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# A daily egg production method estimate of snapper biomass in Hauraki Gulf, New Zealand

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Snapper (*Pagrus auratus*, Sparidae) are an abundant finfish in waters off northern New Zealand and important in commercial and recreational fisheries, the largest stock being in the Hauraki Gulf. A daily egg production method (DEPM) survey was used to estimate Hauraki Gulf snapper biomass in Nov.–Dec. 1992, during the peak of the spawning season. Snapper are multiple spawners with indeterminate fecundity, and it is possible to estimate the proportion of females spawning each day in the population using trawl samples, making the DEPM appropriate for estimating biomass. Daily egg production was estimated using egg counts-at-age data from 298 plankton samples fitted to a maximum-likelihood model. Spawning proportion (the proportion of females with hydrated oocytes sampled before the onset of daily spawning), batch fecundity (counts of hydrated oocytes in ovaries) and sex ratio were estimated from trawl samples. Average fish weight was estimated from a mixture of longline market sampling, longline catch-at-sea sampling and trawl sampling. The estimated mean biomass (24 499 t, 95% confidence interval 17 994–48 650 t) was similar to that estimated from a tagging programme in the Hauraki Gulf one year after the DEPM survey. Possible sources of error and bias are discussed.



Key words: daily egg production method, snapper, *Pagrus auratus*, biomass, indeterminate fecundity, Hauraki Gulf.

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## Introduction

Snapper (*Pagrus auratus*, Sparidae) are the most abundant of the inshore demersal finfish off northern New Zealand (Francis, 1994). They occupy a variety of coastal habitats, from rocky reefs to areas of sand and soft bottom, with highest densities at depths between 15 and 60 m (Annala and Sullivan, 1996). The species sustains important recreational and commercial fisheries and aquaculture through the temperate and subtropical western Pacific, where it is also known as *P. major* in Japan and *Chrysophrys auratus* and *C. unicolor* in Australia (Paulin, 1990).

In New Zealand, snapper have had a long history of commercial exploitation and are the third highest earner of export revenue among New Zealand finfisheries (Zeldis, 1993). They are also the most popular fish for non-commercial fishers in the country (Annala and Sullivan, 1996). The largest stock of snapper in New Zealand is in the Hauraki Gulf (Fig. 1). By the mid-1980s this stock was showing signs of over-exploitation, with the fishery becoming more dependent on newly recruited year classes. Recent assessments of this stock have been based on biomass estimates from tagging programmes carried out in 1983–1984 and 1993–1994, projected forward using CPUE and recruitment indices (Annala and Sullivan, 1996). Although the tagging programmes have been successful in measuring snapper stocks, they have uncertainties over factors such as tag-induced mortality and incomplete mixing (J. R. McKenzie, NIWA, pers. comm.), and they are expensive to carry out. For these reasons, a daily egg production method (DEPM) survey was carried out in November–December 1992 in the Hauraki Gulf, to measure snapper biomass and to assess the method as an alternative or complement to tagging programmes.

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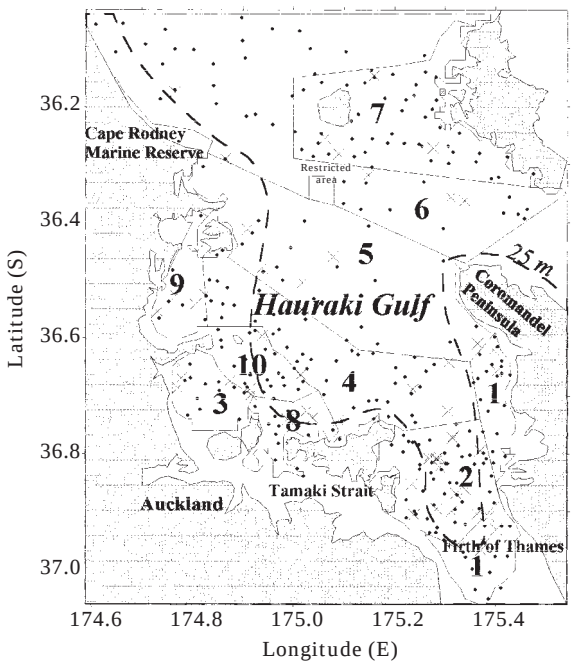


Figure 1. Location diagram of Hauraki Gulf, with place names, strata (numbered), plankton stations (dots) and trawl stations (crosses) used in the DEPM survey. Coordinates are in decimal degrees.

Zeldis (1993) discussed aspects of the reproductive biology of snapper, with respect to applying egg production methods for biomass estimation. He showed that annual fecundity in snapper is indeterminate. That is, the potential annual fecundity of a female is not fixed prior to the onset of spawning, and unyolked oocytes continue to mature and be spawned through multiple releases during the spawning season. Therefore, the annual egg production method, in which the annual planktonic egg production is divided by the annual fecundity to estimate biomass (Hunter and Lo, 1993), is inappropriate for snapper biomass estimation. The DEPM instead relies on being able to identify the average proportion of females in the population that releases a batch of eggs on a given day. Scott *et al.* (1993) and Zeldis (1993) showed that the proportion of females spawning $d^{-1}$ could be determined by sampling fish in the early morning and determining the proportion of females with oocytes in the hydrated state. Because all these fish spawn in the afternoon of the day they hydrate their oocytes, they constitute the spawners of the day, and since virtually all hydrated oocytes are ovulated, the number of hydrated oocytes in the ovaries of these fish constitutes the batch fecundity (Scott *et al.*, 1993). When batch fecundity is combined with estimates of other parameters of the daily stock fecundity, and divided into the estimate of the amount of planktonic eggs produced by the stock $d^{-1}$, it is possible to estimate the average biomass during the DEPM survey.

In this paper we describe how the DEPM was applied to snapper in the Hauraki Gulf, comment on how the resulting biomass estimate relates to a subsequent estimate derived from tagging, and discuss possible sources of error and bias.

## Methods

The DEPM used was an adaptation of that described by Lasker (1985) and Hunter and Lo (1993). It estimates the spawning biomass as the ratio of the daily production of planktonic eggs over the survey area and the weight-specific daily fecundity:

$$B = \frac{P \times k}{S \times F \times R} \quad (1)$$

where
B = biomass (t),
P = egg production over survey area (eggs $d^{-1}$),
k = conversion factor (kg to t),
S = mean proportion (by weight) of mature females spawning a batch of eggs on any day during the survey,
F = weight-specific batch fecundity (eggs spawned $d^{-1}$ $kg^{-1}$), and
R = sex ratio (by weight) of mature females to mature fish.

In this application of the DEPM, the daily planktonic egg production parameter (P) was estimated using a plankton survey over the area and the daily fecundity parameters (S, F, R) were estimated using a coincident trawl survey. All parameters except E were estimated using stratified–random sampling designs over the Hauraki Gulf. The DEPM was used to estimate the mature biomass (taken to be all fish with fork length $\geq$23 cm, the length at 50% maturity). The plankton and trawl surveys were done from 19 November to 4 December 1992 during the peak months of the snapper-spawning season in the Hauraki Gulf (Crossland, 1977; Scott and Pankhurst, 1992; Zeldis, 1993). The survey designs, and field and analytical methods for estimating the DEPM parameters are described below.

