

**Abstract.** – Batch fecundity, weight-specific fecundity (number of eggs per gram somatic weight), size of ripe ovarian eggs, and the somatic and gonadal conditions of adult female queenfish *Seriphus politus* were estimated for five spawning seasons during an 8-year (1979–86) period. The effects of female somatic weight were evaluated in analyses of covariance comparing batch fecundity, egg size, and gonadal condition among years.

Batch fecundity was positively (and allometrically) related to female somatic weight. Fecundities were remarkably similar during four of the five years evaluated. After adjustment for annual differences in female size, fecundities were still significantly lower (by about one-fifth) during 1984, a major El Niño year, compared with the preceding (1979–80) or following (1985–86) pairs of years. Gonadal condition also was uniquely low in 1984. The 1984 declines in fecundity and gonadal condition co-occurred with low somatic condition during 1984, particularly for larger females. Mean size (diameter, dry weight) of eggs was indistinguishable among years. There was a positive relation between egg size and female body size, and a general decline in egg size as the spawning season advanced for females of all sizes.

Likely links between declines in fecundity, gonadal and somatic condition, and the crash in planktonic production during the 1982–84 El Niño are discussed.

## Annual Variations in Fecundity, Egg Size, and the Gonadal and Somatic Conditions of Queenfish *Seriphus politus* (Sciaenidae)

Edward E. DeMartini

Honolulu Laboratory, Southwest Fisheries Science Center  
National Marine Fisheries Service, NOAA  
2570 Doie Street, Honolulu, Hawaii 96822-2396

Few data exist on annual variations in reproductive traits (fecundity, egg size, gonadal allocation) of marine fishes. At a minimum, however, such data are necessary if fisheries ecologists are to begin to understand the many processes, including the vagaries of planktonic transport, that influence the large annual and longer-term temporal fluctuations in the recruitment and subsequent year-class abundance of marine fish stocks (Sinclair 1988, Bailey and Almatar 1989). The influences of egg size and quality on the early growth and survivorship of most species are poorly understood (Ware 1975).

The queenfish *Seriphus politus* is a small croaker abundant in the inner-shelf waters off southern California. It has planktonic egg and larval stages prior to the recruitment of juveniles to epibenthic habitat. Individual females are indeterminate serial spawners that produce as many as 20 batches of eggs during a protracted (6-month) spawning season (DeMartini and Fountain 1981). Juvenile and small adult, including male, queenfish feed on zooplankton (copepods and mysids), and large adults, females in particular, specialize on juveniles of the northern anchovy *Engraulis mordax* (DeMartini et al. 1985).

In this paper, I present data on batch and relative (weight-specific) fecundities, egg size, and the gonadal

and somatic conditions of adult female queenfish collected during five spawning seasons spanning an 8-year period from 1979 to 1986. Fecundity, egg size, and condition indices are compared among years and related to concurrent variations in female body size. Because data are available prior to, during, and immediately following a major El Niño event, I interpret my observations in terms of known interannual variations in planktonic production and potential food limitation.

### Methods

#### Sample collection

Queenfish were collected during the March–August reproductive seasons (DeMartini and Fountain 1981) of 1979, 1980, 1984, 1985, and 1986. Nighttime (2000–0200 hours), bi-weekly to fortnightly collections with a lampara seine, made at 5–16 m bottom depths at three longshore locations in San Onofre–Oceanside waters (DeMartini et al. 1985), were used to index the abundance and to describe the size (length, weight) composition of the nearshore queenfish stock. Sample fish for gonad analyses were provided by daytime lampara seining, otter trawling, and gillnetting at <16-m depths in the same area, and by screenwell samplings of the San Onofre Nuclear Generating Station,

near San Clemente, California. Night-time samples were used to characterize abundance and size composition, because net avoidance is less at night (Allen and DeMartini 1983). Fish analyzed for reproductive variables and condition were collected during daylight hours, because oocytes destined for imminent spawning are macroscopically recognizable within ovaries only as they hydrate during the half-day preceding dusk spawning (DeMartini and Fountain 1981).

#### Processing of samples

Queenfish were refrigerated until processed within one day of collection. Sex and maturity were determined from macroscopic characteristics of gonads (DeMartini and Fountain 1981). Adult females were measured (standard length, SL, in mm), and their gonadectomized, wet body weights (as a proxy for somatic weight) were determined to 0.1 g.

