

An Approach to Modeling Crustacean Egg-Bearing Fractions as a Function of Size and Season

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We present an approach to the analysis of crustacean egg production ogives with emphasis on detecting seasonal trends. The relationship between the proportion of gravid females (by size) and season is a prerequisite to the estimation of egg production potentials of populations. The basic method consists of relating, for each sample, the proportion of berried females with their size through a three-parameter logistic function where the asymptote may be less than 1. We then provide guidance for detecting seasonal trends in the estimates of the parameters for the individual samples. This is accomplished by restricting the basic model such that some parameters are considered to be either fixed for all samples or as simple functions of time or environmental variables such as temperature. Parameter estimates are obtained via maximum likelihood methods, and comparisons between alternative models are presented graphically and using likelihood ratio tests. We illustrate the approach and its application with data for a tropical shrimp, *Penaeus esculentus*, from northern Australia.

Nous présentons une approche pour l'analyse des enveloppes d'oeufs de crustacés qui insiste sur la détection des tendances saisonnières. Le rapport entre la proportion de femelles gravides (par taille) et la saison est un prérequis pour l'évaluation du potentiel de production d'oeufs des populations. La méthode de base est basée sur l'établissement de rapports, pour chaque échantillon, entre la proportion des femelles porteuses d'oeufs avec leur taille grâce à une fonction logistique à trois paramètres dont l'asymptote peut être inférieure à un. Nous donnons ensuite des conseils permettant de déceler les tendances saisonnières dans les évaluations des paramètres d'échantillons individuels. On y arrive en restreignant le modèle de base de façon à ce que certains paramètres soient considérés comme étant soit fixes pour tous les échantillons, ou soit de simples fonctions du temps de variables environnementales comme la température. Des évaluations de paramètres sont obtenues par la méthode de la vraisemblance maximum et des comparaisons entre plusieurs modèles possibles sont présentées graphiquement et utilisent des tests de rapports de ressemblance. Nous illustrons cette approche et son application avec des données obtenues pour une crevette tropicale, *Penaeus esculentus*, provenant du nord de l'Australie.

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Determination of an individual's average egg production is essential to obtain estimates of the reproductive potential of a population. Physiologically, a crustacean's production of eggs at any given time is the result of numerous complex interactions between internal and external factors. Among the internal factors are size (age), biochemical and metabolic changes, and hormonal factors. Environmental factors may include temperature, light, salinity, and food (Sastry 1983).

In modeling egg production at the population level for stock assessment purposes, it is often useful to calculate the reproductive potential of every size class in the population separately (see Campbell and Robinson 1983; Fogarty and Idoine 1988; Cobb and Caddy 1989). For tropical and subtropical species that spawn more than once annually, it is particularly important to consider seasonal changes in spawning frequency. For instance, the average number of eggs produced by females of size x at time t , E_{xt} , can be modeled as

$$(1) E_{xt} = N_{xt} B_{xt} G_{xt}$$

where N_{xt} = number of females of size x present at time t , B_{xt}

= fraction of females of size x that are carrying eggs at time t (berried females), and G_{xt} = number of eggs produced by a female of length x in each egg batch (fecundity).

Typically, N_{xt} can be obtained from research surveys or fishery-dependent data (e.g. via virtual population analysis), or it may simply be a variable in a simulation model. Given samples of individual egg counts and size measurements, knowledge about the form of and estimation of the relevant parameters in G_{xt} can be straightforward. For many decapods, fecundity is a linear or exponential function of body length.

In contrast, knowledge about the form of the function relating berried fractions with size and season may not be obvious. Ideally, the data used to postulate an appropriate empirical relationship should provide information on two aspects: (a) the proportion of physiologically mature animals (defined here as those capable of producing viable gametes) and (b) the proportion of these that are actually producing eggs at a given time.

