The daily fecundity reduction method: a new procedure for estimating adult fish biomass

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A new method was developed for estimating adult fish biomass from the daily decline in reproductive potential of the population and the numbers of planktonic eggs. Decline in reproductive potential was estimated from the product of the daily decline in the standing stock of advanced oocytes in ovaries and the daily decline in the numbers of females with reproductively active ovaries. Daily production of planktonic eggs was estimated from the number of eggs in quantitative oblique plankton tows. The method is restricted to fishes in which the potential annual fecundity becomes fixed prior to the onset of the spawning season, that is, fishes with determinate annual fecundity. The method was applied to data for *Microstomus pacificus*, commonly known as Dover sole, a pleuronectid flatfish of the upper continental shelf (200–1500 m) of the west coast of North America.

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Introduction

The annual egg production method (Saville, 1964) has been widely used for estimating the biomass of adult fish from the numbers of planktonic eggs. Parker (1980) showed how a daily egg production method could also be used to estimate adult fish biomass. Subsequently, the daily egg production method has been used to estimate the biomass of sardines and anchovies (Santander *et al.*, 1984; Lasker, 1985; Wolf and Smith, 1986).

The principal difference between the daily and annual methods is in the way fecundity is estimated. In the annual method, one measures the standing stock of advanced yolked oocytes in the ovaries of females taken prior to spawning season. This estimate of fecundity is considered to be equivalent to the potential annual fecundity of the stock. This condition is called determinate annual fecundity (Hunter *et al.*, 1985; Horwood and Greer Walker, 1990), because the annual fecundity is assumed to be fixed prior to the onset of spawning. In contrast, the daily method uses daily fecundity which is the product of spawning frequency and the number of eggs released per spawning (batch fecundity). The daily method may be preferable because less cruise time is required but may be costly because estimation of spawning frequency of the population requires either laboratory calibration or a series of samples of the spawners taken over 24 hours at sea. In addition, it may be more difficult to obtain representative samples of the adult population during the spawning season than before it begins. Thus, adult sampling from research vessels may be required for the daily method while for the annual method samples drawn from the commercial fishery may suffice.

The objective of this paper is to describe the daily fecundity reduction method (DFRM), a new method for estimating adult fish biomass from the numbers of planktonic eggs. This method is a daily method designed for fish of determinate annual fecundity and involves measuring the daily decline in the standing stock of advanced yolked oocytes (total fecundity) and the daily decline in numbers of females with reproductively active ovaries during a part of the spawning season. Fish biomass is estimated by linking the decline in the two reproductive variables (fecundity and ovarian activity) to the production of planktonic eggs. The chief advantage of the DFRM is that estimates of spawning frequency are not required. The DFRM is inappropriate for fishes with indeterminate annual fecundity, such as anchovy and sardine (Hunter

et al., 1985), because a key assumption underlying the model is that no new advanced oocytes are recruited to the ovary during the survey period. It may also be inappropriate to apply the DFRM to fishes having extensive spawning migrations since the DFRM requires representative samples of both spawning and spent females during the spawning season.

Material and methods

The general form of the model for the DFRM is:

$$B = \frac{P_o \times A}{(R/W) \times D_t \times 10^6} = \frac{P_o \times A}{K},\qquad (1)$$

with approximate coefficient of variation (CV) of estimate of biomass

$$CV(B) = [CV^2(P_o) + CV^2(K) - 2COV(P_oK)/(P_oK)]^{0.5}, \quad (2)$$

where B is the biomass (mt) for area A.

P_o is the daily production of eggs per 10 m^2 sea surface area estimated from egg abundance adjusted for their development time and mortality during incubation.

