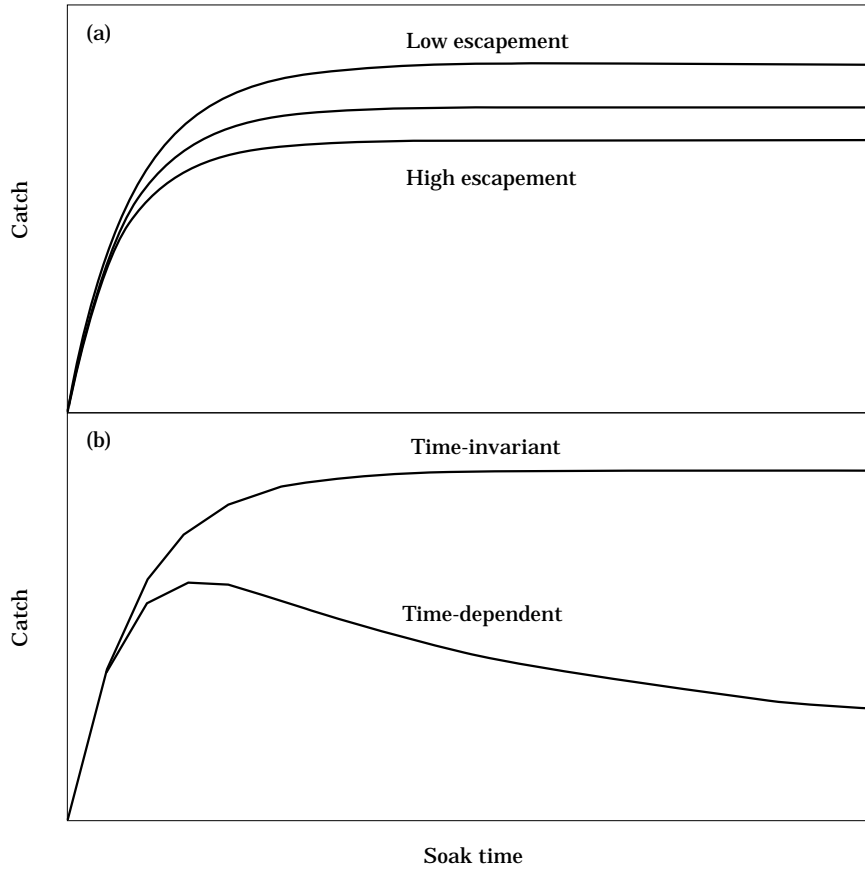
Figure 2. (a) Relationship between catch and soak (immersion) time for the modified Gulland–Beverton–Holt model for three levels of escapement. (b) Illustration of the effects of time-invariant and time-dependent escapement processes.

interval is $\beta_C h + o(h)$ [where $o(h)$ is a quantity such that $\lim_{h \to 0} o(h)/h = 0$ (implying that $o(h) \to 0$ more rapidly than $h \to 0$)]. The probability of two or more events (capture and/or escapement) in the interval is taken to be $o(h)$. The probability of obtaining exactly C individuals in the catch at time $t+h$ is:

$$P_C(t+h) = P_C(t)[1 - \alpha_C h - \beta_C h + o(h)] + P_{C-1}(t)$$
$$[\alpha_{C-1} h + o(h)] + P_{C+1}(t)[\beta_{C+1} h + o(h)] + o(h) \quad (16)$$

The first term on the right hand side gives the probability of no change given that the catch at time t is exactly C individuals. The second term represents the probability of an increase from $C-1$ individuals and the third component is the probability of a decrease from a catch of $C+1$ during the time interval. The probabilities are taken to be independent and therefore additive. Rearranging and taking the limit as $h \to 0$ of $[P_C(t+h) - P_C(t)]/h$ gives:

$$P'_C = -(\alpha_C + \beta_C)P_C(t) + \alpha_{C-1}P_{C-1}(t) + \beta_{C+1}P_{C+1}(t) \quad (17)$$

