

Abstract.—Length-at-sexual-maturity and spawning periodicity of the tuna baitfish *Encrasicholina devisi*, *E. heterolobus*, *Spratelloides delicatulus*, *S. gracilis*, *S. lewisi*, and *Archamia zosterophora* were studied at two exploited fishing grounds and one unexploited site in the Solomon Islands. All species became sexually mature and capable of spawning at 70% of the largest size, except the apogonid *A. zosterophora* which matured at a larger size (80%). There was little site-related variability in length-at-first-spawning, although *S. lewisi* from Tulagi grew to a larger size and was larger than *S. lewisi* from other sites when it spawned for the first time. There was no evidence that length-at-first-spawning was affected by commercial baitfishing.

The timing and intensity of spawning of each species were extremely variable. All species spawned throughout the year, with one or two periods of more intense activity. The spawning peaks of the same species at different sites did not coincide, and no proximate stimuli correlated with spawning by any species at all sites. The timing of major spawning events was not random, nor did fish spawn as soon as they reached maturity. Spawning events at the three sites correlate with particular environmental conditions, especially moon phase and, less importantly, rainfall and temperature. These results are not consistent with the hypothesis that spawning is timed to maximize either local dispersal or the potential for larvae to find suitable food. Lack of clear proximate stimuli for spawning among the six species examined makes it difficult to predict the timing of major spawning events by these species.

Maturation, Spawning Seasonality, and Proximate Spawning Stimuli of Six Species of Tuna Baitfish in the Solomon Islands

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The pole-and-line fisheries for skipjack tuna *Katsuwonus pelamis* in the Pacific are dependent on adequate supplies of suitable bait. Engraulids (genus *Encrasicholina*) and dussumierids (genus *Spratelloides*) are the basis of the Solomon Islands tuna baitfishery, the largest in the region with catches of over 2000 t annually (Anon. 1988).

Knowledge of the reproductive biology of the main bait species may be important in developing management regimes to minimize the impact of the baitfishery on these species. Some aspects have been studied in the Solomon Islands (Evans and Nichols 1984) and elsewhere in the Pacific (Tester 1955; Tiews et al. 1971; Leary et al. 1975; Dalzell and Wankowski 1980; Conand 1985; Dalzell 1985, 1986, 1987ab; Lewis et al. 1983; McCarthy 1985; Clarke 1987) and in southeast Asia (Dharmamba 1960; Tham 1965; Luther 1979; Chen 1984, 1986). These studies suggest both genera spawn year-round, with periods of increased spawning during spring and summer (Leary et al. 1975, Tiews et al. 1971, Luther 1979) or with the change of monsoon (Dalzell and Wankowski 1980, Dalzell 1987b) or periods of high zooplankton production (Sithichockpan 1972). However, timing of peak spawning is variable, both temporally (e.g., Dalzell 1987b) and between regions.

There have been several reviews (e.g., Scott 1979, Lam 1983, Bye

1984) of the importance of various cues which stimulate gonadal development and cause fish to spawn (proximate factors). Among temperate species, temperature and light are the most common cues (Scott 1979, Bye 1984). Other cues, such as food supply, moon phase, and rainfall, have also been suggested as important for spawning by tropical marine fishes (Johannes 1978, Lam 1983, Walsh 1987). However, the proximate stimuli that arouse increased spawning activity among baitfish remain obscure. Tester (1955) found that variations in egg production by *Encrasicholina purpureus* in Hawaii could not be adequately explained by temperature, salinity, or moon phase. Similarly, Muller (1976) showed that fluctuations in salinity and zooplankton biomass accounted for only 30% of the variation in egg production of *E. heterolobus* at Palau. Such poor correlations suggest that spawning may be random, or fish may begin to spawn as soon as they are physiologically capable of doing so.

The length at which *Encrasicholina* and *Spratelloides* become sexually mature appears to be variable both between and within countries of the southwestern Pacific (Dalzell and Wankowski 1980, Conand 1985, Dalzell 1985, McCarthy 1985, Dalzell 1987ab, Wright 1989), and these fish may adjust their life-history parameters to changes in their demography

or environment (Stearns and Crandall 1984). Such variability could have important implications for the baitfishing industry. Juveniles could be caught before they have had a chance to spawn, because the liftnets used in the baitfishery are not size-selective and catch all sizes of *Encrasicholina* and *Spratelloides* (see Evans and Nichols 1984).