#### Ovary and egg analyses

Both ovaries were removed (fresh) from adult females, weighed damp to 0.01 g, and, for fish in ripe(ning) condition, the presence of hydrated-state oocytes noted based on macroscopic criteria ("Stage 3" ovaries: DeMartini and Fountain 1981).

Hydrated-state ovaries were fixed and preserved in modified Gilson's Fluid (Bagenal and Braum 1971) for about three months, after which declines in oocyte diameters and dry weights should have stabilized (Withames and Walker 1987). These specimens are hereafter referred to as "Gilson's-fixed." Batch fecundity was then determined for a maximum of 10 females per month and year of collection. Fecundity was estimated by gravimetric method (Bagenal and Braum 1971, DeMartini and Fountain 1981). Counts from each section were standardized to the total weight of both ovaries and then averaged (Hunter et al. 1985).

In a subsample of the Gilson's-fixed ovaries, I estimated the median diameter (random axis) of hydrated-state eggs: 10 randomly chosen oocytes per ovary pair were measured within  $\pm 25 \mu\text{m}$  ( $\pm 1$  "eyepiece unit" or "EU") using a compound microscope with ocular micrometer at  $40\times$  magnification. I examined a maximum of 10 females per month and year.

A linear dimension such as diameter might not accurately represent egg volume or mass because of variations in chemical composition or density (Blaxter and Hempel 1963). Therefore, I compared the diameter and dry weight of oocytes from Gilson's-fixed ovaries. For

**Table 1**

Size composition and catch-per-net-haul (CPUE) of adult female queenfish *Seriphus politus* collected during the March–August periods of 1979–86, off northern San Diego County, California. All fish were captured by lampara seines of consistent dimensions, mesh sizes, and method of deployment, during the night at 5–16 m bottom depths (DeMartini and Fountain 1981, DeMartini et al. 1985).

Year	SL (mm)		Mean somatic wt (g)	Mean CPUE	Number	
	$\bar{x}$	% > 165 mm			Fish	Net hauls
1979	141	19	45	22	872	40
1980	134	16	40	22	995	45
1984	132	2	35	15	294	20
1985	134	6	38	20	624	32
1986	138	7	40	24	948	40

46 females with hydrated-state ovaries present in March–August 1984 collections, I determined the mean dry weight of hydrated oocytes for one member of each ovary pair. I determined the mean diameter of hydrated oocytes for the other member of the ovary pair. Oocyte diameters were measured as described above. I determined mean oocyte dry weight by drying lots of 100 eggs to constant weight (1–2 days) in a vacuum jar over anhydrous calcium chloride. Eggs were dried at room temperature to avoid weight loss of volatiles (Hay 1984, Hislop and Bell 1987), and an aggregate weight determined to the nearest mg on an analytical balance.

#### Calculation of condition indices

The relative allocation of energy to gonadal tissue was indexed by the RGI of Erickson et al. (1985), as  $RGI = (G/W^b) \times 100$ , where  $G$  = wet weight of ovaries in g,  $W$  = wet somatic weight in g, and  $b$  = the exponent of the power equation,  $G = aW^b$ . The relative gonadal index (RGI) is equivalent to  $100 \times a$ , where  $a$  is defined by the linearized (log-transformed) equation,  $\ln G = \ln a + b \ln W$  (Erickson et al. 1985). It was necessary to adjust the gonadal index for somatic weight because the slope of the logarithmic gonad-to-somatic weight equation was significantly greater than one (i.e., the relation was allometric).

I first attempted to index somatic robustness as relative somatic condition,  $K_n = CW/SL^b$  (Le Cren 1951), where  $W$  = wet somatic weight in g,  $SL$  = standard length in mm,  $C$  = a constant ( $10^5$ ), and  $b$  = the exponent of the regression,  $W = aSL^b$ . However, the exponent, evaluated as the slope of the log-transformed weight-to-length equation  $\ln W = \ln a + b \ln SL$ , differed among years, thereby invalidating the use of such an index in analysis of covariance (Erickson et al. 1985,

Cone 1989). I therefore limited my evaluation of robustness to comparisons of estimates of ordinary least-squares regression parameters (Cone 1989).