A is the area size in 10 m^2 of the survey area. The quantity $K = (R/W) \times D_t \times 10^6$ in the denominator of equation (1) is daily population fecundity in units of eggs mt^{-1} day^{-1}, where R is the female fraction of the population by weight, W is the average female weight (g), D_t is the daily fecundity per female at Julian day t and is expressed as:

$$D_t = d(E \times G)/dt = E_t \, dG/dt + G_t \, dE/dt.$$

The quantity 10^6 converts grams to metric tons, E is the number of advanced yolked oocytes present in the ovary (total fecundity), G is the fraction of females that have ovaries containing advanced yolked oocytes (fraction of females with active ovaries), t is the elapsed time in days over which changes in G and E are monitored.

In the proposed model we use the two variables, G (fraction of females with active ovaries) and E (total fecundity) to measure the seasonal decline in the total fecundity of the population. G is measured on-ship using gross anatomical criteria to distinguish active (advanced yolked oocytes present) from inactive ovaries (no advanced oocytes present) and E is measured in the laboratory using conventional gravimetric fecundity methods. The decline in total fecundity (E) over time measures the rate the standing stock of advanced oocytes declines as batches are spawned; females that have completely exhausted their stock of advanced oocytes are not included in this measurement. The decline in G over time estimates the rate females pass from a reproductively active to an inactive state, i.e. the rate at which females

spawn *all* of their advanced oocytes. Thus the product of the rates of change in G and E measures the daily decline in fecundity of the average female in the population (D). In short, the decline rate of E × G, d(E × G)/dt measures the daily decline in fecundity in the average female. The daily decline in the average female fecundity is converted to the daily decline in the fecundity of the population (K) using the ratio R/W, where R is the weight of female Dover sole (regardless of the level of ovarian activity) divided by the weight of male, female and immature fish of undetermined sex, and W is the average female weight in the sample. Both R and W are estimated for random samples of the trawl catch.

We assume that during a survey ovaries of the females in the population only change from active to inactive states, and not the reverse. Thus the survey must begin after the ovaries of most of the mature females in the population have developed sufficiently to be classified as active. Since any female taken in a trawl can be included in the denominator of G (the fraction of females with active ovaries), it follows that the biomass (B) is an estimate of the total adult biomass vulnerable to our trawl which includes all adult fish and an unknown fraction of the juveniles. This differs from the daily egg production method used for anchovy (Lasker, 1985), where spawning biomass rather than total "trawlable" biomass was estimated.

As in past methods, the daily production of eggs (P_o) is estimated from their abundance adjusted for egg development rates and natural mortality (Sette, 1943; Saville, 1964; Hewitt, 1985). This requires identification and staging of eggs and knowledge of temperature-specific rates of egg development.

Both direct formulas and resampling methods (jack-knife and bootstrap methods) were used to compute estimates of parameters, and their variances. Resampling methods were used primarily for estimation of the variance of biomass, covariances of adult parameter estimates and the bias of parameter estimates (Efron, 1982; Lo *et al.*, in press).

The example

Data sources

To illustrate the method, we used data for *Microstomus pacificus*, a pleuronectid flatfish commonly known as the Dover sole on the west coast of North America (Eschmeyer *et al.*, 1983). Dover sole are an appropriate example because: they do not have extensive spawning migrations (Quirollo and Kalvass, 1987); their potential annual fecundity becomes fixed before spawning begins, that is fecundity is determinate; and they do not spawn all their advanced oocytes at once but spawn about nine batches before using up their stock of advanced oocytes

(Hunter *et al.*, in press). Hunter *et al.* conclude that determinate fecundity is indicated by four lines of evidence: (1) in mature ovaries a hiatus exists between the advanced stock of mature oocytes and smaller, less mature oocytes; (2) total fecundity declines over the spawning season; (3) total fecundity is lower in females with post-ovulatory follicles; and (4) the mean diameter of the advanced oocytes increases over the spawning season (Hunter *et al.*, in press)

In central California 86% of the spawning biomass of Dover sole occurs along the upper continental slope between 600 m and 1000 m depth and some fish occur as deep as 1500 m (Hunter *et al.*, 1990). Their eggs are pelagic and occur at the surface as well as deeper in the water column. Thus, estimation of the biomass of this stock required development of methods for taking quantitative plankton tows from 1500 m to the surface.