The aims of this study were, first, to examine the length at maturity and the spawning seasonality of the six most abundant baitfish species (*Encrasicholina devisi*, *E. heterolobus*, *Spratelloides delicatulus*, *S. lewisi*, *S. gracilis*, and the apogonid *Archamia zosterophora*); secondly, to determine whether spawning is random or correlated with environmental cycles; and, thirdly, to assess the effects, if any, of the commercial fishery on these reproductive parameters.

Methods and materials

Sampling

Samples of six species of baitfish were collected from three sites each month for two years. Fish from commercial bait catches came from Munda and Tulagi, and fish from an unexploited control site came from Vona Vona, Solomon Islands. Sites and sampling methods are described in Milton et al (1990). Samples were usually collected between 2100 and 2200 hours. Two sites, Munda and Vona Vona, were in enclosed coral reef lagoons with little water movement and were approximately 20 km apart. The other site, Tulagi, consisted of a series of protected bays which opened into a narrow channel between two islands and was located over 300 km southeast of the other sites. Each month a random sample of over 100 fish of each species from each site was preserved in 4% formaldehyde and taken to the laboratory for analysis. On each sampling occasion, the water temperature, cloud cover, moon phase, and wind speed and direction were recorded. At least two 5-minute horizontal plankton tows ($\sim 100\text{m}^3$) were made with a 250- μm mesh net (0.5 m diameter) 1 hour prior to fish collection. The daily rainfall at a village adjacent to each site was recorded throughout the study.

Laboratory analyses

Fish were measured (standard length (SL) $\pm 0.5\text{mm}$) and weighed ($\pm 0.001\text{g}$) and the gonads were removed and weighed ($\pm 0.001\text{g}$). The gonads of up to 10 females of each species and of any other females with enlarged

Table 1
Criteria used for staging female gonads of baitfish.

Stage	Histology
(1) Immature	Oogonia present
(2) Developing/resting	Previtellogenic oocytes
(3) Maturing	Yolk precursor stage; some non-staining yolk
(4) Ripe	Non-staining yolk; developed chorion
(5) Running ripe	Homogeneous red-staining yolk; oocytes hydrated; development complete
(6) Spent	Atresion of ripe oocytes plus previtellogenic oocytes; presence of post-vitellogenic follicles

oocytes were randomly subsampled from each site sample each month. Gonads were embedded in paraffin wax, sectioned at $9\mu\text{m}$, and stained with Ehrlich's haematoxylin and eosin (McManus and Mowry 1964). Gonad maturation stages were defined following Cyrus and Blaber (1984) and Hunter and Goldberg (1980). Each gonad was staged, based on the relative numbers of cells at each developmental stage (Young et al. 1987; Table 1), and the presence of any postovulatory follicles was noted. Gonosomatic indices (GSI) were calculated as the ratio of wet gonad weight to somatic weight (total weight minus gonad weight) expressed as a percentage.

Size-at-sexual-maturity was determined from the length at which a fish developed ripe eggs (Table 1: stage 4). Among fish that were only examined macroscopically, the criterion for sexual maturity was a gonosomatic index greater than the minimum GSI of fish that were shown histologically to have ripe eggs.

Fish examined histologically were considered to be in spawning condition if more than 85% of the eggs were fully hydrated, running-ripe (Table 1: late stage 5). The mean GSI ± 2 standard errors of these fish was calculated for each species at each site. The GSI value of the lower 95% confidence limit of the mean GSI of spawning fish was used as the indicator of spawning among fish examined macroscopically. The proportion in spawning condition in each sample was then calculated from the fraction of the sample (examined both histologically and macroscopically) with a GSI greater than this value. This criterion was used, as it was a conservative estimate of the real proportion spawning.

Plankton samples were split in half with a Folsom plankton splitter and one fraction was dried to a constant mass to provide an estimate of relative zooplankton biomass. The other fraction was sorted and the number of *Encrasicholina* eggs and larvae (Delsman 1931), the number of other eggs, larvae, and potential

prey (from those found by Milton et al. 1990) were counted. *Spratelloides* eggs are demersal (Leis and Trnski 1989) so were not sampled by this method.

Data analyses

The proportion of each 1 mm length-class that were sexually mature was compared between sites. The normal approximation to the binomial distribution was used to estimate the 95% confidence limits of the proportion mature in any length-class. Confidence limits of the estimated proportion of the mature population spawning each month were calculated in a similar way.