The relationship between wet and dry body weights might change throughout the spawning season (Love 1970). Therefore, I evaluated seasonal changes in dry somatic weight using 57 females collected at the start of (April–May,  $n = 32$ ) and immediately following (August–September,  $n = 25$ ) the 1985 spawning season. After ovariectomy, fish were frozen in air-tight “zip-lock” bags. Fish were then thawed, and each entire fish was macerated and individually oven-dried to a constant weight at 120°C for 24–32 hours.

### Statistical analyses

I used nonparametric analysis of variance (Kruskal-Wallis One-way ANOVA) to compare the body lengths and somatic weights of females among years. Year was evaluated as a fixed-effect class variable, because I was interested in evaluating potential differences among a pre-established series of years. Analysis of covariance (ANCOVA) was used whenever possible to evaluate the effects of sampling year on batch fecundity, and on relative gonadal condition, after adjustment for year differences in somatic weight. A two-way Model I ANCOVA was used to evaluate sub-seasonal (approximately bimonthly) influences of egg diameter among years for females of differing body lengths. Dry egg weight was related to egg diameter by parametric regression. Dry somatic weight was regressed on wet weight for sample fish collected at the beginning and at the end of the 1985 spawning season; regressions were then compared using ANCOVA with body length as the covariate. Computations were made using the GLM, REGRESS and TTEST software procedures of the Professional Database Analysis System (PRODAS; Conceptual Software Inc. 1986).

## Results

### Variations in female body size and CPUE

The size composition of the nearshore, adult female queenfish stock differed among years. Mean female length and weight were significantly lower in 1985 and especially 1984 (Kruskal-Wallis one-way ANOVA; both

**Table 2**

Summary statistics for adult female queenfish *Seriphus politus* used in analyses of reproductive variables and condition. Gonadal condition (RGI), batch fecundity, and egg diameter variables are least-square means (adjusted for annual differences in the body-size covariate). All variables, including fecundity, refer to sample females only. See Methods for explanations of the covariate used to adjust particular variables. One standard error is given in parentheses below each mean.

Year	N	SL (mm)	Somatic weight (W, g)	RGI*	Batch fecundity <sup>b</sup> (no. eggs)	Egg diameter <sup>c</sup> (EU)
1979	44	165 (5)	77 (7)	3.8 (.2)	14,752 (1)	19.10 (.18)
1980	126	151 (2)	56 (3)	4.7 (.1)	15,019 (1)	20.61 (.18)
1984	71	137 (2)	37 (1)	3.9 (.2)	11,784 (1)	20.11 (.23)
1985	77	141 (2)	44 (2)	5.3 (.2)	14,550 (1)	21.03 (.18)
1986	75	143 (2)	44 (2)	4.1 (.2)	14,199 (1)	21.10 (.18)

\* Estimates ( $\pm$  SE) of the exponent “b” in the power equation, gonad weight ( $G$ ) =  $aW^b$ , were  $1.185 \pm 0.092$  (in 1979),  $1.162 \pm 0.053$  (1980),  $1.232 \pm 0.124$  (1984),  $1.280 \pm 0.102$  (1985), and  $1.011 \pm 0.102$  (1986). Estimates did not differ among years, and were consistently greater than one (ANCOVA; ln somatic  $W \times$  Yr interaction:  $F_{4,333} = 0.87$ ,  $P = 0.48$ ; pooled slope = 1.1810).

<sup>b</sup> Batch fecundity estimates were back-calculated from the means and SE's of ln-transformed data, multiplied by the correction factor of Sprugel (1983).

<sup>c</sup> Using the largest size-class of oocytes (ripe, hydrated-state) present in Gilson's fixed ovaries (see Methods).

$P < 0.001$ ). Large females ( $\geq 165$  mm SL, chosen because they were relatively rare during 1984–86) in fact were nearly absent in 1984, when overall mean female abundance was at an estimated low (Table 1).