In our example we use fish and egg data collected during trawl and ichthyoplankton surveys conducted from 1985 to 1988 (Butler *et al.*, 1989). We combine data from these years to reconstruct 4 months of the spawning season from December through April. The survey design varied between years: in 1987 we used a line transect design; in 1988 we used a random design stratified by bathymetric depth; and in 1985 and 1986 trawls were taken opportunistically and no plankton samples were taken. The survey area in each year was the same, and extended from Point Conception to Monterey Bay, California, an area of 14 172 km^2 (Fig. 1). This area is a small fraction of the total Dover sole habitat that extends from the Bering Sea to Baja California, Mexico (Eschmeyer *et al.*, 1983). Use of these historical data required two assumptions: the timing of the spawning season and the production of eggs were similar in 1985 to 1988 and no net transport of eggs occurs across the boundaries of the survey area.

We used 25–100 Dover sole from each trawl to estimate the four adult reproductive parameters (E, G, R, W). It was necessary to post-stratify the data by bathymetric depth because adult parameters changed markedly with depth (Hunter *et al.*, 1990). Each parameter was computed for each of the following area strata: stratum 1 was an area with bottom depth $\leqslant 456$ m (249 fm), stratum 2 was 457–1004 m (250–549 fm) and stratum 3 was $\geqslant 1005$ m (550 fm).

At each station in 1987 and 1988 we sampled Dover sole eggs with an oblique bongo tow retrieved from 210 m depth, and a deep oblique bongo tow which sampled the entire water column to a maximum of 1500 m depending on bathymetric depth. We attached a conductivity–temperature–depth (CTD) sensor to the deep bongo net to record depth and water temperatures every 20 seconds. The temperature varied from 5°C near the bottom to 15°C at the sea surface.

Estimates of egg production (P_0) are based on the full water column deep bongo tows but the comparison of egg

densities between deep bongo and 210 m bongo tows allowed us to allocate the eggs taken in each deep bongo tow into an upper segment (depth < 200 m) and lower segment (depth > 200 m) of the water column. This stratification was necessary because egg development rates are a function of temperature and temperature varies with depth. We used a temperature-dependent egg development model to assign ages to staged eggs on the basis of the mid-depth temperature in the upper 200 m segment and the lower depth segment of water column. Abundance of eggs at age was used to model egg mortality curve and to estimate egg production at age zero (P_0).

Results and discussion

The daily egg production ($P_0 = 1.97/10$ m^2, CV = 0.19) was computed from a Pareto survival function, and the daily population fecundity (K = 0.28/g, CV = 0.15) was computed from a depth-stratified sampling design. The bootstrap method was used to compute the variance of each estimate (Lo *et al.*, in press).

To illustrate the magnitude of fecundity reduction, the daily decline in the standing stock of advanced yolked oocytes (total fecundity, G) and the daily decline in fraction of females with reproductively active ovaries (E) during a segment of the spawning season for stratum 2 (457–1004 m) are shown in Figures 2 and 3. In stratum 2 an active female spawns 255 eggs d^{-1} and the fraction of the females with active ovaries is reduced by 0.5% d^{-1}. For example, if 60% of females were active at the beginning of January, 45% would be active at the end of January (Fig. 2). The parameter D_t can be also estimated by $(G_t E_t - G_{t+dt} E_{t+dt})/dt$ which would provide an estimate of the average rate of decline in daily fecundity for the season. This alternate method requires G and E to be estimated simultaneously for G > 0. We believe this alternate approach is disadvantageous because the sources of variability of G and E are masked. In addition, since the true form of the decline in G with time is likely to be non-linear, the estimate of the average rate for the season provided by the alternate method may have greater bias than estimates of the instantaneous rate at time t provided by our model.