where $P'_C = dP_C/dt$ and

$$P'_0 = -\alpha_0 P_0(t) + \beta_1 P_1(t) \quad (18)$$

This is the basic system of equations for a linear birth–death stochastic process. Here, the birth component is equated with ingress and the death component relates to escapement or other sources of loss. We assume that there is no waiting time in the capture process. The terms α_C and β_C can, in general, be specified as functions of catch. Whether the above system of equations can be solved in closed form depends on the exact functional forms and the initial conditions specified. Below, we provide results for the Gulland–Beverton–Holt model and a variant of the Munro model. To simplify both the notation and the discussion, we will consider only the time invariant case. However, the results easily generalize to include time-varying parameters as in the deterministic case.

We will first consider a version of the Munro model (m=0). We then have $\alpha_C = a$ and $\beta_C = bC_t$ and the basic

system of equations is:

$$P'_C = -(a+bC)P_C(t) + aP_{C-1}(t) + b(C+1)P_{C+1}(t) \qquad (19)$$

and

$$P'_0 = -aP_0(t) + bP_1(t) \qquad (20)$$

This system of equations is amenable to solution using the method of probability generating functions. We take the initial conditions to be $P_0 = 1$ and $P_C(0) = 0$ for all $C \neq 0$. The probability density function (PDF) for this model is Poisson:

$$P_C(t) = \{e^{-(a/b)[1-e^{-bt}]}\} \frac{\{(a/b)[1-e^{-bt}]\}^C}{C!} \qquad (21)$$

with mean:

$$E(C_t) = \frac{a}{b}(1-e^{-bt}) \qquad (22)$$

Recall further that for the Poisson distribution, the mean and variance are identical. Note also that the stochastic mean is identical to the deterministic model. An illustration of the probability distribution of catch with increasing soak time is provided in Figure 3 for this model.

For the stochastic version of the Gulland–Beverton–Holt model we have $\alpha_C = k(C^* - C)$ and $\beta_C = 0$. The catch model is then:

$$P'_C(t) = k[(C^* - C)]P_C(t) + [k(C^* - (C-1))]P_{C-1}(t) \qquad (23)$$

where $(C+1)$ cannot exceed C^* and

$$P'_0 = -kC^*P_0(t) \qquad (24)$$

This model can again be solved in closed form by the method of probability generating functions. The initial conditions are taken to be $P_0(0) = 1$ and $P_C(0) = 0$ for all $C \neq 0$ (i.e. the catch at time 0 is 0). The probability density function for this model is binomial:

$$P_C(t) = \binom{C^*}{C}(e^{-kt})^{(C^*-C)}(1-e^{-kt})^C \qquad (25)$$

with mean:

$$E(C_t) = C^*(1-e^{-kt}) \qquad (26)$$

and variance:

$$V(C_t) = C^*(e^{-kt})(1-e^{-kt}) \qquad (27)$$

Notice that the stochastic mean is again identical to the deterministic solution. An illustration of the form of the probability density function for this model is provided in Figure 3. Note that the general shape of the distribution with increasing soak time differs markedly from the Poisson model examined earlier. The probability mass becomes concentrated near the maximum catch value but, of course, does not exceed the maximum.

Example

Application of these principles are described below for the American lobster, *Homarus americanus*. Auster (1985) set strings of 16 traps in Long Island Sound, USA and monitored ingress and escapement from these traps over immersion times of up to 7 d. Observations by SCUBA were made daily and each individual in the trap was tagged for subsequent identification. Some entries could have gone unrecorded if the individual exited the trap prior to the census, resulting in an underestimate of the true entry and exit rates (Auster, 1985).

For the purposes of the present analysis, we combined data from individual sets collected during two distinct area/time period combinations. Catch levels within these two area/time combinations were relatively homogeneous but were distinctly different between area/time combinations. The first group, comprising two sets (n=32 traps) was characterized by relatively low catch rates. In contrast, the second group of three sets (n=48 traps) had higher catch levels. Daily ingress and egress from each trap for these sets were available for both area/time periods. The observational periods for groups 1 and 2 were 7 d and 5 soak days respectively. We assumed that the catch of each trap is independent of others in the string and can be treated as replicates.