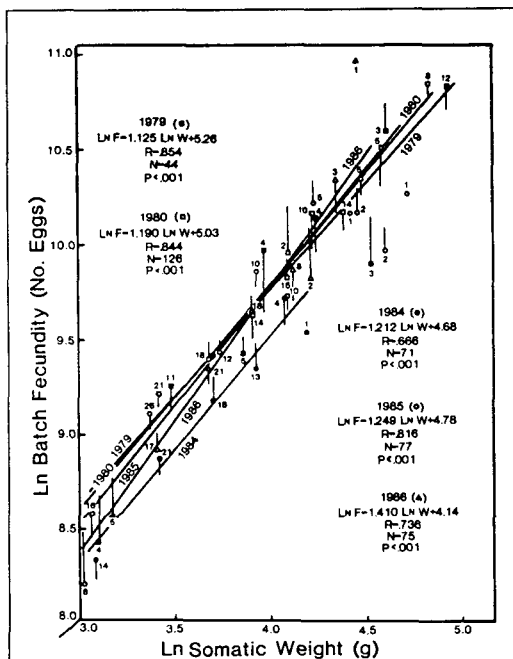
Females used in analyses of reproduction and condition also differed in mean body size (both somatic weight and length) among sample years (Kruskal-Wallis ANOVA, both  $P < 0.001$ ; Table 2).

### Dry vs. wet somatic weight

The dry somatic weight of female queenfish averaged 24% of wet weight for fish collected at the beginning and at the end of the 1985 spawning season. Body length obviously influenced dry weight; sub-season, however, had no significant effect on dry weight (ANCOVA of effects of body length and sub-season on dry weight: length effect— $F_{1,54} = 346$ ,  $P < 0.0001$ ; sub-season effect— $F_{1,54} = 0.42$ ,  $P = 0.52$ ). Wet weight, therefore, could be used as an accurate proxy for dry weight throughout the queenfish spawning season, once adjusted for variations in female body size.

### Batch fecundity

Batch fecundity in queenfish was positively related to female body size in each year (Table 3; Fig. 1). Fecundity was generally better related (based on higher  $R^2$  values) to somatic weight than body length. Batch fecundity was disproportionately large in heavier females, as indicated by the value of the slope in the linear double-log plot (Fig. 1). Fecundity also differed among years, even after adjustment for annual differences in female size, with mean fecundity in 1984 significantly lower (by 20%) than mean fecundity in the other four years (Tables 2, 3, 5; Fig.1).



**Figure 1**

Relationship between the log of batch fecundity ( $\ln F$ ) and log female somatic weight ( $\ln W$ ) during each of the five study years. For illustration, mean fecundity data ( $+1$  SE) are plotted for each 10-g weight class. The allometric equation,  $F = aW^b$  (in log-linear form as  $\ln F = \ln a + b \ln W$ ), and its summary statistics are provided for each fitted regression line.

**Table 3**

Summary of ANCOVAs<sup>a</sup> testing the effects of female somatic weight and year on batch fecundity ( $F$ , no. eggs) and relative gonadal index (RGI). Both model  $R^2$  are significant at  $P < 0.001$  ( $\ln F$ ,  $R^2 = 0.694$ ; RGI,  $R^2 = 0.114$ ).

Dependent variable	Source	df	SS	MS	F	P
$\ln F$	$\ln W$	1	118.1	118.1	693	<0.0001
	Yr	4	3.4	0.8	4.9	<0.0001
	Error	387	65.9	0.2		
RGI	$\ln W$	1	0.06	0.06	0.03	0.87
	Yr	4	111	27.7	12.5	<0.0001
	Error	387	860	2.2		

<sup>a</sup> $\ln W \times Yr$  interaction terms deleted for analysis of  $\ln F$  ( $P = 0.61$ ) and for analysis of the RGI ( $P = 0.84$ ).

### Weight-specific fecundity

Patterns of weight-specific fecundity (WSF, no. eggs per g somatic weight) resembled those of batch fecundity. WSF appeared to increase with female body weight (ANCOVA of effects of somatic weight and year on WSF: weight effect— $F_{1,387} = 13.1$ ,  $P < 0.001$ ), and also seemed to vary among years ( $F_{4,387} = 2.84$ ,  $P = 0.025$ ). However, main effects were confounded by a weakly significant weight-by-year interaction ( $F_{4,387} = 2.57$ ,  $P = 0.038$ ). This heterogeneity of slopes prevented adjustments for annual variations in female weight and invalidated comparisons of intercepts among all five years. Although WSF generally increased with body weight, the disproportionate effect of larger females varied among years. Most notable was the particularly strong, positive influence of somatic weight on WSF in 1986. If the 1986 data are deleted and the ANCOVA analysis rerun, the slope heterogeneity disappears ( $F_{3,310} = 0.82$ ,  $P = 0.49$ ). When main effects are reanalyzed, a strong year effect ( $F_{3,313} = 6.02$ ,  $P < 0.001$ ) becomes apparent, in addition to that of somatic weight. This year effect disappears ( $F_{3,243} = 0.56$ ,  $P = 0.57$ ) if the 1984 data are removed. Size-adjusted WSF in 1984 (mean  $\pm$  SE =  $264 \pm 15$  eggs per g) clearly was less than that in 1979, 1980, and 1985 ( $336 \pm 8$  eggs per g).