The direct estimate of Dover sole biomass using equation (1) was 9971 mt (Table 1) with a coefficient of variation of 24%. The bootstrap estimate was 8725 mt with a coefficient of variation of 36%. The CV using the bootstrap method was higher than the direct method because the bootstrap estimate of P_0 was more variable (Table 1). It appears that some upward bias may exist in the direct computation of K because the bootstrapped estimate (0.32) was higher than the direction computation (0.28). As a result, the bootstrap estimate (8725 mt) was different from one based on the direct computation (9971 mt). If the direct computation was corrected for
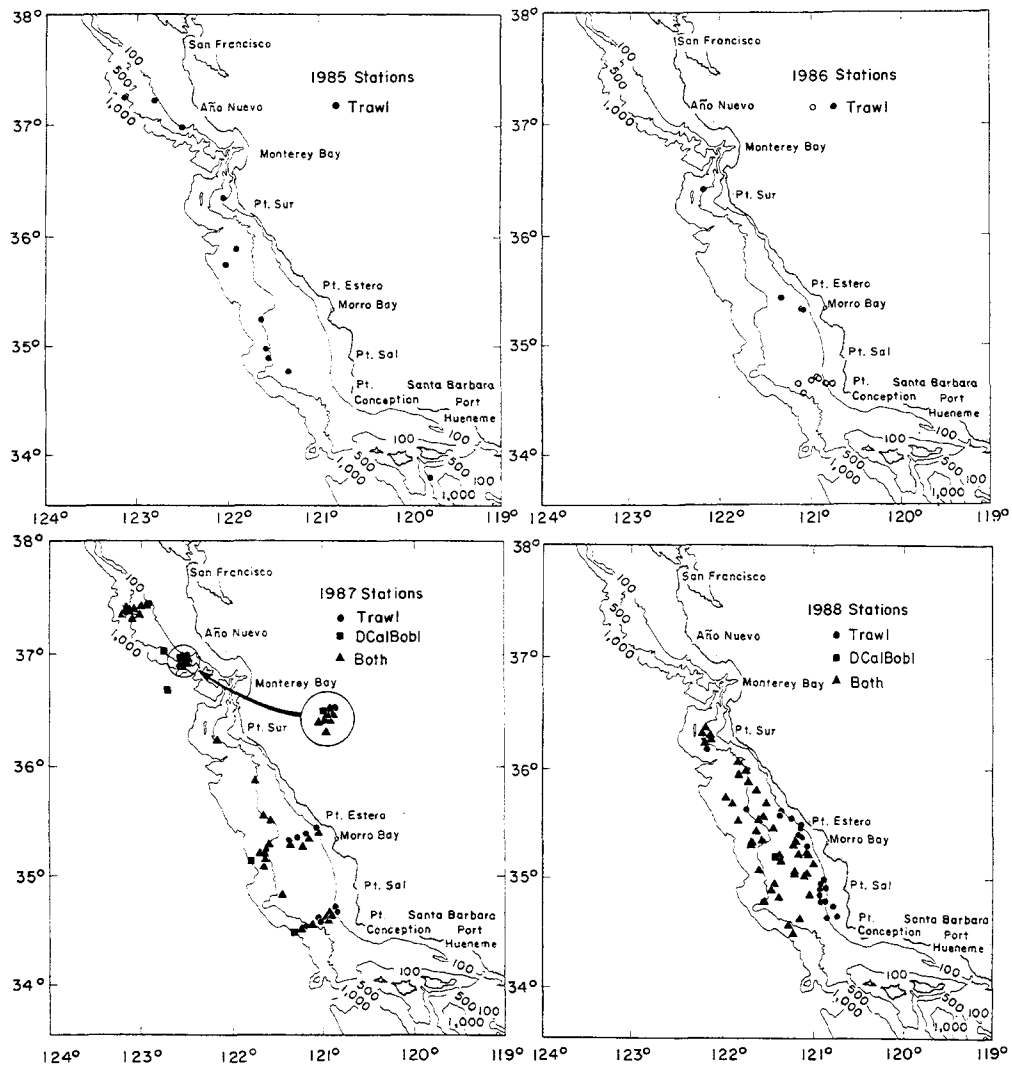
Figure 1. Survey patterns of Dover sole trawls and plankton tows in 1985–1988. In the 1986 survey open circles are stations occupied on cruise 8604, and solid circles are stations occupied on cruise 8606 (DCalBobl is deep bongo net tow).

this bias, the estimate (B_c) of biomass became 11 217 mt [$= 9971 - (8725 - 9971)$] (CV $= 0.51$) (Efron, 1982).