Reproductive maturity is generally a nonlinear function of size (Sastry 1983; Hartnoll 1985; Wenner et al. 1985). In species that extrude eggs only once during the course of a brief

reproductive season, a maturity–size relationship can be attained if an egg production ogive occurs during the reproductive season. A plot of proportion of berried females in each size class typically results in an S-shaped relationship with an asymptote approaching 1.0 for the largest sizes (see Wenner et al. 1974). Problems may be encountered, however, with some species in which not all physiologically mature females actually extrude eggs. In species that lay eggs several times during a longer reproductive season, the relationship between maturity and size cannot be estimated in the same fashion because not all mature females will be ovigerous at all times. Plots of the egg production ogives will also be sigmoid, but the observed asymptotes will differ from 1.0, depending on the time at which the samples are taken.

In this study we propose a simple approach to model berried fractions as a function of size and season. The general model assumes that egg production ogives obtained during sequential samples are independent of each other. We also present a maximum likelihood method to estimate the parameters of such a model and illustrate its application with data for a tropical shrimp, *Penaeus esculentus* (Haswell, 1879), in Torres Strait, Australia.

Model

Consider a sample taken during the course of a brief time period (e.g. 1 mo or less) in which a large number of females are measured and the presence or absence of eggs in each individual is recorded. The fraction berried in each size, B_{xt} , is estimated by

$$\frac{r_{xt}}{N_{xt}}$$

where r is the number of females with eggs and N is the total number of females. Considering the binomial nature of the data (i.e. eggs are either present or absent in an individual), the probability distribution for the fraction berried in each length group is (Welch and Foucher 1988; Schnute and Richards 1990):

$$(2) \quad \Pr(B_{xt}) = \binom{N_{xt}}{r_{xt}} (B_{xt})^{r_{xt}} (1 - B_{xt})^{N_{xt} - r_{xt}}$$

The likelihood associated with the sample is the product of the probability distributions at each length class. Given that individuals are measured in lengths indexed 1 to M , the likelihood is

$$(3) \quad \Lambda = \prod_{x=1}^M \Pr(B_{xt})$$

We propose the use of a simple, three-parameter sigmoid function to model changes in the proportion berried as a function of x (and also as a function of t in the next section):

$$(4) \quad B_{xt} = \frac{C_t}{1 + e^{(a_t - b_t x)}}$$

Disregarding the numerator in equation (4), this is a simple logistic equation that is commonly employed to study maturity as a function of size in finfish and crustaceans. The parameter C_t ($0 \leq C_t \leq 1$) allows for the maximum fraction of berried females to be less than 1. Note that other equations such as a

modified logistic (Welch and Foucher 1988), a cumulative normal (Wenner et al. 1974), or a function of the hyperbolic tangent (Polovina 1989) can be used instead. Ratkowsky (1983) presented a comparison between the estimation properties of the parameters in equation (4) and other parameterizations of the logistic curve.

For a given sample, the parameters a_t , b_t , and C_t can be estimated by finding the values that maximize the logarithm of the likelihood function (from equations (3) and (4)):

$$(5) \quad \ln(\Lambda) = \sum_{x=1}^M \ln \binom{N_{xt}}{r_{xt}} + r_{xt} \ln \left(\frac{C_t}{1 + e^{(a_t - b_t x)}} \right) + (N_{xt} - r_{xt}) \ln \left(1 - \frac{C_t}{1 + e^{(a_t - b_t x)}} \right)$$

The binomial coefficient, the first term in the right-hand side of equation (5), can be ignored because its value is independent of the parameters a_t , b_t , and C_t . Estimates of the parameter values that maximize the log-likelihood function can be obtained with a numerical search algorithm. In the examples below, we used the implementation of the simplex search of Nelder and Mead (1965) given in Press et al. (1987). There are a number of ways to derive variance estimates and confidence regions for the parameter estimates (Kendall and Stuart 1973; Seber and Wild 1989). In this study, we used the inverse of the large sample information matrix, evaluated at the maximum likelihood estimates, to approximate the variance–covariance matrix of the parameter estimates.

Extensions of the model to cases in which egg production ogives are obtained for S time periods are straightforward. The obvious first choice involves the use of equation (5) to estimate three parameters independently for each sample. From a modeling point of view, it may not be desirable to require $3 \cdot S$ parameters to model the fractions of berried females during S time periods. It is, however, useful to follow this approach as a first step because plots of the parameter estimates over time may reveal a well-defined seasonal behavior.