### Daily planktonic egg production

*Survey design*

The plankton survey area stratification (Fig. 1) was determined by plotting catch rates of seven trawl surveys targeting adult snapper carried out from 1984 to 1990 (NIWA unpublished data, Francis *et al.*, 1995), on a chart of the Hauraki Gulf. Areas with different catch rates were separated by stratum boundaries on the

assumption that the relative abundance of trawl-caught adult fish across the Gulf during the spawning season would correspond to the egg production rate. The resulting stratification was very similar to that from the trawl survey time series used for adult fish (Langley, 1994). The total plankton survey area was made similar to the Hauraki Gulf trawl survey area, and included all areas $\geq$10 m depth, excluding the Cape Rodney Marine Reserve and a small naval testing range (Fig. 1).

The allocation of stations to strata (Fig. 1) was carried out using planktonic egg catch rate data from 12 plankton surveys done in the Gulf during the peak spawning months of Nov.–Dec., from 1985 to 1987 (J. Zeldis, NIWA unpublished data, Zeldis, 1992; Zeldis *et al.*, 1995). These survey data were pooled, and laid over the strata. Mean egg counts for each stratum were determined and the stations were allocated in proportion to the product of these means and the stratum areas. Allocation was done in proportion to the stratum means because these means were highly correlated with the stratum standard deviations and are probably more reliably estimated than the standard deviations (Francis, 1984).

To predict the precision of egg abundance estimates using this allocation, the station counts in each stratum were randomly sampled with replacement (bootstrapped) to estimate the stratum mean, where the number of samples taken from each stratum was the allocation size. These were scaled by stratum size and summed across strata to estimate the mean egg abundance for each simulated survey. This was repeated 500 times and the standard deviation of the 500 estimates, divided by the mean, was taken as the coefficient of variation (c.v.) of the mean. This suggested that 300 stations was appropriate for the final design, because it was considered that this was a tractable number of stations to occupy within the available survey period, and was predicted to yield an acceptable c.v. of about 15% on the egg abundance estimate. It was assumed that optimizing the allocation for estimating egg abundance would be similar to optimizing for egg production.

*Field methods*

The plankton net used had a cylinder-cone design with 3.5 $m^2$ mesh area in the cylinder and 3.0 $m^2$ mesh area in the cone. The mouth area was 0.5 $m^2$, and the mesh size was 346 μm. The net was fished from the starboard area of the 28 m R.V. ''Kaharoa'', with the ship stationary (i.e. not under power) and starboard beam-on to the wind, by lowering it to within 2 m from the bottom and then hauling it to the surface. The cod end was weighted to ensure that the net descended with the cod end below the net mouth. By design, the net meshes near the cod end regularly touched the sea bottom, so the net was encased in a protective sheath of stronger, heavy mesh (2000 μm). Plankton captured in the samples was preserved in 4% borax-buffered formaldehyde.

Net depth was monitored with a Guildline conductivity-temperature-depth probe (CTD) mounted in the centre of the net mouth and the length of warp payed out was monitored with a counter on the winch. Net deployment rate was 0.5-m depth change $s^{-1}$ and retrieval rate was 1-m depth change $s^{-1}$. It was not possible to monitor the distance travelled by the net (and therefore, volume filtered) by using a Tsurumi-Seiki-Kosakusho (TSK) flowmeter within the net mouth because the impellor in the meter often revolved in the forward direction during the net descent, due to surging from waves (subsequently verified using data logging devices on these meters (J. Zeldis, NIWA unpublished data)). Therefore, filtered volumes were not estimated from flowmeter counts, but from the length of towing warp deployed (see below).

Warp length will be an underestimate of the distance travelled by the net if the ship was drifting downwind during net retrieval. Failure to account for this will underestimate volume filtered, and will therefore overestimate egg densities and biomass. To form a sensitivity analysis to examine the volume filtered problem, the following assumptions were made: (1) the net dropped vertically through the water during deployment so that when retrieval started it was directly below the vessel position at the time of deployment; (2) ship drift rate was constant during the entire tow; (3) the warp was straight during retrieval and the net mouth was orthogonal to it; and (4) the trajectory of the net during retrieval was straight (this was verified by the net-mounted CTD data showing that net depth change by time was constant). Using the Pythagorean theorem with maximum net depth and warp length as a side and hypotenuse of a right triangle, respectively, the drift distance during deployment was calculated. Because the tow retrieval durations were half of the deployment durations, the drift distance during retrieval was calculated as half the deployment distance. The proportional difference between the drift distance and the warp length was taken as the bias in the volume filtered calculation due to ship drift.

Net efficiency (E) was estimated for 45 tows in which a TSK meter was attached to the tow warp 1.35 m above the net ring, and its measured distance travelled was compared with that of a TSK meter in the net mouth (after correcting for its higher position on the warp). In this calculation it was assumed that errors in the TSK readings due to surge affected each meter equally.

Plankton sampling was done around the clock, and sampling rate (45 to 75 min $station^{-1}$) was set such that each stratum took a whole number of days to complete (except strata 4, 5, 8, and 9; see Discussion). This was

Table 1. Descriptions of snapper egg stages used in DEPM survey.

| Stage | Description |
|---|---|
| 0 | Unfertilized |
| 1 | Undifferentiated, 1 cell |
| 2 | 2 cell to 16 cell, single layer of cells |
| 3 | >32 cell, multilayered |
| 4 | Individual cells still visible |
| 5 | Individual cells indistinct, in cap |
| 6 | Blastodisc starting to enlarge |
| 7 | Blastodisc covers 1/3 of yolk, germ ring forming |
| 8 | Blastodisc covers 1/2 of yolk, germ ring more distinct |
| 9 | Blastodisc covers 3/4 of yolk, gastrulation |
| 10 | Blastopore, rudimentary embryonic head, embryo 2/5 around yolk |
| 11 | Blastopore closed, optic vesicles and tail formed |
| 12 | Tail blunt, myotomes visible, embryo 1/2 around yolk |
| 13 | Early pigmentation visible, embryo 3/5 around yolk |
| 14 | Pronounced pigmentation, tail starting to lift at root, embryo straight |
| 15 | Tail lifted and still blunt, embryo straight |
| 16 | Tail starting to curl and more pointed |
| 17 | Tail longer and sharply pointed |
| 18 | Ready to hatch, very long tail, oil drop at ventral end of yolk sac |

done to sample as many daily egg cohorts as possible, within each stratum.

*Laboratory analysis*

In the laboratory, snapper eggs were identified and staged according to the stages illustrated by Crossland (1980) and described in Table 1. The raw counts of abundance at stage were converted to densities (numbers $m^{-2}$ sea surface area) by multiplying the counts $m^{-3}$ filtered (warp length × net mouth area) by the water column depth at each station. It was assumed that the samples taken from 2 m above the bottom to the surface represented the egg densities from the bottom to the surface.