### Diameter vs. dry weight of eggs

The median diameter of Gilson's-fixed, hydrated-state eggs was significantly related to the mean dry weight of these eggs (dry weight [ $\ln g, \times 10^{-6}$ ] =  $7.2 + 0.4931$  egg diameter;  $r = 0.47$ ,  $n = 46$  females,  $P = 0.001$ ). The mass of hydrated-state eggs therefore was approximately predicted ( $R^2 = 0.22$ ) by egg diameter. While appropriate, I acknowledge that a more direct and

accurate measurement of egg mass would have been preferable.

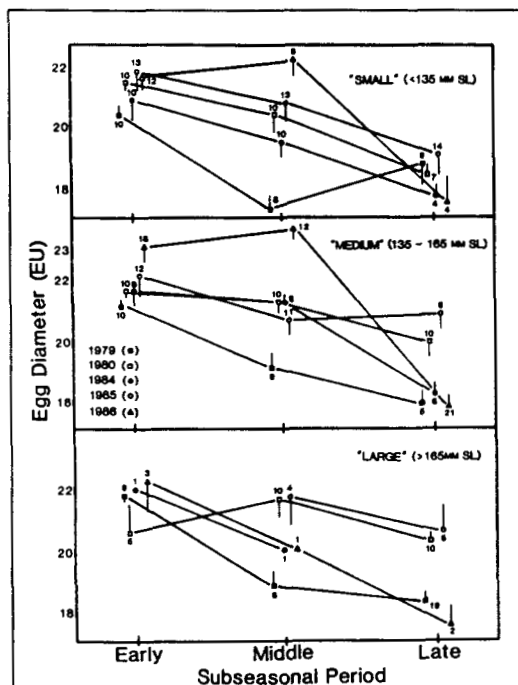
### Egg size

Egg size varied with female body length and period within spawning season, with larger eggs produced by larger females, and all females producing larger eggs earlier in the season (Table 4; Fig. 2). The mean size of eggs did not vary among years, after adjustments for annual differences in female size and a significant

**Table 4**

Results of two-way ANCOVA testing the effects of female body length (SL, as covariate), study year (spawning season), and bimonthly period within the spawning season on size of ripe ovarian eggs. See Methods for explanation of egg size measurements. Model  $R^2$  (0.510) significant at  $P < 0.001$ .

Dependent variable	Source	df	SS	MS	F	P
Egg diameter	SL	1	57	57.0	22.5	<0.0001
	Period	2			(inestimable)	
	Yr	4			(inestimable)	
	Period × Yr	8	226	28.2	11.2	<0.0001
	Error	372	942	2.5		



**Figure 2**

Relationship between mean ( $\pm 1$  SE) egg size (diameter of Gilson's-fixed, hydrated oocytes) and bimonthly period within spawning season for female queenfish of three arbitrary body sizes (small  $< 13.5$  cm, medium 13.6–16.5 cm, and large  $\geq 16.5$  cm SL), by sample year. See Tables 4 and 5 for results of ANCOVA testing the effects of subseasonal period (within year) on egg size, with female body lengths evaluated as a covariate. Data were pooled by bimonthly period to increase sample sizes.

**Table 5**

Summary of a posteriori Bonferroni  $t$ -tests for identity of year effects detected by ANCOVAs summarized in Tables 3 and 4. Means connected by underlines are not significantly different at  $P = 0.05$ . See Table 2 for values of adjusted means and SEs.

Variable	Year contrasts
ln F	<u>1984 &lt; 1985 = 1986 &lt; 1980 &lt; 1979</u>
Egg diameter	<u>1979 = 1984 = 1980 = 1985 = 1986</u>
RGI	<u>1979 = 1984 = 1986 &lt; 1980 = 1985</u>

period  $\times$  year interaction (Tables 4,5). The latter interaction illustrates that the pattern of subseasonal decline in egg size varied among years (Fig. 2). Adjusted for female length, mean egg diameter appeared to vary 10% among years (Table 2). This difference in egg diameters, expressed in terms of volume (as  $4/3 \pi r^3$ , the volume of a sphere), was 35% of the smaller value.