We fit the generalized Munro model to the catch as a function of soak time by non-linear least squares. The catch was asymptotic or increasing within the range of soak times observed and no independent information on time-varying entry or escapement rates was available. We assumed that the parameters were time-invariant for the purposes of this analysis. Although it was possible to estimate all three parameters simultaneously, we found that the parameter estimates were highly correlated, resulting in high standard errors for the estimates. We therefore fit the model for a range of fixed m values, varied in increments of 0.05, and estimated the remaining two free parameters (a and b). The model with the lowest residual mean square error was selected as the best model. This approach does unfortunately preclude testing for whether the shape parameter differs significantly from zero. However, we have found that the variability of the estimates for the full parameter model is generally too high to allow an adequate test for the
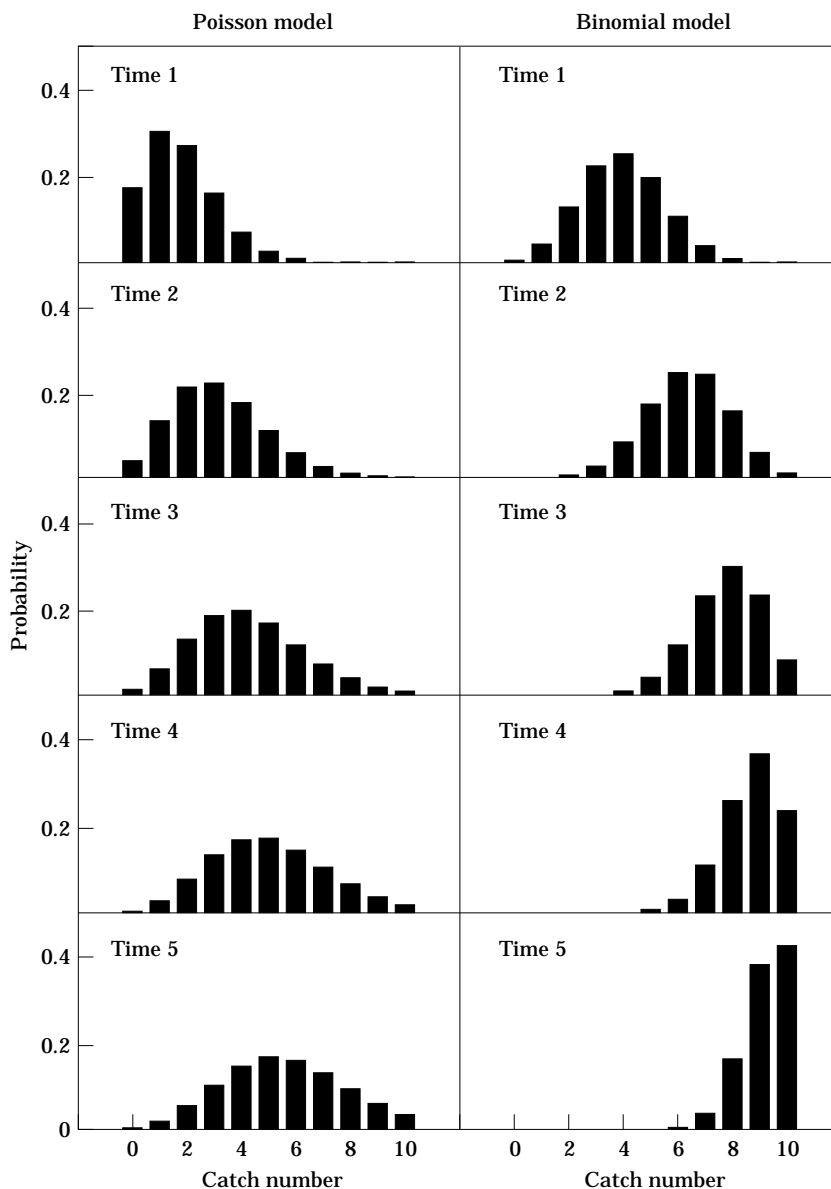
Figure 3. Illustration of the probability distribution of catch levels for stochastic version of the Munro model with increasing soak time (*left*) and the probability distribution of catch levels for stochastic version of the Gulland–Beverton–Holt model with increasing soak time (*right*).

shape parameter. Non-parametric bootstrap estimates (Efron, 1982) of the parameter errors were made.