When the egg densities by stage where plotted against the time of capture (Fig. 2), very distinct daily cohorts of eggs were evident. Early stage eggs appeared first in samples taken about midday, and spawning appeared to finish by about 1800 h. Eggs finished hatching after about 60 h. Therefore, samples taken after midday usually showed eggs spawned over three consecutive days, and those taken before midday usually showed eggs spawned over two days.

The eggs in each cohort in each sample were given ages based on the time difference between a nominal peak spawning time of 1400 h, and the time and day the sample was taken. The cohort densities at age were fitted to an exponential mortality model using a maximum likelihood procedure that assumed lognormally distributed errors (Appendix 1). The procedure minimized the differences between observed and expected values of counts at age, to estimate $P_k$, the daily production of eggs at age zero (time of spawning), and $Z_k$, the mortality rate, for each stratum, k.

The total daily egg production in the survey area, P, was estimated as

$$P = \frac{\Sigma_k (P_k A_k)}{E} \quad (2)$$

where

$A_k$ = the area of stratum k, and

E = plankton net efficiency.

A bootstrap procedure (Appendix 2) was used to estimate coefficients of variation and confidence intervals for the production estimates.

## Daily fecundity: sex ratio, spawning proportion, batch fecundity and average female weight

*Survey design*

The trawl survey stratification was the same as used for the plankton survey. This stratification was optimal for estimating mean catch rate of adult snapper, so it was assumed that it would also be optimal for estimating parameters of the daily fecundity. There were, however, enough spawning proportion pilot data from 1988 and 1989 ''Kaharoa'' trawl surveys (Zeldis, 1993) to predict optimal sample numbers and within-trawl subsample sizes for an unstratified sampling estimate of spawning proportion (Picquelle, 1985). This modelling predicted that a c.v. on the spawning proportion estimate of about 0.05 was achievable with 30 trawls and subsamples of about 15 mature females per trawl. However, because this prediction was sensitive to the true value of spawning proportion, the actual survey had 50 trawls, and catch size allowing, subsamples were taken of 30 females or 75 staged fish (whichever occurred first). The 50 stations were allocated to strata in proportion to mean catch rates and stratum areas, from the pooled catches in the seven ''Kaharoa'' trawl surveys, although un-trawlable ground had to be avoided. For batch fecundity, data from a previous study of snapper spawning (Scott, 1991) were used to predict that sampling one ovary from each of 80 females would yield a c.v. on the estimate of batch fecundity of about 0.05. In the actual DEPM survey, however, ovaries with hydrated oocytes were removed from 134 fish.

*Field and laboratory methods*

Trawling was carried out from R.V. ''Kaharoa'', using a high-opening otter trawl with cod end mesh size = 40 mm, headline height = 5.5 m, wing width = 16.0 m, and door width = 79 m (Francis *et al.*, 1995). Trawl tow length was typically 1.3 km. Trawling was done from 0300 h to 0900 h, because previous studies (Scott *et al.*, 1993; Zeldis, 1993) had shown that this was

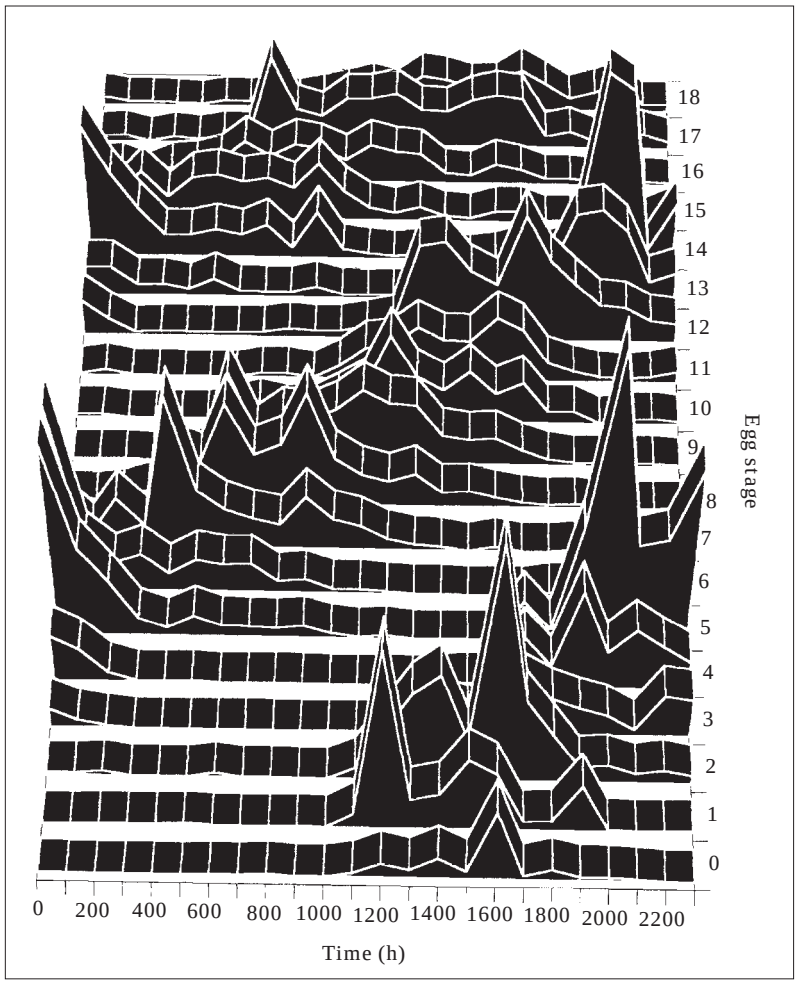


Figure 2. Relative egg density ($m^{-2}$) by time of day and stage (Table 1) from the DEPM survey. Time axis covers a full day so samples taken after midday contained eggs spawned over 3 consecutive days (0, 1 and 2 day-old eggs) and those taken before midday usually showed only 1 and 2 day-old eggs.

the time of day when maximal numbers of females would be in the hydrated ovarian state. Generally, four or five trawls were done per morning, interspersed with plankton tows.

All sub-sampled snapper were measured. Fish $\geq 23$ cm were sexed and their gonads were staged macroscopically using the staging system of Pankhurst *et al.* (1987). The estimator used for sex ratio, R, was:

$$R = \frac{\Sigma_i \left( R_i \frac{C_i A_i}{n_i} \right)}{\Sigma_i \frac{C_i A_i}{n_i}} \qquad (3)$$

where

$R_i$ = catch rate (kg $km^{-1}$ trawled) of females/total catch rate of fish $\geq 23$ cm fork length at station i,

$C_i$ = the catch rate of fish at station i,

$A_i$ = the area of the stratum containing station i,

$n_i$ = the number of stations in the stratum containing station i.