### Condition indices

Somatic condition varied with body size. Larger females usually were more robust (Table 6), but somatic condition also varied among years; the slopes and intercepts of length–weight relations were lower in 1984 and 1985 than in the other three years (Table 6). Larger females in particular were less robust in 1984 and 1985 (i.e., there was a highly significant  $\ln SL \times$  year interaction; Table 6), and this invalidated a straightforward interpretation of the effects of body size and year on a summary index of somatic condition.

As indicated by values consistently greater than one for the exponent "b" in the equation,  $G = aW^b$ , percentage gonad-to-somatic weight allocation increased for larger females (Table 2; Fig. 3). However, relative

gonadal condition, as described by the RGI of Erickson et al. (1985) in which gonad weight has been standardized by female somatic weight, did not vary with female size (Table 3). The RGI did differ among years in concert with size-adjusted variations in fecundity; mean RGI in 1984 was about 14% lower than the RGI averaged over the other four years (Tables 2, 5). An identical pattern of annual variation in gonadal condition is observed if the classical gonadal index ( $GSI = [G/W] \times 100$ ) is used as the dependent variable in ANCOVA instead of the RGI.

### Potential biases of condition indices

These differences in somatic and gonadal conditions were not the result of year variations in condition-selective collection methods. Lampara-seined fish comprised 84–100% of the specimens examined for condition in each year; among non-lampara fish, a maximum of 14% of the fish examined (in 1984) were collected by otter trawl. The somatic conditions ( $K = 10^5 W/SL^3$ ; Le Cren 1951) of fish collected by lampara seine and otter trawl during April–June 1984, the only period when testable numbers of fish were collected using more than one method, were indistinguishable (seine: mean  $\pm$  SE condition =  $1.40 \pm 0.016$ ; trawl: mean  $\pm$  SE =  $1.39 \pm 0.010$ ; Student's  $t = 0.28$ ,  $df = 151$ ,  $P = 0.78$ ).

## Discussion

### Annual variations in body size

Interannual variations in the body size of adult female queenfish were marked, with the percentage contribution of large fish varying tenfold and mean somatic weights of the nearshore female stock varying by 25% over the study period. Clearly, potential year effects on fecundity and other size-sensitive variables are confounded with the effects of annual variations in body size, necessitating the use of size as a covariate in analyses.

### Fecundity and female body size

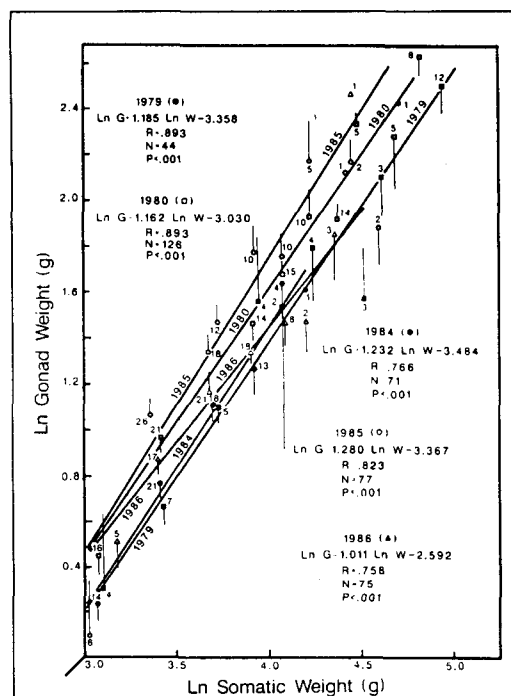
During each of the queenfish spawning seasons monitored, batch fecundity was positively related to female body size, especially somatic weight. The overall mean value of  $b$  in the equation,  $F = aW^b$  was 1.2087, which is significantly greater than unity.

**Table 6**

Least-squares regression parameters for length-weight relationships of adult female queenfish in each\* of the study years. Ordinary least-squares regressions were calculated for the double-log transformed equation,  $\ln W = \ln a + b \ln SL$ , where  $\ln a$  is the intercept and  $b$  is the slope.