The entry rates for the first group was relatively constant and the cumulative entry was approximately linear over time, although there was clear evidence of reduced entry on the final day of observation (Table 1 ; Fig. 4a). In contrast, the cumulative catch was clearly non-linear with increasing soak time (Fig. 4a). The value of the shape parameter providing the lowest mean square error was $m = -0.15$, suggesting a slight reduction in entry with increasing catch. For comparison, we

also provide parameter estimates for $m = 0$ (corresponding to the Munro model; Table 2). We note that the changes in the residual mean square in the vicinity of $-0.2 < m < 0.2$ are very small. A comparison of the observed and expected catch with increasing soak time is provided in Figure 4b.

The cumulative entry for individuals in the second group was markedly non-linear (Fig. 5a) and the number of lobsters entering the traps declined sharply following the first soak day (Table 1). The lowest residual mean square error was obtained with

Table 1. Summary of mean entry and catch for each soak day (variance estimate in parentheses below) for American lobster in Long Island Sound (Auster, 1985) for two periods (September–October 1982; group 1; n=32 and October–November 1982; group 2; n=48).

Soak day	Group 1		Group 2	
	Entry	Catch	Entry	Catch
1	0.188 (0.157)	0.188 (0.157)	0.521 (0.468)	0.521 (0.468)
2	0.188 (0.157)	0.188 (0.157)	0.313 (0.390)	0.667 (0.780)
3	0.125 (0.113)	0.313 (0.286)	0.208 (0.211)	0.708 (0.722)
4	0.156 (0.201)	0.375 (0.371)	0.250 (0.277)	0.750 (0.830)
5	0.156 (0.136)	0.375 (0.565)	0.125 (0.112)	0.792 (0.807)
6	0.188 (0.286)	0.500 (0.903)		
7	0.063 (0.060)	0.500 (0.838)		

m= −1.30, again suggesting that the presence of lobsters in the traps following the initial high entry rate inhibited the further entry of individuals. This effect was substantially stronger for group 2 relative to group 1 where catch levels were much lower. A comparison of the observed and predicted catch with increasing soak time is provided in Figure 5b. The reduction in entry rates with increasing catch is consistent with experimental observations in which lobsters were pre-stocked in traps (Richards *et al.*, 1982). Traps in which 3 and 8 lobsters were stocked had significantly lower catches than control traps. Addison (1995) found similar results for traps stocked with a single lobster (*H. gammarus*).

We further examined the data for group 1 in the context of the stochastic catch model. For this set, catch levels were relatively low and the apparent effect of individuals already in the trap on entry rates was relatively small. We compared empirical catch for each day against expected levels according to a Poisson distribution for the Munro model. The observed and predicted probability distribution of number of individuals per trap for the Poisson model is provided in Figure 6.

Discussion

Trap-based fisheries present unique challenges for the development of standardized measures of abundance. Catch rates in these fisheries are determined by the interplay of factors affecting capture and escapement or loss from the gear. The exact nature of the capture and loss processes determines the most appropriate strategy for development of an abundance index. For stationary gear fisheries, the behavior of the target species plays a vital role in the capture process. Physiological and environmental factors have a dominant effect on the behavior of the species sought and therefore must be considered in the development of abundance indices based on catch rate information. For broad scale fishery-dependent information, this may require stratification based on temporal/spatial units where environmental conditions and physiological state of the target species can be considered relatively homogeneous. Alternatively, models that incorporate these factors explicitly can be developed.