To assess whether the timing of spawning was random, we calculated the proportion of the population spawning from the fraction of the entire sample of each species at each site during the study. This proportion was then compared with the proportion spawning each month. Monthly proportions greater than the 95% confidence limits to the normal approximation to a binomial distribution were scored as a plus sign. A non-parametric runs test (Sokal and Rohlf 1981) was used to test whether the distribution of plus signs was random.

The relationship between the proportion of fish in each monthly sample (of each species at each site) that were longer than the mean adult length at that site, and the proportion in that sample that were spawning, was examined using linear regression. A significant positive relationship between these proportions was used to assess whether fish spawned as soon as they were physiologically capable of doing so.

The relationships between possible proximate stimuli and the proportion spawning were compared by stepwise regression analysis. Variables that improved the fit were added to the model until the best three-variable model was obtained or the most significant fit was found. The proportion of each sample of each species in spawning condition was transformed by its arcsine square-root to reduce possible bias due to an excess of low values (Sokal and Rohlf 1981). The following 11 variables were compared for each species at each site: (1) sea-surface temperature, (2,3) prey biomass and density, (4) moon phase, (5) tide range, (6) cloud cover, (7) wind speed, and (8–11) rainfall between samples. Previous studies of spawning by these species (Dalzell 1985, 1987b) and other tropical inshore fishes (e.g., Johannes 1978, Walsh 1987) suggested that these variables may be important cues for these species. Initially, salinity and current speed were also measured, but as they varied little, they were not included in the analysis.

The variable moon phase was calculated by fitting a curve of the form $y = \sin(2\pi x) + \cos(2\pi x)$ where x = number of days since the last full moon prior to the

start of sampling divided by 29.5 (days in a lunar month). This variable has higher values about the new and full moon. Rainfall data were regressed in several ways to assess the influence they may have on baitfish spawning: total rainfall since previous sample (usually 1 month)(Total); number of days since rain (Days); number of days since rain >25 mm (Days 25 mm); and number of days of rain since previous sample (Rain). Rainfall, cloud cover, and wind variables were transformed by their square root to normalize skewed values. Except for moon phase, positive relationships between the proportion of each species spawning and proximate variables are indicative of greater spawning activity at higher values.

To assess whether all variables were independent, proximate variables were correlated with one another. Principal component analysis (Sokal and Rohlf 1981) was also used to help identify variables that covaried within and between sites. A subset of proximate variables that behaved independently was identified and analysed separately. Where a potential stimulus had been measured in several ways (e.g., rainfall), the most biologically appropriate was chosen.