Year	Intercept		Slope		$R^2$	N	P
	Estimate	SE	Estimate	SE			
1979	-11.864	0.246	3.151	0.048	0.990	44	<0.0001
1980	-11.660	0.178	3.106	0.036	0.984	126	<0.0001
1984	-10.450	0.378	2.853	0.077	0.952	71	<0.0001
1985	-10.433	0.206	2.862	0.042	0.984	77	<0.0001
1986	-11.888	0.616	3.152	0.124	0.898	75	<0.0001

\* Estimated slopes of the  $\ln W - \ln SL$  relations differed among years (ANCOVA;  $\ln SL \times Yr$  interaction:  $F_{4,393} = 6.10$ ,  $P < 0.0001$ ).



**Figure 3**

Relationship between the log of ovary weight ( $\ln G$ ) and log female somatic weight ( $\ln W$ ) during each of the five study years. For illustration, mean ovary weight data ( $+1$  SE) are plotted for each 10-g weight class. The equation,  $G = aW^b$  (in log-linear form as  $\ln G = \ln a + b \ln W$ ), and its summary statistics are provided for each fitted regression line.

In another detailed study, Parrish et al. (1986) detected allometric weight-specific fecundities in a size-(age-) structured stock of the northern anchovy. Empirical data for additional species of "weedy" (fast-growing, high-fecundity) fishes suggest that allometric fecundity-weight relations may be a general phenomenon (Blaxter and Hunter 1982, Clarke 1987). Reiss (1987), in a review and interpretation of relevant data, calculated that larger (older) fish in general have disproportionately large reproductive investments. Williams (1966), Wootton (1979), and Reiss (1987) have argued that disproportionate investments by older individuals should be adaptive for many iteroparous fishes with indeterminate growth. The queenfish data further suggest that allometry in gonadal allocation may be more common than is generally appreciated. Adjustments for allometry are required when calculating egg-based stock size estimates for species like queenfish and northern anchovy (Parrish et al. 1986).

### Covariates of egg size

Egg size was positively related to queenfish body length, but declined for females of all sizes as water temperatures increased between the beginning (March–April) and end (July–August) of the spawning season. Egg size has been observed to increase with female body size, and decreases in egg size have been related to increases in water temperature during spring–summer production cycles, for diverse marine fishes (Williams 1967, Ware 1977, Blaxter and Hunter 1982 and references, Kashiwagi et al. 1985, Knutsen and Tilseth 1985, Daoulas and Economou 1986 and references, Imai and Tanaka 1987, Tanasichuk and Ware 1987). A positive female size–egg size relation and a seasonal decline in egg size with increasing water temperatures, the latter either ecophenotypic or genetic responses to the changing prey or predator (Clarke 1989) spectra confronting larvae, are now recognized as general phenomena in marine pelagic-spawners (Ware 1975; Markle and Frost 1985). It is obvious that estimates of mean egg size (and fecundity) must account for the effects of female body size and subseasonal variation.

### Annual variations in fecundity and egg size

Batch fecundities of queenfish (adjusted for annual variations in female size) varied less than 6% during four out of the five years of this study. A marked change in batch fecundity, after adjustments for variations in female size, occurred only in 1984. Weight-specific fecundities paralleled batch fecundities.

Queenfish egg size varied little among the five years studied. Apparent egg volume averaged about 24%

smaller in 1979 than during the other four years.

Few data exist on annual variations in the egg production of marine fishes (Bagenal 1957 and references, Antony Raja 1971, Pinhorn 1984, Hunter et al. 1985, Bailey and Almatar 1989). As one might expect, the size-specific fecundity of individuals varies among years, but sometimes fecundities are remarkably similar within a short series of years (Antony Raja 1971, Pinhorn 1984, Hunter et al. 1985). Observational and experimental studies (e.g., Tyler and Dunn 1976, Wootton 1979, Hunter and Leong 1981, Hay and Brett 1988) demonstrate that fluctuations in fecundity can and do result from naturally occurring food limitation. Food rations can also affect egg size (Hislop et al. 1978, Le Clus 1979). The trivial inference is that food can sometimes, although not invariably, limit egg production. Of greater interest is that, for queenfish, the maximum observed deviation from long-term average fecundity was only a 20% decline in a single year of unique oceanographic conditions, as described in the following section.