We have described approaches to modelling the performance of an individual trap. However, further application of these models in the development of indices of abundance requires explicit linkage to local population size. In particular, we require an index of catch per unit effort which is proportional to population size: $C/f=qN$ where C/f is the catch per unit effort, q is the catchability coefficient, and N is population size. Clearly, the catch per trap is not proportional to abundance at long soak times where the limiting catch has been attained. However, catch per trap for short immersion times before interactive effects are manifest could be used. For example, Miller and Hunte (1987) demonstrated that the catch per trap of selected reef fish at short soak times was proportional to abundance measured by visual census in the vicinity of the trap. The choice of this soak time would, of course, be species-specific. Application of this general approach will require calibration based on experiments and/or carefully designed observational studies in which the effects of factors such as changes in bait attractiveness, inter- and intraspecific interactions,
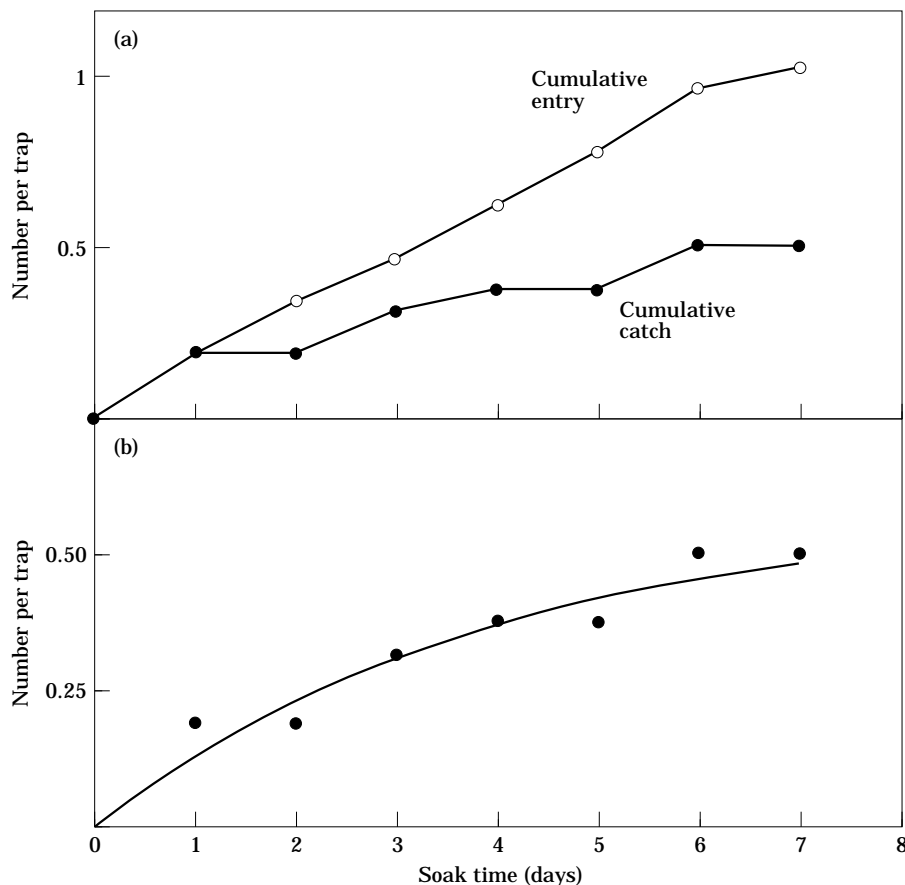
Figure 4. (a) Cumulative entry and catch (mean number per trap) for American lobster in Long Island Sound (Auster, 1985) in experimental fishing operations during September–October 1982 and (b) observed (closed circles) and predicted mean catch per trap as a function of soak time.

the effective fishing area of a unit of gear, potential interference among units of gear, and the effects of local population depletion can be quantified. The effects of the existing catch on new entrants and time dependence of the entry and escapement parameters are likely to be confounded in field data. It will therefore be crucial to conduct controlled experiments in which varying numbers of individuals are stocked in traps (e.g. Richards *et al.*, 1982; Castro and DeAlteris, 1990; Addison, 1995) with entry and escapement continually monitored and bait freshness or attractiveness controlled over time (e.g. Miller, 1980; Smith and Jamieson, 1989). In addition,

Table 2. Parameter estimates and associated asymptotic standard errors for trap catch model applied to American lobster in Long Island Sound (Auster, 1985) for two time periods: September–October 1982 (group 1; number traps=32) and October–November 1982 (group 2; number traps=48). For both groups, model parameter estimates were made fixing the shape parameter (m) at zero and by incrementally varying m and selecting the model with the lowest residual error (see text).