Results

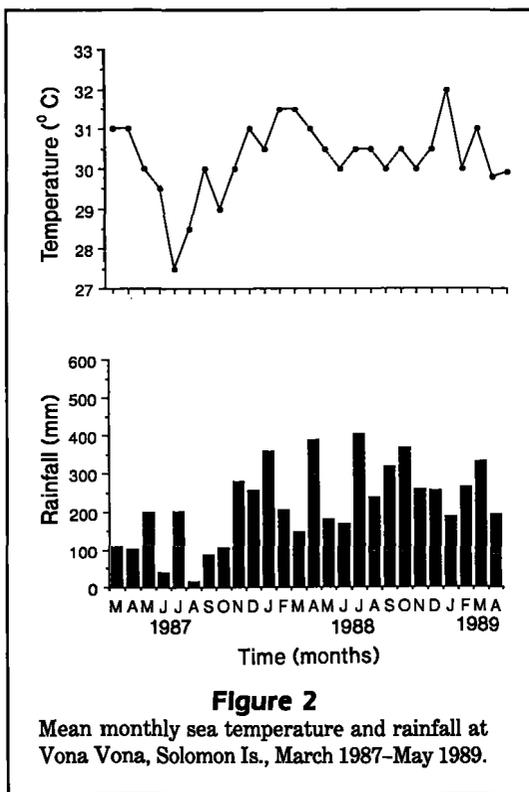
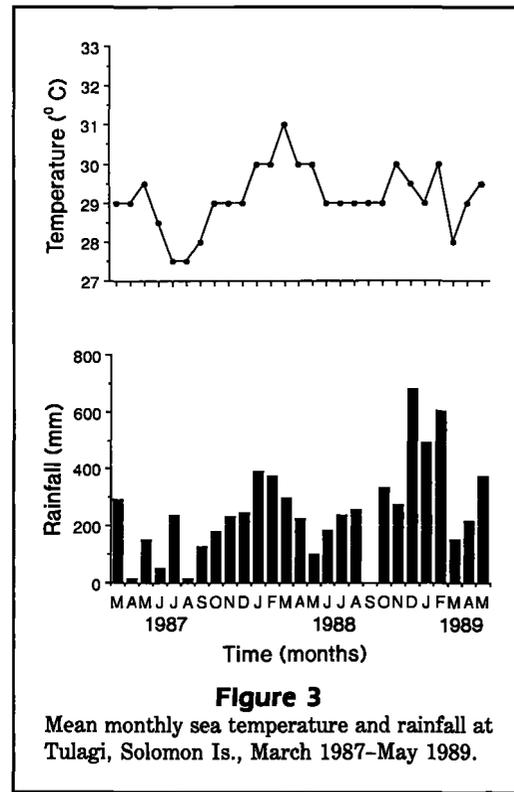
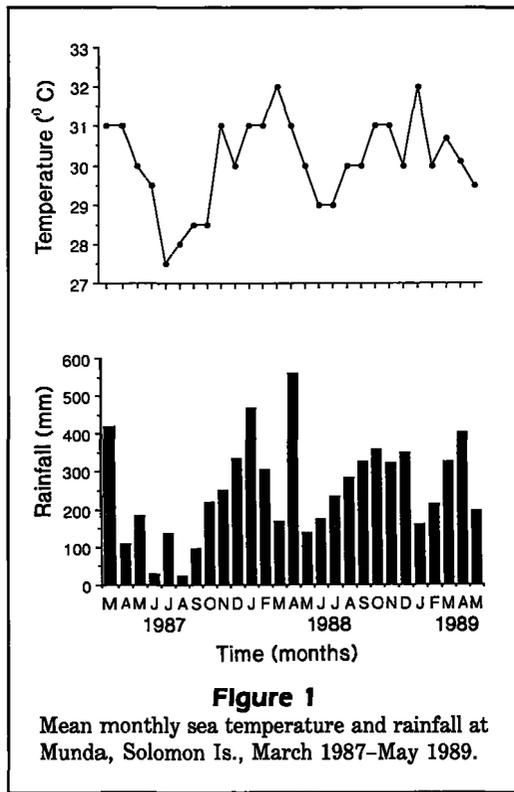
Physical environment

The mean sea-surface temperature and monthly rainfall at each site varied seasonally during the sampling period (Figs. 1–3). The temperature ranged from 27.5° to 32.5°C at all sites, with lower temperatures during the dry season (May–September). Temperatures were lower in 1987 than 1988 at all sites. Rainfall occurred in all months at all sites. The amount of rainfall and its monthly distribution pattern were similar at the two closest sites, Munda and Vona Vona (r^2 0.48, $P < 0.05$), but Tulagi had a higher rainfall and different pattern of distribution.

Maturation

A total of 1159 fish of six baitfish species from the three sites were examined histologically, including over 200 of each of the four most abundant species: *Encrasiicholina devisi*, *E. heterolobus*, *Spratelloides delicatulus*, and *S. lewisi*.

Encrasiicholina Histological examination of ripe ovaries of *E. devisi* and *E. heterolobus* showed that almost all oocytes were in the most advanced stage of development, with a few at the yolk precursor stage (Table 1) or less developed. Although many females (~15%) of those examined had hydrated eggs, no post-vitellogenic follicles or spent fish (Stage 6) were observed.