The precision of the estimate of R was estimated using the following bootstrap procedure. For each station, the pair $(X_i, R_i)$ was calculated, where $X_i = C_i A_i / n_i$. Then, 1000 simulated survey data sets were generated by sampling random pairs with replacement. Each simulated data set contained the same number of stations as the original trawl survey and produced one bootstrap estimate of R using Equation (3). A c.v. for R was calculated as the standard deviation of the 1000 bootstrap estimates divided by its mean.

The estimator for spawning proportion (S) was the similar to that for R, with $C_i$ replaced by the catch rate of female fish $\geq 23$ cm, and $R_i$ replaced by $S_i$, the catch rate of ovarian stage 4 (hydrated) females/catch rate of

female fish $\geq$23 cm. An analogous bootstrap procedure was used to estimate the precision of S.

For batch fecundity (F), both ovaries were removed from hydrated fish and frozen. In the laboratory, the ovaries were thawed and weighed, and a 0.2 g subsample of ovarian tissue was removed from the middle of a randomly chosen ovary in each pair. The hydrated oocytes were clearly identifiable under the dissecting microscope because of the wrinkled appearance of the chorion, caused by freezing of the watery oocyte contents, and the presence of a single, fully formed oil droplet (Scott, 1991).

Analysis of variance showed that samples from the middle of each ovary provided a batch fecundity estimate insignificantly different from samples taken from the anterior or posterior of 28 ovaries sampled in all three positions (the middle position mean estimate was only 0.5% lower than the mean of these three positions, and had c.v. = 0.046). Taking the sample from the middle of each ovary, therefore, was considered to provide an unbiased estimate of batch fecundity of that ovary. The relationship of batch fecundity (hydrated eggs batch$^{-1}$) to fish weight was modelled by a weighted linear regression (weighting by 1/fish weight, to remove the dependence of the variance on the mean).

The weight-specific batch fecundity (F) was estimated by determining the batch fecundity at the mean weight of mature females in the population, and then scaling this to the fecundity of a 1 kg mature female by dividing by this mean weight. The estimate of batch fecundity at mean weight was not available directly from the samples obtained for F, because the ''Kaharoa'' trawl undersampled fish larger than 25 cm (Davies *et al.*, 1993) and therefore the fish obtained from the trawls were not a random sample (by weight) of the mature female population.

The mean weight estimate for the mature female population was estimated from a mixture of longline market sampling, longline catch-at-sea sampling and trawl sampling during the period of the DEPM survey (Davies *et al.*, 1993). This combined approach was necessary, because while longline market samples are considered to give an unbiased catch frequency for fish lengths $\geq$30 cm fork length, longliner ''high grading'' at sea and reduced longline gear selectivity for fish <30 cm results in a mean weight estimate which is biased high. Therefore, these authors used an at-sea sampling programme on commerical longliners to correct for fisher selectivity for lengths between 25 and 30 cm. They also used a trawl survey, done in the Hauraki Gulf immediately before the DEPM survey (''Kaharoa'' voyage KAH9212), to obtain unbiased catch frequencies for fish $\leq$25 cm. These results were combined (Davies *et al.*, 1993) to estimate mean weight of mature females ($\geq$23 cm fork length) in the Gulf, corrected for fisher and gear selectivity.

### Biomass estimates

The biomass of mature snapper was estimated using Equation (1). The precision of the biomass estimate was estimated by generating 1000 estimates of biomass using Equation (1) where the parameter estimates were obtained by random resampling with replacement from distributions around the estimates. The distributions of S, F and R were all assumed to be normal and represented by their parametric variance, and the distribution of P was directly resampled from the bootstrap distribution of estimates of that parameter. The estimate of E was assumed to have no error. The upper and lower 95% confidence intervals of the biomass estimate were taken to be the 0.975 and 0.025 percentiles, respectively of the 1000 biomass estimates. Two sensitivity analyses were conducted by estimating biomass (1) without planktonic data from strata 8 and 9 (because these strata were poorly sampled; see Discussion), and (2) using only the error in P (to illustrate the proportion of the error in biomass due to error in P).

## Results

### Daily egg production

Egg abundance (Fig. 3a, b, c) was highest in the inner Gulf (strata 1–3 and 8–10), very low in the central and outer Gulf (strata 4–6), and at intermediate levels in stratum 7. The spatial distributions of early, middle and older aged eggs were nearly congruent (Fig. 3a, b, c), suggesting that there was little advection of eggs across stratum boundaries as they aged.

For the plankton net efficiency parameter, E, the mean of the ratios of the counts of upper and lower meters was 0.89 (c.v. = 0.007) with the upper meter registering more counts.

Plots of egg density against age for each stratum (Fig. 4) suggested that the youngest and oldest eggs were under-sampled. According to the exponential mortality model such plots should show a linear decline. In fact, the plots typically showed an initial increase in abundance followed by a gradual decline and then, for the oldest eggs, a rapid decline (Fig. 4, broken lines). Accordingly, densities for eggs of ages $\leq$12 h and $\geq$55 h were omitted from the data before the mortality model was fitted. With this restriction the data fitted the model reasonably well with homogeneity of standardized residuals around zero (not shown).

The estimated production rates $P_k$ (Table 2) for the inner Gulf (strata 1–3 and 8–10) were considerably higher than rates in the central and outer Gulf (strata 4–7). The Gulf-wide egg production rate estimate ($P \times A$) was $450 \times 10^9$ eggs d$^{-1}$, with the 95% confidence interval ranging from $350 \times 10^9$ to $860 \times 10^9$ eggs d$^{-1}$ (Table 3).

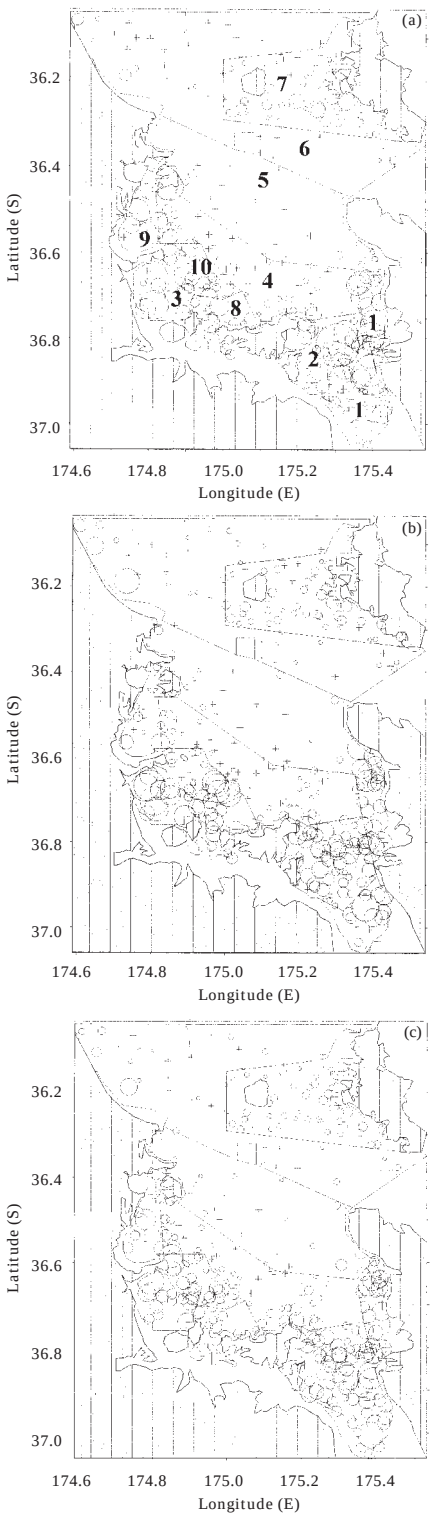


Figure 3. Maps of snapper egg abundance (proportional to circle size) from the DEPM survey for (a) stage 0–6 eggs, (b) stage 7–12 eggs and (c) stage 13–18 eggs. Largest circle = 888 eggs $m^{-2}$ and crosses show stations with no eggs at each stage range. Strata are numbered.