Abundance estimates for Dover sole in the same study area from trawl surveys range from 14 000 to 17 000 mt (Butler *et al.*, 1989). Thus, the DFRM estimate is close to the lower limit obtained by application of the swept area method to trawl catch data for the same area. Our estimates of biomass were probably too low because ichthyoplankton surveys did not extend to the offshore boundary of Dover sole eggs. Eggs were taken in the outermost stations of the survey pattern, indicating substantial offshore transport of eggs.

In addition to extending the offshore boundaries of our survey pattern, we need to improve our estimation of the ages of eggs. The temperature coefficient for incubation rates for Dover sole needs to be estimated in the laboratory. We also need to improve our method for assigning temperatures to eggs. We used the mean temperature over each of two depth ranges (depth < 200 m and depth > 200 m) to assign ages to the eggs taken in each of these ranges. This method underestimates the age of the eggs in the upper depth range since the eggs are spawned at the bottom and rise through the lower range before reaching the upper one. Although we believe the current method
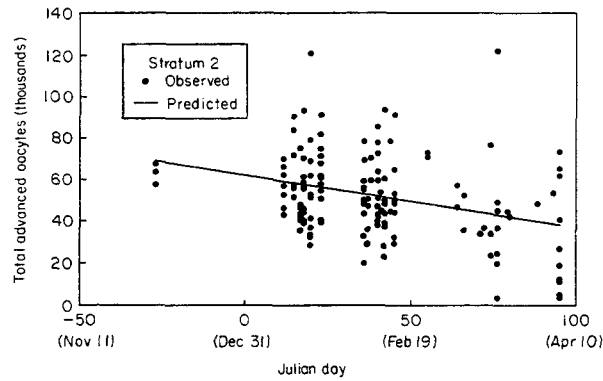
Figure 2. Decline in total advanced oocytes with time for stratum 2 (area with bottom depth 457–1004 m). Each point is one fish. Equation for the line showing the predicted value = 62 082 − 255.16 Julian day.
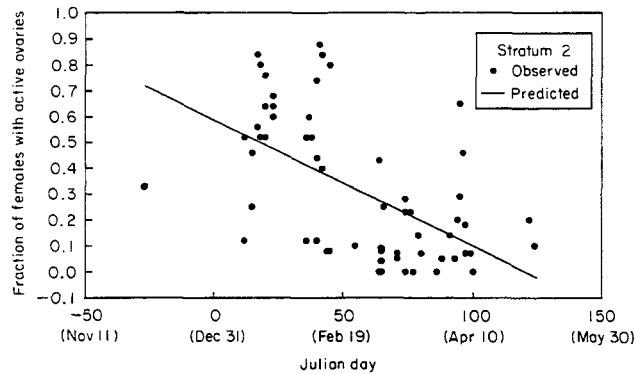

Figure 3. Decline in fraction of females with active ovaries with time for stratum 2 (area with bottom depth 457–1004 m). Each point is a trawl sample. Equation for the line showing the predicted value = 0.58 − 0.0049 Julian day.

produces only a minor bias in the estimates of biomass, a temperature-dependent, vertical transit model for eggs would be preferable.