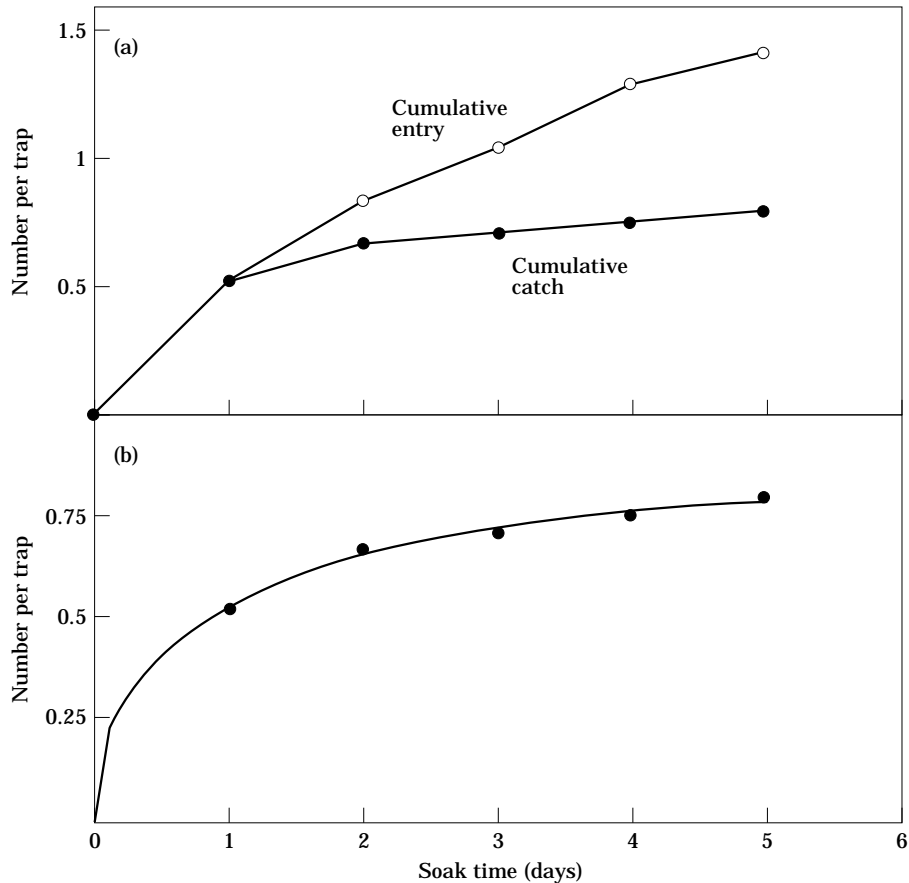| Parameter	Group 1		Group 2	
a	0.1457 (0.0901)	0.1456 (0.0622)	0.8457 (0.2034)	0.1209 (0.1226)
b	0.2490 (0.3427)	0.2162 (0.2892)	0.1094 (0.3197)	0.1877 (0.3602)
m	0	− 0.15	0	− 1.30

Figure 5. (a) Cumulative entry and catch (mean number per trap) for American lobster in Long Island Sound (Auster, 1985) in experimental fishing operations during October–November 1982 and (b) observed (closed circles) and predicted mean catch per trap with m = − 1.30 as a function of soak time.

the issue of interference among units of gear as a function of the spacing between traps needs to be carefully considered (e.g. Sinoda and Kobayasi, 1969; Williams and Hill, 1982). It is further necessary to demonstrate the relationship between the proposed abundance index and actual abundance (e.g. Miller, 1975, 1978; Yamane and Itaka, 1985; Miller and Hunte, 1987; Recksiek *et al.*, 1991) in calibration studies. Finally, variation in the catchability coefficient as a function of environmental factors must be considered (e.g. McLeese and Wilder, 1958; Paloheimo, 1963; Morgan, 1974). Given the large number of potentially interacting factors that can affect trap catches, we concur with Miller (1990) that trap-based measures of abundance should be based on controlled fishing experiments rather than commercial fishing operations.