### Daily fecundity

High adult catch rates (Fig. 5a) corresponded with high planktonic egg abundance (Fig. 3a, b, c). In the inner Gulf (strata 1–3 and 8–10) trawl catches were moderate to high, while those in the central and outer Gulf (4–7) were consistently small, if not zero. Spawning proportion, S (Fig. 5b), was also much higher in the inner Gulf strata, while sex ratio, R, did not show any particular spatial pattern.

The average mature female weight was 0.725 kg. It was not possible to calculate a c.v. of this estimate (N. Davies, NIWA, pers. comm.), but it was assumed to be relatively small (0.05), because c.v.s on conventional snapper weight frequencies are generally very small (Davies *et al.*, 1993).

The batch fecundity of a fish of average weight was 45 785 hydrated eggs $batch^{-1}$, with c.v. = 0.05. The weighted linear regression predicting batch fecundity, F, from fish weight, W, was $F = 73.9W - 7793$ ($r^2 = 0.72$, $n = 133$). The batch fecundity was predicted from fish weight by the regression with no pattern in standardized weighted residuals. Most of the ovaries (87%) were collected from inner Gulf strata, and a wide range of fish weights were sampled in most of these strata. This meant that the estimated weight-specific batch fecundity was representative of the general fish population in the Gulf during the survey period.

### Biomass estimates

The estimate of mature ($\geq 23$ cm fork length) snapper biomass was 24 499 t, with 95% confidence interval of 17 994–48 650 t (Table 3). The 95% confidence interval of biomass estimated using only the error in P was 18 783–46 603 t, so clearly most of the variation was from this source.

## Discussion

The 1992 DEPM biomass estimate of about 25 000 t is within the range of the 1993 Hauraki Gulf tagging estimates, which ranged from 20 700 to 27 900 t (c.v. $\simeq 0.09$), depending on which of a number of sensitivity analyses were considered (J. McKenzie, NIWA pers. comm., Dec. 1995). The DEPM and tagging estimates are not strictly comparable, however, because the tagging estimate was for fish $\geq 25$ cm, while the DEPM was for fish $\geq 23$ cm, and there was a difference of one year in the timing of the two estimates. Nevertheless, these effects would be expected to be relatively minor, especially considered in the context of the potential bias and error associated with each of the biomass estimates.

The DEPM biomass estimate had a high variance, associated primarily with the planktonic egg production estimates. Clearly, the assumption that optimizing the

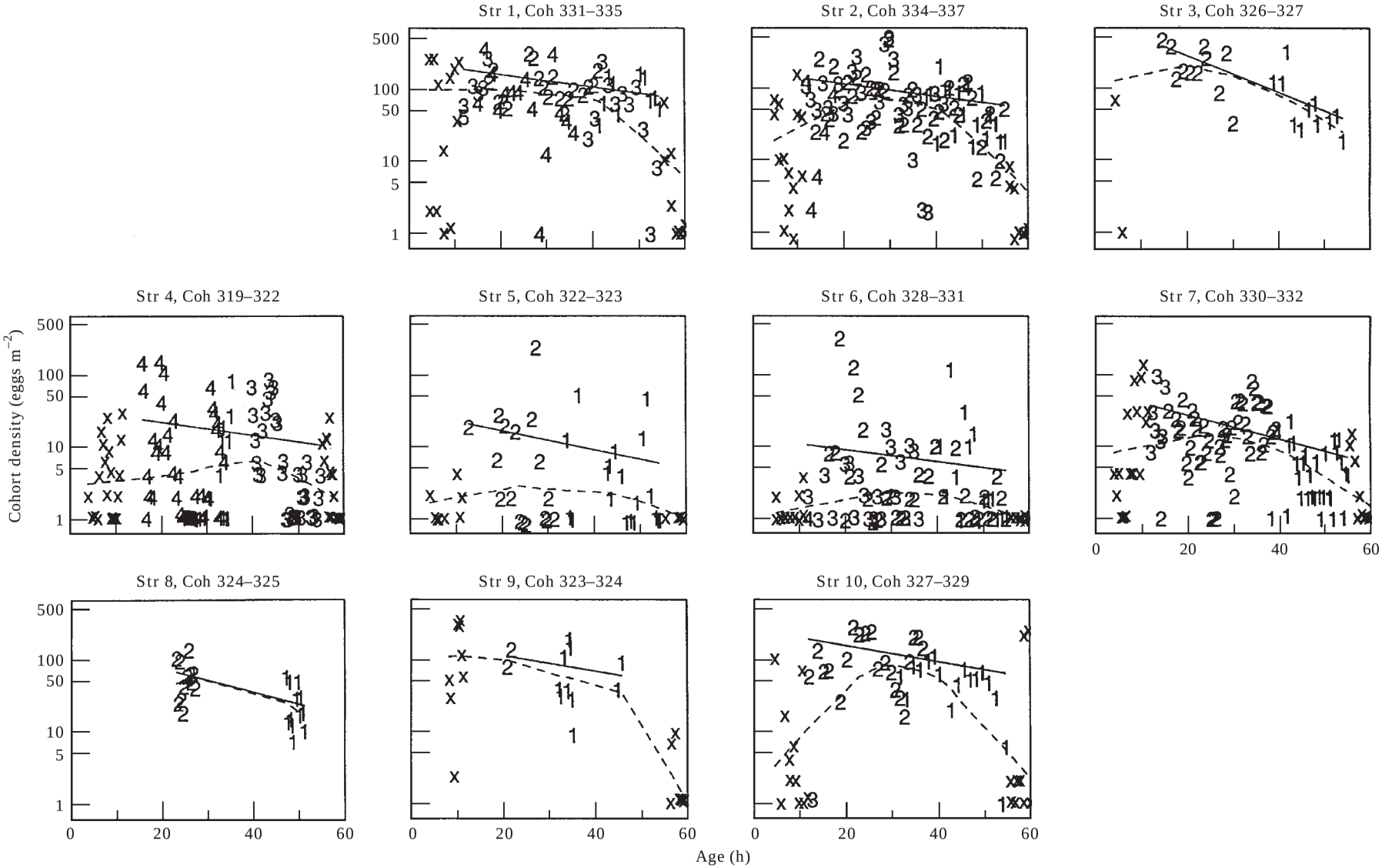


Figure 4. Plots of cohort egg density vs. age (h) by stratum (one point for each valid cohort-station combination in the stratum) from the DEPM survey. Cohort numbers given above each panel refer to the day of the year when the cohort was spawned. Points included in the estimation of production are plotted as ''1'', ''2'', etc., according to which cohort they belong to (''1'' indicates the earliest cohort); points excluded (see text) are plotted as ''x''. The broken lines are smooth curves fitted to all the data; the solid lines indicate the fit to the maximum-likelihood model.