Following such an exploratory analysis, further restrictions can be imposed on the simple model to reduce the number of parameters. For instance, one possibility is that the location and curvature of the logistic function (given by parameters a and b) remain relatively unchanged while the asymptote varies with time. Equation (4) becomes

$$(6) \quad B_{xt} = \frac{C_t}{1 + e^{(a - b x)}}$$

and the likelihood function is given by

$$(7) \quad \Lambda = \prod_{t=1}^S \prod_{x=1}^M \Pr(B_{xt})$$

In this case, a total of $S + 2$ parameters are estimated: one C_t for every sample plus one a and one b . Note that while in the previous model the parameters can be estimated independently for each sample, the parameters in equation (7) must be estimated simultaneously. More general formulations, requiring the estimation of more parameters, could also be hypothesized by specifying time-specific a 's or b 's.

The adequacy of a restricted model can be assessed by plotting the predicted functions against the observed berried percentages for each sample. Likelihood ratio tests (Seber and Wild 1989) can also be used for this purpose. If the analyses suggest

TABLE 1. Sample sizes (N) for the *Penaeus esculentus* data used, and results of likelihood ratio tests between fits of two-parameter (asymptote = 1.0) and three-parameter (asymptote estimated) logistic functions; $\log(\Lambda)_3$ and $\log(\Lambda)_2$ are the values of the log-likelihood function for the two fits, respectively. Values of the test statistic ($\chi^2 = 2[\log(\Lambda)_2 - \log(\Lambda)_3]$) greater than 3.84 indicate that the varying-asymptote model is preferable at the 5% level.

Month	N	$\log(\Lambda)_3$	$\log(\Lambda)_2$	χ^2
Jan. 1986	291	-154.36	-155.38	2.03
Feb. 1986	547	-246.58	-257.75	22.34
Mar. 1986	400	-232.52	-236.62	8.20
Apr. 1986	535	-235.27	-236.93	3.31
May 1986	342	-177.21	-181.09	7.76
June 1986	407	-139.73	-147.33	15.20
July 1986	104	-55.32	-57.05	3.46
Aug. 1986	282	-137.26	-137.48	0.44
Sept. 1986	85	-35.28	-36.15	1.75
Oct. 1986	173	-89.43	-92.17	5.49
Nov. 1986	236	-123.92	-134.41	20.99
Dec. 1986	303	-140.26	-145.02	9.51
Jan. 1987	352	-172.20	-179.36	14.33
Feb. 1987	558	-206.64	-226.19	39.11
Mar. 1987	478	-122.29	-122.29	0.00
Apr. 1987	269	-40.00	-40.00	0.00
May 1987	2507	-1070.03	-1077.49	14.90
June 1987	990	-398.90	-401.21	4.63
July 1987	239	-121.82	-123.47	3.30
Aug. 1987	167	-87.15	-87.34	0.38
Oct. 1987	418	-236.36	-252.08	31.43
Nov. 1987	310	-163.41	-178.23	29.64
Dec. 1987	450	-219.00	-247.20	56.40
Jan. 1988	674	-301.56	-321.37	39.61
Feb. 1988	790	-400.64	-414.72	28.16
Apr. 1988	650	-268.06	-270.81	5.49
June 1988	353	-50.07	-51.33	2.53
Sept. 1988	221	-78.09	-81.43	6.66
Oct. 1988	373	-203.46	-209.56	12.19
Nov. 1988	272	-148.66	-148.73	0.15
Jan. 1989	491	-153.84	-166.70	25.72
Feb. 1989	736	-144.43	-156.57	24.27
Mar. 1989	404	-150.87	-154.16	6.59
Apr. 1989	843	-380.20	-380.31	0.21
May 1989	452	-217.55	-217.78	0.45
June 1989	369	-145.08	-147.76	5.35

that the model given by equation (6) is adequate, it is possible to further simplify the model to fewer than $S + 2$ parameters. For instance, if temperature data or other relevant environmental indices are available, a plot of C_t against these other data may reveal the presence of a linear or nonlinear relationship. Thus, if a second-degree polynomial seems appropriate, the C_t in equation (6) could be substituted by $(c_0 + c_1 T + c_2 T^2)$ where T denotes the variable of interest (such as temperature). In this case, only five parameters would require estimation ($c_0, c_1, c_2, a,$ and b), regardless of the number of samples.