### El Niño effects

The anomalously low fecundities and somatic condition of queenfish in 1984 occurred at a time when the 1982–84 El Niño was still evident in the Southern California Bight (McGowan 1985). During 1983–84, zooplankton production was at unusually low levels in inner-shelf waters (Petersen et al. 1986), mirroring the nadir in phyto- and zooplankton production in the California Current, farther offshore (McGowan 1985). This decline in planktonic production off southern California lagged the more extreme declines in production that resulted from the parent El Niño that occurred off the western coast of South America during 1982–83 (Barber et al. 1985).

During the 1982–84 California El Niño, tropical pelagic fishes migrated northward; many species became abundant off southern California, with some noted as far north as Washington–British Columbia (Smith 1985, Mysak 1986). El Niño effects on subtropical and cold-temperate fishes are poorly understood. Bailey and Incze (1985) and Mysak (1986) summarized the fragmentary data then available on distributional shifts and fluctuations in stock sizes of temperate fishes. Bailey and Incze (1985) speculated that El Niño effects on water temperature, nutrients, and planktonic production could effect egg and larval physiologies, disrupt the transport of early-life-history stages, and impact the somatic condition and egg production of adults. For vagile species, major impacts such as these should prompt movements to regions more favorable for growth and reproduction (Bailey and Incze 1985).

My data on interannual variations in body size composition suggest that large female queenfish (those individuals whose somatic condition and reproduction were particularly stressed by reductions in their anchovy prey) responded to El Niño conditions in part by emigrating out of the study area. The observed 1984 nadir in females >165 mm, followed by the return of fish of this size in 1985-86, demonstrates that emigration had to have occurred, because 165-mm long queenfish are more than 3 years-old (E. DeMartini, unpubl. data). Large fish might have emigrated to deeper depths, tracked colder water masses upcoast, or done both; unfortunately, lack of data prevent discrimination among these possibilities.

The only published evidence thus far for El Niño effects on adult fish condition and egg production off the west coast of North America are for the central stock of the northern anchovy (Fiedler et al. 1986), yellowtail rockfish *Sebastes flavidus* (Lenarz and Echeverria 1986), and for Pacific herring *Clupea harengus pallasi* (Tanasichuk and Ware 1987). In anchovy, individual egg production was lower in 1983-84 than in 1980-82 and 1985; this reflected lower spawning frequencies more than declines in batch fecundity (Fiedler et al. 1986). Specific fecundity (the daily production of eggs per unit biomass) of anchovy was low in 1983 (although high in 1984, the second El Niño year) compared with other years between 1980 and 1985. Growth rates of juvenile-adult anchovy were low in 1983-84 (Fiedler et al. 1986). For yellowtail rockfish off the central California coast, the visceral fat and gonad volumes of adults were lower in 1983 than in 1980 (Lenarz and Echeverria 1986). Off British Columbia, Pacific herring responded to the El Niño with increased batch fecundities coincident with reductions in mean egg size (Tanasichuk and Ware 1987). Adults of the anchovy and rockfish do not regularly occur in inner-shelf waters: most anchovy frequent the California Current, tens to several hundred kilometers offshore of central and southern California. Adult yellowtail rockfish are an epibenthic predator of continental borderlands offshore of the coasts of British Columbia-California.

It is tempting to speculate that the observed decrease in fecundity and somatic condition of queenfish during 1984 reflects lower production of the planktonic and anchovy prey of adults during a major El Niño year, compared with the 1979-80 and 1985-86 periods. If true, these data are among the first to show annual variations in egg production resulting from differences in size-specific batch fecundity, rather than changes in the duration of the spawning season or changes in the spawning frequency of females (Hunter et al. 1985). Interestingly, queenfish egg mass was not detectably lower in 1984, concurrent with the 20% decline in the

number of eggs produced per batch, so the impact on egg production may have involved only the quantity, not the quality of eggs. Total number of spawnings per female season, whether due to changes in the duration of the spawning season or frequency of spawning by individual females, also might have varied for queenfish during 1979-86, but data are lacking. Length of spawning season and the interval between batches are unlikely to cancel out the batch fecundity pattern, though, since they might be expected to vary in concert with fecundity, if they covary at all (Hunter et al. 1985).

My observations also provide one of the first suggestions of food web impacts of the 1982-84 California El Niño on an inner-shelf fish species. Unfortunately, data on potential El Niño effects on the survivorship of early-life stages and year-class establishment are lacking for queenfish, as for offshore fishes. Future studies should concurrently measure survivorship and recruitment, together with population fecundity and egg production of the stock, in addition to individual fecundity and condition.

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