We have contrasted a generalized version of the Munro model with an extension of the Gulland–Beverton–Holt model to allow for escapement. We note however, that the maximum catch (C*) often cannot be defined unambiguously for traps, limiting

the general utility of the Gulland–Beverton–Holt model for trap data. Yamane and Itaka (1985) defined the maximum catch as the volume of the trap divided by the space occupied by an individual. A trap clearly has a maximum physical holding capacity. However, it is unlikely to be realized because of behavioral interactions of animals inside and outside the trap and other factors (Miller, 1990). However, Hancock and Simpson, 1962, and Hancock, 1963, report that traps for whelks are often filled to capacity and High and Worlund, 1979, note that king crab traps are sometimes completely filled. We further note that although a trap may, in principle, be filled to apparent capacity, this limit will depend on the size composition of the catch and other factors and will not represent a finite number of individuals which can be consistently specified. Von Brandt (1984) described primitive eel traps used in artisanal fisheries consisting of cylindrical compartments (e.g. sections of bamboo) joined together. Here, the number of compartments in a unit could be used to define C* (assuming multiple occupancy of a
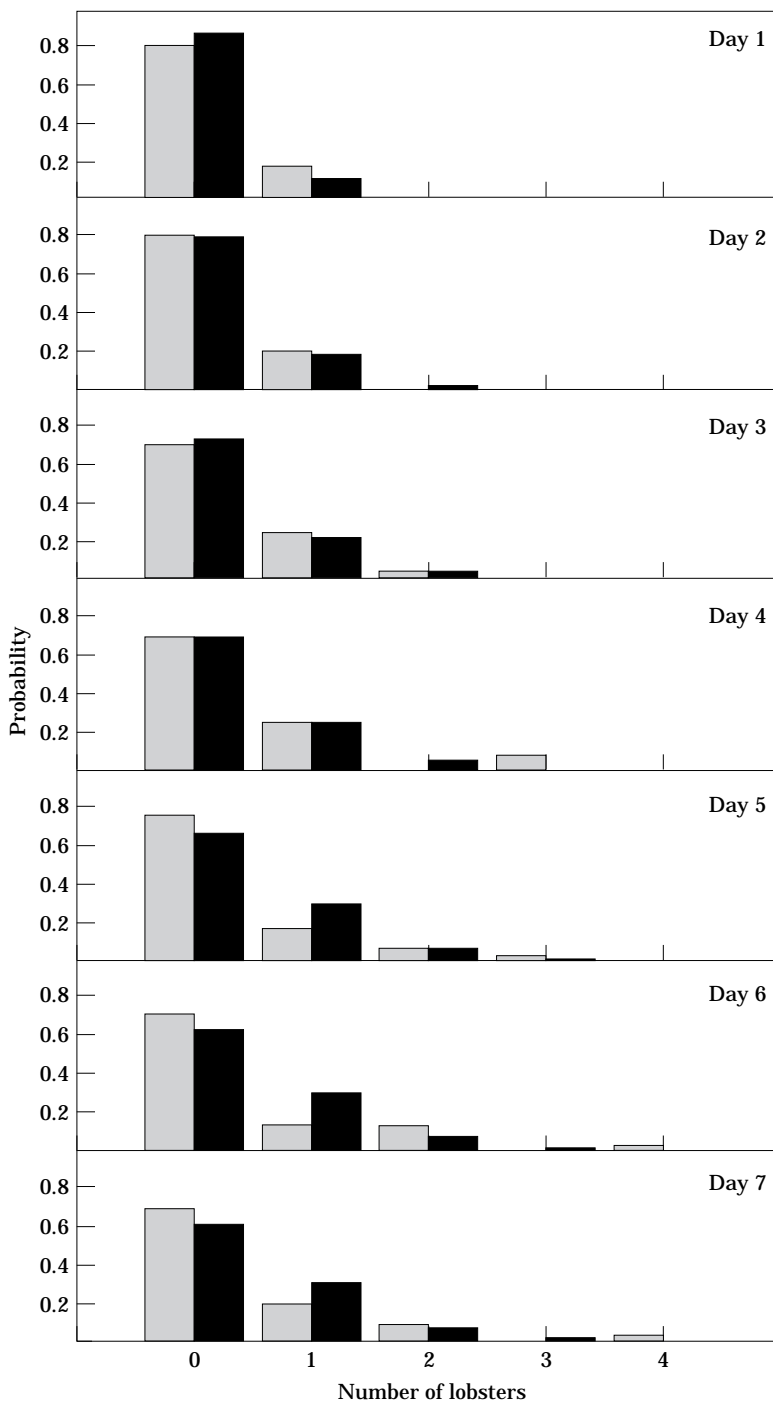
Figure 6. Observed (shaded bars) and predicted (solid bars) probability distribution of catch levels American lobster in Long Island Sound (Auster, 1985) at immersion times of up to seven days in experimental fishing operations during September–October 1982.