Table 2. Station numbers (n), stratum areas ($A_k$), egg production rates ($P_k$), c.v.s $P_k$, egg mortality rates ($Z_k$), and stratum production rates ($P_k \times A_k$) for DEPM survey.

| Stratum | n | $A_k$ ($m^2 \times 10^{-6}$) | $P_k$ (eggs $m^{-2}$ $d^{-1}$) | c.v. $P_k$ | $Z_k$ ($d^{-1}$) | $P_k \times A_k$ ($\times 10^{-9}$ eggs $d^{-1}$) |
|---|---|---|---|---|---|---|
| 1 | 34 | 300 | 225 | 0.38 | 0.5 | 67.5 |
| 2 | 50 | 355 | 165 | 0.31 | 0.5 | 58.7 |
| 3 | 11 | 154 | 871 | 0.42 | 1.4 | 134.2 |
| 4 | 52 | 641 | 33 | 0.55 | 0.5 | 21.1 |
| 5 | 20 | 983 | 30 | 0.86 | 0.7 | 29.4 |
| 6 | 40 | 1604 | 13 | 0.67 | 0.5 | 20.9 |
| 7 | 46 | 619 | 59 | 0.42 | 0.9 | 36.5 |
| 8 | 12 | 130 | 158 | 0.79 | 0.9 | 20.6 |
| 9 | 10 | 136 | 182 | 1.81 | 0.6 | 24.8 |
| 10 | 23 | 146 | 251 | 0.50 | 0.6 | 36.6 |

plankton station allocation for estimating egg abundance would be sufficient to optimize the estimation of egg production was not supported, due to the additional requirement of estimating Z (the egg mortality rate). The data were inadequate to test the assumption (see Appendix 1) that production rate and mortality rate of each egg cohort sampled within each stratum did not vary during the time each stratum was occupied. However, this is not thought to be a stringent assumption for the reasons given in Appendix 1. Daily changes within strata in spawning proportion and batch fecundity were examined, to determine if egg cohort size was consistent from day to day. Only strata for which sampling extended over at least 2 d and for which >1 ovarian sample or trawl station was made each day, were used (strata 1, 2 and 3 for batch fecundity and strata 1 and 2 for spawning proportion, respectively). One-way ANOVA showed no significant difference (alpha = 0.05) between days, for any of the strata-day combinations, for either parameter.

The confidence interval for the biomass estimate (Table 3) was not well estimated. This interval derives from uncertainty in the estimates of all the parameters in Table 3, but is determined primarily by uncertainty in egg production, P (which was estimated by the procedure of Appendix 2). Unfortunately, the plankton survey data were inadequate to test the assumptions on which this procedure was based (e.g. lognormal distribution of egg densities, and the relationship between $\sigma_k$ and $P_k$). The bootstrap method used to estimate coefficients of variation for R and S is crude in that it effectively ignores the stratum structure in the data (which means it will tend to over-estimate). A referee suggested that it would be better to use a more sophisticated procedure as recommended by Smith (1997). However, it is not clear how these procedures perform when estimating a ratio of biomasses (which is what R and S are). Also, this appears to be of little importance because the effect of these c.v.s is swamped by the much greater uncertainty in P (Table 3).

Table 3. DEPM parameter estimates for the Hauraki Gulf, November–December 1992. P = egg production over survey area (eggs $day^{-1}$), A = survey area ($m^{-2}$), S = mean proportion (by weight) of mature females spawning a batch of eggs on any day during the survey, F = weight-specific batch fecundity (eggs spawned $day^{-1}$ $kg^{-1}$), W = mean weight of mature females (kg), R = sex ratio (by weight) of mature females to mature fish, E = plankton net efficiency, B = biomass (t). The c.v. of W was assumed (see text).

| Parameter | Estimate | 95% c.i. or c.v. |
|---|---|---|
| P × A | $450 \times 10^9$ | $350–860 \times 10^9$ |
| S | 0.76 | 0.07 |
| F | 63 152 | 0.05 |
| W | 0.73 | 0.05 |
| R | 0.43 | 0.03 |
| E | 0.89 | 0.01 |
| B | 24 499 | 17 995–48 650 |

The egg production rate c.v.s from strata 8 and 9 were large (Table 2). This may have been due to small sample numbers in these strata (Table 2), and little contrast in estimated egg ages amongst the observations (recall that these strata were sampled only over part of one day, rather than a full day (Fig. 4). As a sensitivity analysis the egg production estimate was re-calculated without strata 8 and 9 to observe the sensitivity of the c.v. to data from these strata. The distribution of P estimates was considerably narrowed with the mean at $410 \times 10^9$ eggs $d^{-1}$ and a 95% confidence interval of 310 to $610 \times 10^9$ eggs $d^{-1}$, resulting in a biomass estimate with 95% confidence interval of 15 753 to 36 254 t (compare with Table 3). Imprecision can arise from various sources including high intrinsic variability and low sample size, which may explain the high c.v. of stratum 5. For stratum 3, it is notable that although sample size was low, the c.v. was relatively small, possibly because sampling was spread over a fully day in this case (Fig. 4).

A source of bias, which probably caused some overestimation of DEPM biomass, was the method of estimating volume filtered by the plankton net, based on