Seasonal trends in C_t could be dealt with in a number of different ways. For instance, it may be reasonable to assume that C_t will vary between months but remain constant from year to year for any particular month. This would entail estimating 12 C_t 's or one for each month of the year. Because the limited number of years of data restrict our ability to obtain consistent estimates of monthly C_t 's, this particular approach has not been adopted. In this study, the annual peaks and troughs in egg

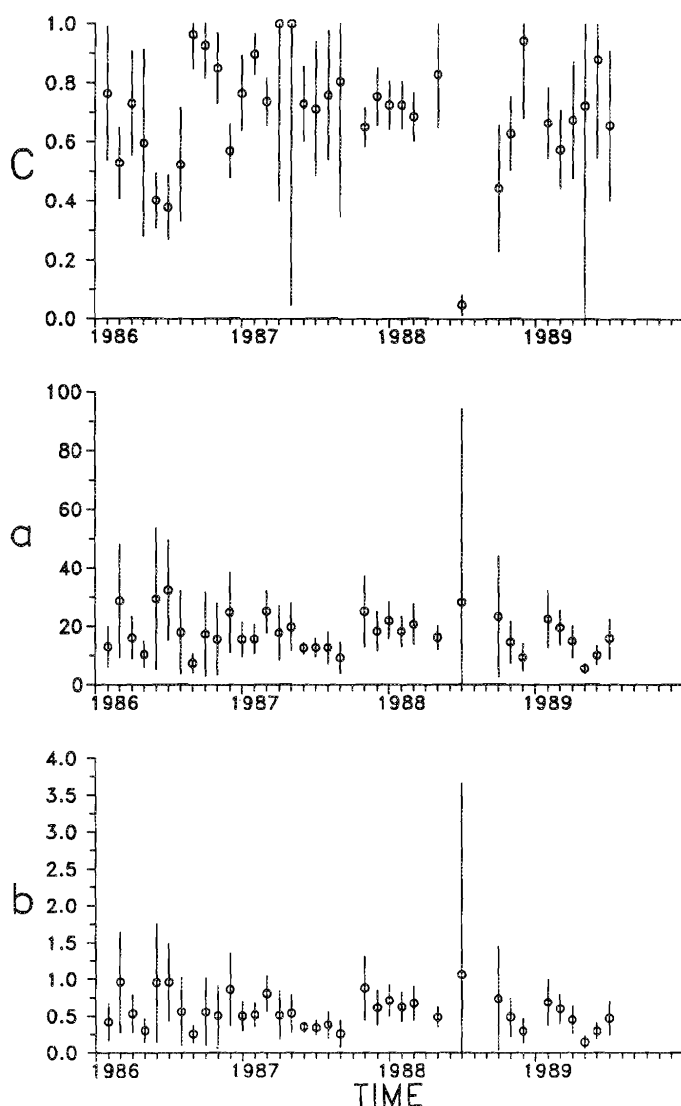


FIG. 1. Monthly trends in the estimates of the parameters $C_t, a_t,$ and b_t (equation (4)) fitted to the 36 samples of *Penaeus esculentus* data. The vertical bars represent approximate 95% confidence limits.

production potential appear to be sinusoidal in nature. A useful model for the asymptote is thus

$$(8) \quad C_t = d_0 + d_1 \cos\left(2\pi \frac{t}{12}\right) + d_2 \sin\left(2\pi \frac{t}{12}\right)$$

where t takes on the sequential values for the months when sampling took place starting at $t = 1$. Similarly, numerous other models could be postulated where the parameters in the equation relating egg-bearing fractions to size are either fixed, sample specific, or functions of environmental variables. Examples are given below to illustrate the application of some of those already mentioned.