compartment does not occur). We suggest that unless C^* can be readily defined for a trap as in the above example, that alternative models be considered.

Few published studies to date have provided information on the probability distribution of the number of individuals per trap. Williams and Hill (1982) examined

catch frequency distributions and variance to mean ratios for the portunid crab *Scylla serrata*. The variance/mean ratios were significantly less than one, suggesting a non-random distribution of individuals per trap. The variance and mean are equal for the Poisson distribution (see Stochastic models) and a variance/mean ratio of one indicates a random distribution. Williams and Hill (1982) noted that the presence of a crab in a trap reduced the probability of additional entries. Addison (1995) reported similar results for the European lobster, *H. gammarus*; the variance was consistently less than the mean in these studies although the null Poisson distribution could be rejected for only one case. Consideration of the catch distribution and its mean and variance provides important additional diagnostic information on the underlying processes affecting trap catches. The expected probability distribution for the stochastic version of the Munro model is Poisson which provides a useful point of comparison with the observations of Williams and Hill (1982) and Addison (1995). Although it does not appear to be possible to obtain closed form solutions for the PDF of the generalized Munro model ($m \neq 0$), numerical solutions can be obtained for a given set of initial conditions and these can be compared with empirical observations.

We have not included the effects of interspecific interactions (e.g. Richards *et al.*, 1982; Addison, 1995) or intraspecific interactions among size classes (Smith and Jamieson, 1989) in the development of trap models. In most stationary gear fisheries, several species may be caught by the gear, and there may be competitive interactions that influence the capture process. Richards *et al.* (1982) showed that the catch rates of crabs (*Cancer* spp.) are reduced in traps stocked with lobsters (*H. americanus*) but not the converse. Addison (1995) noted that traps stocked with *H. gammarus* caught significantly fewer crabs (*C. pagurus*). It is clear that a trap-based model for *Cancer* spp. would require explicit consideration of lobster catch levels. Castro and DeAlteris (1990) demonstrated that traps stocked with *Callinectes toxotes* caught significantly fewer conspecifics but no significant interspecific interactions with its congener *C. arcuatus* were noted in reciprocal stocking experiments. Smith and Jamieson developed a model incorporating size-specific intraspecific interactions for the Dungeness crab (*C. magister*). Extensions of the models described in this paper would be necessary to account for inter- and intraspecific interactions but would not present any conceptual difficulties.

These considerations highlight the importance of a detailed understanding of the ethology of the target species in stationary gear fisheries. Catch rates in trawl fisheries depend considerably on the behavior of fishermen. In contrast, factors affecting the behavior of the target species dominate catch rates in traps and other forms of stationary gear. A refined understanding of these factors is requisite for interpreting catch rates in fixed gear fisheries.

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