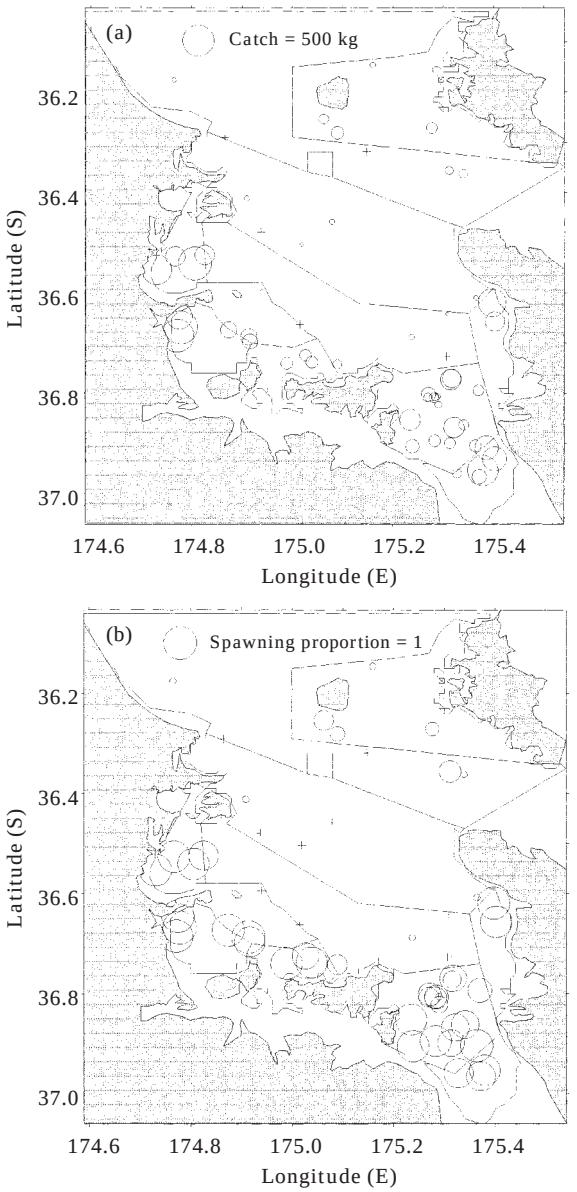


Figure 5. Maps of (a) mature snapper catch rate (kg $km^{-1}$ trawled), and (b) spawning proportion from the DEPM survey, both proportional to circle area (maximum values and circle areas are shown at the top of each panel). Crosses indicate zero catch in (a) and zero mature fish in (b).

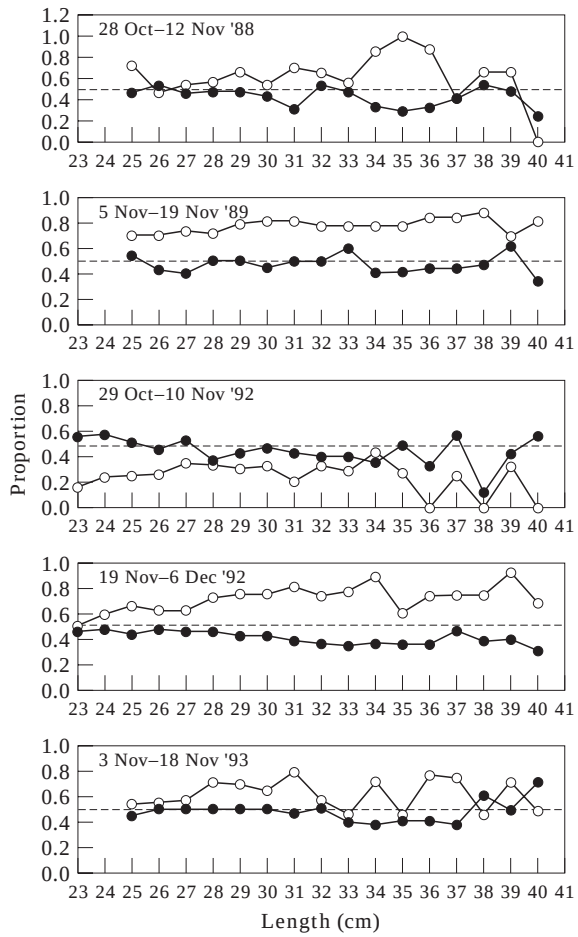


Figure 6. Spawning proportion of mature females (open circles) and sex ratio (proportion females of all mature fish; filled circles) by numbers and length, for 5 ''Kaharoa'' trawl surveys from 1988 to 1993 (NIWA unpublished data). Only 1992 surveys sampled fish below 23 cm. Proportion 0.5 is dotted for reference. The proportions become imprecise at $\geq$ about 34 cm because of low sample sizes at length.

warp length. The sensitivity analysis (see methods) showed that additional distance added to tow length due to ship drift during retrieval made the actual retrieval distance 13% longer than the warp length, on average, over the survey period. This translated into an approximate 13% reduction of biomass to about 21 300 t.

Another source of bias could arise if spawning proportion, S, or sex ratio, R, were not constant for all lengths $\geq$23 cm. In the present analysis it was assumed that the trawl samples (which undersample larger fish) for S and R were representative of the whole mature population. To test this assumption, S and R from all Hauraki Gulf trawl surveys from which ovarian stage and sex data were available were analysed by length (Fig. 6). In general, it was found that S and R had little dependence on fish length, at least for lengths $\geq$25 cm. Spawning proportion may decline somewhat for females between 23 and 25 cm.

R was not consistently related to whether the data were collected before or after the onset of daily spawning (Table 4) which occurs at about 1100 h (Scott *et al.*, 1993; Zeldis, 1993 and Fig. 2). Also, there was no consistent relationship between R and S (Table 4). These results suggested that the relative catchability of males

Table 4. Sex ratio (R) and spawning proportion (S) from Hauraki Gulf ''Kaharoa'' trawl surveys. Sex ratios are compared for samples taken before daily spawning commenced (1100 h) and after that time. Spawning proportions are calculate only for samples taken before daily spawning commenced.

| Date | R pre-spawning | | | R post-spawning | | | S | | |
|---|---|---|---|---|---|---|---|---|---|
| | Mean | c.v. | n | Mean | c.v. | n | Mean | c.v. | n |
| 28 Oct.–12 Nov. 1988 | 0.52 | 0.19 | 28 | 0.56 | 0.15 | 43 | 0.51 | 0.24 | 28 |
| 5 Nov.–19 Nov. 1989 | 0.49 | 0.08 | 39 | 0.35 | 0.10 | 42 | 0.52 | 0.35 | 39 |
| 29 Oct.–10 Nov. 1992 | 0.46 | 0.08 | 38 | 0.52 | 0.08 | 38 | 0.32 | 0.20 | 38 |
| 19 Nov.–6 Dec. 1992 | 0.43 | 0.03 | 50 | 0.33 | 0.09 | 2 | 0.76 | 0.07 | 50 |
| 3 Nov.–18 Nov. 1993 | 0.50 | 0.05 | 41 | 0.41 | 0.07 | 32 | 0.59 | 0.12 | 41 |

and females was not affected by intensity of spawning behaviour. This was a source of sampling bias in DEPM biomass estimates for northern anchovy (Picquelle and Stauffer, 1985), where it appeared that females became much more susceptible to capture while actively spawning. For snapper, it appears that the duration of the daily ovulated stage is very brief (Zeldis, 1993). Diver observations (Scott *et al.*, 1993) suggest that snapper are strongly demersal at most times and therefore accessible to trawl gear. Since the data in the present study were all collected before daily spawning, and did not include the time of ovulation, it is unlikely that they were biased by spawning behaviour.

The S estimates varied substantially between surveys (Table 4, Fig. 6). Most of this variation was probably due to the timing of each survey relative to the onset of seasonal spawning in each year (typically in October; Crossland, 1980; Scott and Pankhurst, 1992; Zeldis, 1993). S was also quite sensitive to data from stations with moderate catch rates and extremely low spawning proportions, if they were in large strata. These stations tended to occur in stratum 7 and east of Coromandel Peninsula (Fig. 1). This effect was pronounced in one trawl survey (the 1989 survey; Table 4) where removal of one station east of Coromandel Peninsula from the estimate increased the spawning proportion to 0.69 (from 0.52) and lowered the c.v. to 0.14 (from 0.35).