Data and Biological Background

Egg production data for *Penaeus esculentus* were available for 36 monthly samples taken near Warrior Reef in Torres Strait, northern Australia, between January 1986 and June 1989. Each female was measured to the nearest millimetre (car-

apace length) and those with ovary stages III and IV (Tuma 1967) were considered ripe. Monthly sample sizes averaged 474 females (Table 1), with carapace lengths ranging between 15 and 52 mm.

In *Penaeus esculentus*, a single spawning usually occurs after fertilization and before the next molt. At the population level, molting and spawning appear to take place asynchronously throughout the year and at a nearly constant level throughout each lunar month (Crococ 1985). Crococ (1985) suggested that in order to obtain a reliable index of spawning frequency, the duration of the ripe stage should be shorter than the period of sampling. Our monthly data meet this criterion because the duration of ripe stages is reported to be approximately 66% of the mean intermolt period of 28 d. If our samples had represented shorter time periods (e.g. days), then biased estimates of spawning activity would be more likely.

Results

Estimates of the parameters in equation (4) for each of the 36 monthly data sets followed the trends in the data closely (Fig. 1 and 2). Estimates of the asymptote, C_i , ranged from a

low of 0.046 to a high of 1.0 (Fig. 1). Estimates of parameters a_i and b_i were also variable (Fig. 1) and highly correlated ($r_{ab} = 0.981$ for the 36 samples).

We tested the possibility that a conventional two-parameter model would adequately describe the data by fixing C_i to a value of 1.0 for every sample, instead of estimating it, and comparing the resulting fits with those of equation (4) (Fig. 1) via likelihood ratio tests. The null hypothesis that $C_i = 1.0$ was rejected in 23 (64%) of the samples (Table 1). Of the remaining 13 samples, eight had estimates of C_i whose 95% confidence limits included 1.0 (see Fig. 1). Thus, it is expected that the null hypothesis would fail to be rejected in these eight samples. Fisher's test for combining independent significance levels (Fisher 1970, p. 99–101) indicated that the probability of the aggregate of the 36 tests in Table 1 occurring by chance is less than 0.0001 ($\chi^2_{72} = 542.79$). Overall, it is apparent then that the three-parameter model fits the data better than does the two-parameter logistic function with a fixed asymptote equal to 1.

We then examined the possibility of reducing the number of parameters necessary to model egg production potential for the 36 samples. We did this by estimating an individual asymptote for each sample and common a and b values for all samples