One of the chief advantages of the DFRM over the annual method was that sampling could be done over a short survey period. The DFRM does not require plankton samples be taken throughout the season as does the annual method so it may also save cruise time. Plankton sampling need not cover as long a period as we used in our example. In the example plankton samples were taken throughout a series of cruises spanning a period of 93 days, but a shorter period would be adequate for estimating P_o. If P_o was obtained from samples taken during a short period of time, D_t can be easily computed for the mid-point of that period. On the other hand, owing to the long spawning season of the Dover sole (5–6 months), and low batch fecundity, we needed an extended period to detect a change in fecundity (E) and the fraction of females with active ovaries (G). The fraction of females

with active ovaries declines only 15% per month and consequently a long time span is needed to detect a time dependent change in this variable. Our data indicate that 50 positive trawls (trawls in which some fish are caught) over a 100 day interval would provide an estimate of the daily rate of decline of the fraction active (G) with a coefficient of variation = 0.30. On the other hand, if the 50 positive trawls were taken over 30–40 days the coefficient for elapsed time is not detectable (CV = 2.50) (Lo *et al.*, in press). In many species having determinate fecundity, spawning seasons may be much shorter than the Dover sole. In such cases, probably a change in G could be detected during a short survey period.

Despite the problems with the available data, our example indicates that the DFRM is an appropriate method for estimating the biomass of Dover sole and other species of determinate fecundity. Formal application of the method to Dover sole would require that all samples be taken in the same year, that the offshore

Table 1. Estimates of parameters associated with adult reproduction of Dover sole, egg production (P$_0$), daily egg mortality (z) and biomass estimate (B) in central California by depth stratum 1985–1988[1].

Method[3]	Depth stratum							
	0–456 (m) 0–249 (fm)		457–1004 (m) 250–549 (fm)		1005–1280 (m) 550–700 (fm)		Weighted mean[2]	
	1	2	1	2	1	2	1	2
W (g)	250.53	253.22	776.07	763.7	1056.7	1063.5	668.51	659.5
S.E.	29.81	17.36	31.11	26.13	20.49	26.3	25.06	22.24
n	38		62		19			
R	0.67	0.7	0.76	0.79	0.92	0.85	0.74	0.78
S.E.	0.033	0.023	0.031	0.023	0.053	0.07	0.025	0.02
n	38		62		16			
$D_{50} = d(E \times G)/dt$	100.38	145.93	288.60	282.93	463.52	451.13	250.82	255.84
S.E.	26.98	33.88	61.63	22.64	92.68	50.83	48.41	18.52
n	37		60		16			
$k \times 10^{-6} = (R/W) \times D_{50}$	0.27	0.40	0.28	0.30	0.40	0.36	0.28	0.32
CV	0.30	0.23	0.182	0.07	0.21	0.14	0.15	0.09
A (area, km^2)	4049		7204		2919		total = 14 172	
Mean catch (lbs) per trawl	67.39		140.14		5.2			
Weighting factor	0.21		0.78		0.01			
P$_0$/10 m^2	1.97	1.97						
S.E.	0.38	0.70						
β[4]	0.6	0.54						
S.E.	0.10	0.17						
B (mt)	9971	8725						
CV	0.24	0.37						
B$_c$ (mt)	11 217							
CV	0.51							

[1]Abbreviations are as follows: W, the average female weight (g); R, female fraction of the population by weight; E, the total fecundity for average female weight; G, the fraction of females with yolked eggs; D$_{50}$, the number of eggs spawned per female per day for t = 50 (the mid-point of survey); (R/W) × D$_{50}$, the daily population fecundity per gram; S.E., standard error; n, number of trawls. The biomass estimate (B) was computed based on equation (1). B$_c$ is the bias-corrected biomass estimate.
[2]Weighted by the product of area and mean catch of trawl.
[3]Method 1 is the direct computation from formulas described in Lo et al. (in press). The standard error (S.E.) was from non-linear regression for P$_0$, the jack-knife method for R and W, and formulas for D$_{50}$ and K given in Lo et al. (in press). The S.E. of B was from equation (2). Method 2 is the bootstrap method.
[4]β is the mortality coefficient in age dependent daily instantaneous mortality rate $z = \beta/(t + 1)$, where t is days.

boundary of the planktonic eggs be enclosed within the survey pattern and that planktonic eggs and adults be sampled contemporaneously.

Acknowledgements

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