The present study provided much information on how the precision and accuracy of the method could be improved in future DEPM surveys on snapper. First, reliable flowmeter data must be acquired to overcome ship drift effects, and data logging flowmeters have been developed at NIWA to achieve this. There should be investigation of why the youngest eggs appeared to be undersampled, possibly using depth-stratified plankton tows in spawning areas. Possible causes of this were that the youngest eggs were close to the bottom, or were extremely patchy. Older eggs would have been undersampled because some would have already hatched. Planktonic egg production and mortality rate estimate precision could be improved by taking more plankton samples during the DEPM survey and targeting more daily cohorts. It was found during the present survey that sampling rate (samples taken per hour) could have been approximately doubled within the voyage period. Also, certain stratum boundaries could be better located within the Gulf for the planktonic egg survey, for example, between strata 9 and 4 (Figs 1 and 3) to better separate high and low egg production areas. Finally, trawl survey stratification in the outer Gulf could be modified to isolate areas where moderate catch rates but low spawning proportions may occur.

This is the first application of the DEPM in New Zealand, and the first on a sparid, worldwide. Although there are reasonably wide confidence intervals, the mean biomass estimate agrees closely with the results of the tagging study carried out in the following year. These DEPM results show that the method is a viable assessment tool for snapper stocks and is probably applicable to other types of demersal finfish with spawning biology and behaviour similar to snapper (e.g. Lutjanids; Davis and West, 1993).

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## Appendix 1: Maximum-likelihood estimation of egg production

Let $O_{ijk}$ be the observed egg density (eggs $m^{-2}$) at station i in stratum k for the cohort spawned on day j. We assume that the $O_{ijk}$ are indepenent and are distributed lognormally with parameters $\mu_{ijk}$ and $\sigma_k$ (being the mean and standard deviation, respectively, of the $\ln(O_{ijk})$). Then the log-likelihood, $\lambda_k$, given the observations $O_{ijk}$ is, ignoring constants,

$$\lambda_k = -\Sigma_{ij} \ln O_{ijk} - n_k \ln \sigma_k - 0.5\sigma^{-2}_k \Sigma_{ij} (\ln O_{ijk} - \mu_{ijk})^2 \quad (A.1)$$

where $\Sigma_{ij}$ denotes summation over all combinations of i and j for which an egg density is possible and $n_k$ is the number of such combinations in stratum k.

It is convenient to replace $\mu_{ijk}$ by $\ln M_{ijk} - 0.5\sigma_k^2$, where $M_{ijk}$ is the expected value of $O_{ijk}$. Assuming exponential mortality at rate $Z_{jk}$ ($day^{-1}$),

$$M_{ijk} = P_{jk} e^{-A_{ijk}Z_{ik}} \quad (A.2)$$

where $P_{jk}$ is the production of cohort j in stratum k and $A_{ijk}$ is the estimated age of this cohort at the time of sampling of station i (assuming spawning occurs at 1400 h each day). With these assumptions,

$$\lambda_k = -n_k \ln \sigma_k - n_k\sigma_k^2/8 - 1.5\Sigma_{ij} \ln O_{ijk} + 0.5\Sigma_{ij} \ln P_{jk} - 0.5\Sigma_{ij} A_{ijk} Z_{jk} - 0.5\sigma_k^{-2}\Sigma_{ij}\left[\ln\left(\frac{O_{ijk}}{P_{jk}}\right) + A_{ijk}Z_{jk}\right] \quad (A.3)$$

In principle, given sufficiently intense sampling, it is possible to estimate production and mortality for all observed cohort-stratum combinations. However, this was not possible for the present survey. Thus, it was necessary to make the further assumptions $P_{jk} = P_k$ and $Z_{jk} = Z_k$ for all j and k. Note that this assumption is not as stringent as it might appear because each stratum was sampled over just a few days so the number of cohorts observed in any one stratum was small (typically 2 to 4 – see Fig. 4).

It is straightforward (though messy) to show that the maximum-likelihood estimates of $Z_k$, $\sigma_k$, and $P_k$ are given by

$$\hat{Z}_k = -\frac{\Sigma_{ij}(A_{ijk} - A_{..k})(\ln O_{ijk} - \ln O_{..k})}{\Sigma_{ij}(A_{ijk} - A_{..k})^2}, \quad (A.4)$$

$$\hat{\sigma}_k^2 = \frac{1}{n_k}\Sigma_{ij}[(\ln O_{ijk} - \ln O_{..k}) + \hat{Z}_k(A_{ijk} - A_{..k})]^2, \text{ and} \quad (A.5)$$

$$\hat{P}_k = \exp[\ln O_{..k} + \hat{Z}_k A_{..k} + 0.5 \times \hat{\sigma}^2{}_k] \quad (A.6)$$

where $A_{..k} = (\Sigma_{ij}A_{ijk})/n_k$ and $\ln O_{..k} = (\Sigma_{ij} \ln O_{ijk})/n_k$.

In the bootstrap procedure (Appendix 2) it sometimes occurred that the maximum-likelihood estimate for $Z_k$ was negative. As this makes no biological sense, $Z_k$ was set equal to zero in these cases, and $\sigma_k$ and $P_k$ were estimated using the following modified versions of (A.5) and (A.6)

$$\hat{\sigma}_k^2 = \frac{1}{n_k}\Sigma_{ij}(\ln O_{ijk} - \ln O_{..k})^2 \text{ and} \quad (A.5')$$

$$\hat{P}_k = \exp(\ln O_{..k} + 0.5 \times \hat{\sigma}^2{}_k) \quad (A.6')$$

## Appendix 2: Bootstrap procedure

The following parametric bootstrap procedure was used to calculate coefficients of variation for the estimates of $P_k$ and a 95% confidence interval for P.

For each stratum, 1000 sets of simulated survey data (the $O_{ijk}$) were generated using the estimated values of $P_k$ and $Z_k$ as ''true'' values. That is, the $O_{ijk}$ were generated as lognormal variates with mean $M_{ijk}$ (calculated from $P_k$ and $Z_k$ using Equation (A.2)). The standard deviation of the logarithm of these variates was taken from a regression of $\sigma_k$ on $\log(P_k)$ ($\sigma_k = 1.94–0.187 \log(P_k)$).

From each simulated data set the maximum-likelihood procedure (Appendix 1) was used to produce bootstrap estimates of production and mortality, $P_k$* and $Z_k$*. The c.v. of the original estimate of $P_k$ was estimated from the distribution of the 1000 bootstrap estimates, $P_k$*.

Finally, Equation (2) was applied 1000 times, using the bootstrap estimates $P_k$*, to obtain 1000 bootstrap estimates P*. The 2.5 and 97.5 percentiles of this set of 1000 P* values was taken as a 95% confidence interval for the estimate of overall production, P.