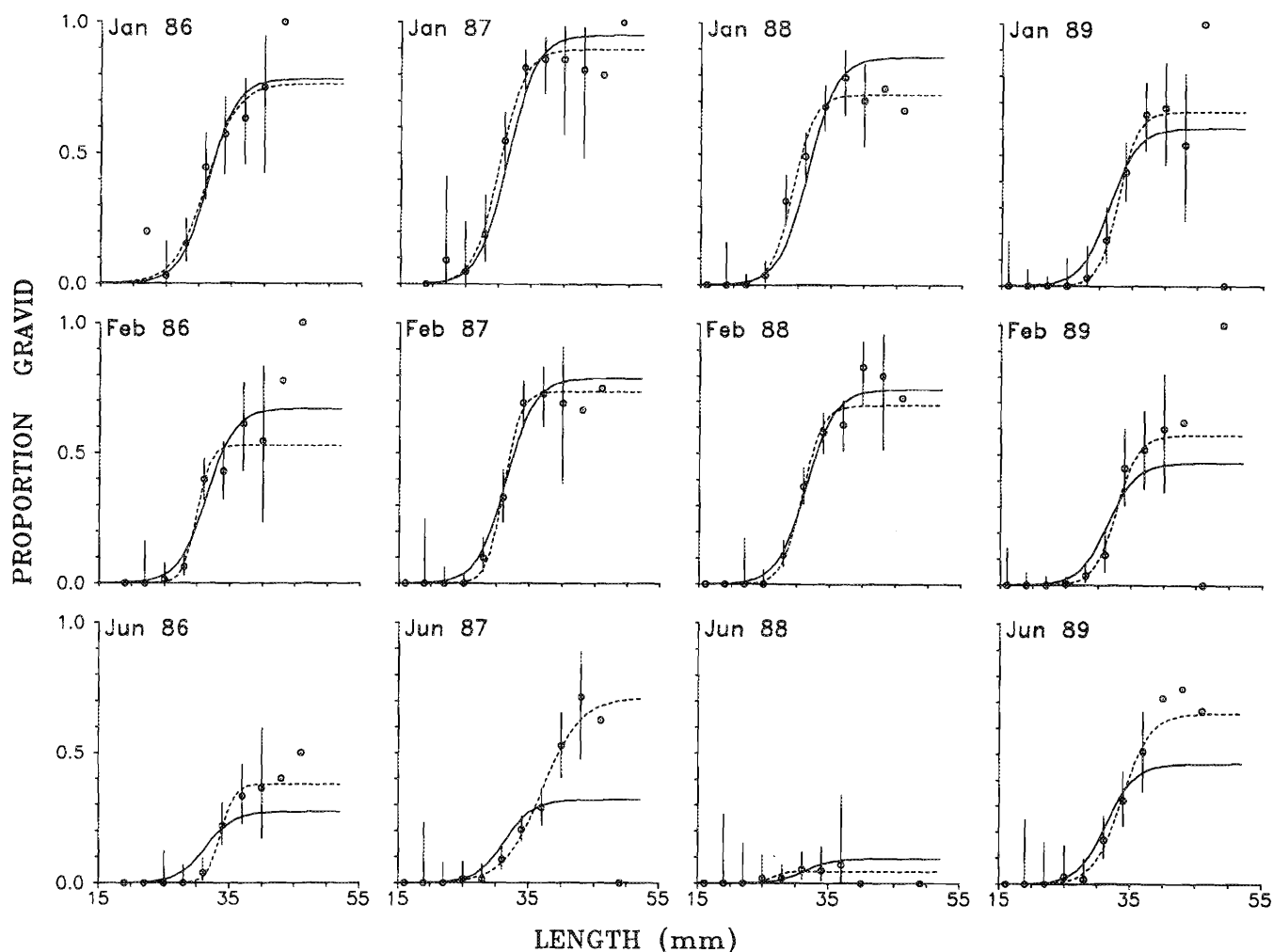


FIG. 2. Observed proportions of egg-bearing females (circles) and fitted equations (lines) for 12 samples of *Penaeus esculentus*. For clarity, the raw data were grouped into 3-mm intervals (ungrouped data were used for parameter estimation). Fractions made up of 10 or more observations include approximate 95% binomial confidence limits (vertical lines) computed with the Paulson–Takeuchi method described by Fujino (1980). The broken lines represent the individual fits of equation (4) to the samples. The solid lines represent the fit of the more constrained model (equation (6)) in which the asymptote varies but the curvature parameters remain fixed and are estimated with data from all available samples.

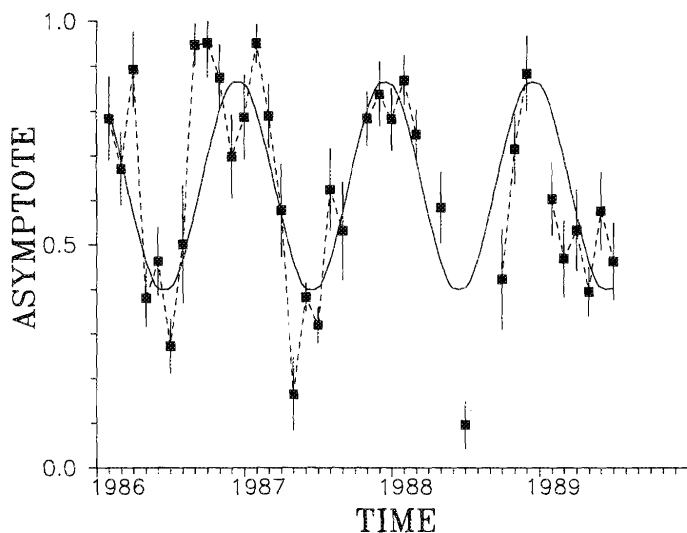


FIG. 3. Estimates of the asymptote for two models of egg-bearing fractions fitted to 36 samples of *Penaeus esculentus*. The broken line and solid squares show the estimates of the asymptote from the model given by equation (6), in which one value is obtained for every sample (vertical bars are approximate 95% confidence limits). The solid line represents the fit of a more constrained model (equation (8)) in which the asymptote is a sinusoidal function of time.

(i.e. 38 parameters were estimated with equation (6)). Trends in the estimates of the asymptote are shown in Fig. 3. The estimates of a and b were 14.56 and 0.463, with variances of 0.196 and 0.0002, respectively. A likelihood ratio test indicated that the fit of equation (4) to the individual monthly samples (108 parameters, $\log(\Lambda) = -7247.45$) may be statistically preferable to that of the more constrained model given by equation (6) (38 parameters, $\log(\Lambda) = -7499.44$) (likelihood ratio statistic $\chi^2_{72} = 503.98$, $P < 0.0001$).

Upon visual examination, the fit of the constrained model appeared to be reasonable for most samples (a subset of the fits is shown in Fig. 2). However, for the samples taken during August 1986 and January 1988, the constrained model tended to underestimate berried percentages for the smaller sizes and to overestimate them for the larger sizes. The opposite occurred with the samples taken in June 1986, March 1987, May 1987, and June 1987. In particular, the results for these last two samples were poor considering that they contained the largest number of observations (2507 and 990, respectively).

While the observed monthly variability is more accurately described by individual fits of equation (4) to each sample, equation (6) may be adequate to represent the general seasonal trends in the observed data. The latter has intuitive appeal because the only sample-specific parameter in it is the asymptote. Thus, variations in the estimated values of this asymptote can be thought of as seasonal changes in the egg production potential of the population. (Note that changes in actual egg production must also take into consideration size structure and population numbers.)

We also estimated the parameters of the sinusoidal model for the asymptote given by equation (8). The estimates of a and b were 14.64 and 0.465, respectively, values that are similar to those obtained with the 38-parameter model (equation (6)). In general, the asymptote values predicted by the sinusoidal function coincided well with the estimates from equation (6), although the simple function failed to predict the low egg pro-

duction potentials typical of winter months such as June 1988 (Fig. 2 and 3).

Discussion

The conventional method of using annual samples and assuming the egg-bearing fractions are asymptotic to unity may be sufficient for species with brief reproductive seasons. The approach we have presented requires more data and is computationally intensive but is more useful for species that reproduce throughout the year and exhibit within-year fluctuations in reproductive potential. Use of a model with a seasonal component can provide insight into important management questions. For instance, incorporation of a relationship for monthly egg-bearing fractions into an egg-per-recruit model can aid in determining the optimum time to set seasonal closures for a fishery when the goal is to enhance the reproductive output of a stock.

The basic model (equation (4)) is most useful when one desires to explain accurately the observed variability in the proportion of berried females by size, for a given sample. When modeling equilibrium egg production potential, this model is undesirable because it requires too many parameters. In contrast, the more restricted models (e.g. equation (6) and (8)) sacrifice precision but provide estimates that are more useful in an equilibrium modeling framework. To illustrate this idea, consider the examples above where equations (4) and (8) were fitted to the 36 monthly samples of egg-bearing females. Given additional data for fecundity relationships and the size frequency distributions every month, the monthly magnitudes of egg production can be estimated with equation (1). These values could then be used in conjunction with recruitment estimates to examine the presence of a stock-recruitment relationship. The berried proportions used in such a study should preferably be the sample-specific estimates (equation (4)). In contrast, estimates of the sinusoidal function (equation (8)) would be preferable for a simulation of equilibrium egg production per recruit because they consist of fewer parameters and predict a long-term relationship. Currently, this approach may have limited applicability because the large number of samples necessary to capture seasonal fluctuations are not typically available for most crustacean fisheries. However, quantifying reproductive data is a relatively simple task with some species and such measurements can be incorporated into a routine sampling program.

As we have illustrated with some examples, other models that fall between the two extremes in the previous paragraph are straightforward to formulate. The parameters could be treated as constants or as functions of time or of some environmental variable. In any case, the applicability of the selected model would be largely dictated by its intended purpose.

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