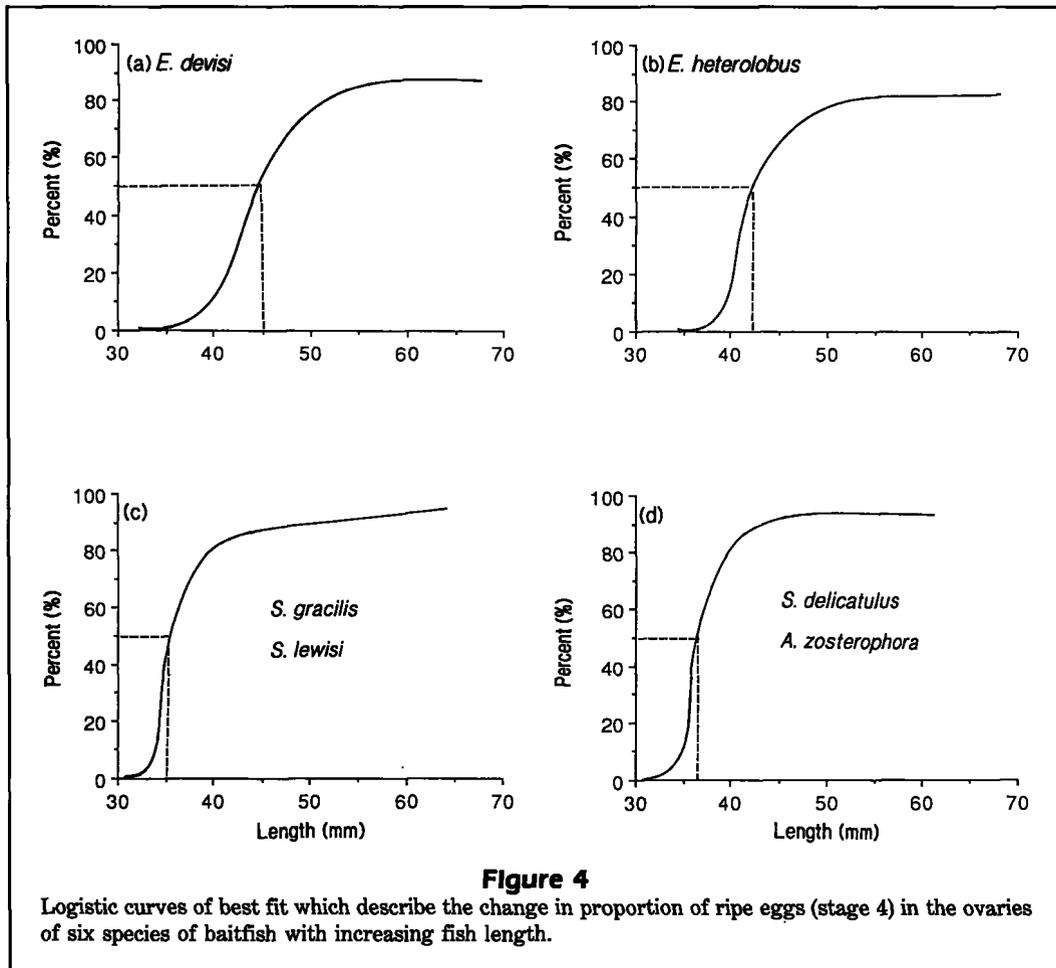
In both *Encrasicholina* species, fish with a GSI greater than 2% (Table 2) were sexually mature. The size at maturation of *E. devisi* was similar at all sites with 50% of the fish being sexually mature at 44–45mm (Fig. 4a). At Munda and Vona Vona, fish beyond this length were capable of spawning, but at Tulagi the smallest *E. devisi* in spawning condition was 52mm (Table 2). Sexual maturity in *E. heterolobus* was reached at approximately 43mm at Munda and Vona Vona (Fig. 4b) and 45mm at Tulagi. Hydrated eggs were not observed in *E. heterolobus* less than 50mm, except at Munda where the smallest potential spawner was 45mm (Table 2).

Spratelloides The three *Spratelloides* species at the three sites were mature at similar lengths. *Spratelloides gracilis* and *S. lewisi* were sexually mature and had hydrated eggs at 35mm (Table 2, Fig. 4c), except at Tulagi where the smallest *S. lewisi* with running ripe eggs was 40mm. *Spratelloides delicatulus* reached sexual maturity at 37mm (Fig. 4d), and running-ripe eggs were found in fish beyond this length. However, their length-at-maturity was not significantly different from the other *Spratelloides* species ($P > 0.1$). For all species, a gonosomatic index of over 2% correlated with fish having ripe eggs (stage 4) in the ovary. Most oocytes in the ovaries of females of these species were at a

Table 2

Minimum gonosomatic index (GSI) values used as criteria to estimate proportion of sexually mature fish (stage 3) and proportion of fish spawning (late stage 5) at each site, and minimum size (SL, mm) of fish in spawning condition (based on values obtained from fish examined histologically). *N* = sample size.

Species	Site	Sexual maturity		Spawning		
		GSI (%)	<i>N</i>	GSI (%)	Length	<i>N</i>
<i>Archamia zosterophora</i>	All	2.5	57	3.8	37	23
<i>Encrasicholina devisi</i>	Munda	2.0	86	9.0	45	39
	Vona Vona	1.8	80	7.0	45	41
	Tulagi	1.8	58	5.7	52	11
<i>Encrasicholina heterolobus</i>	Munda	2.0	134	8.5	45	26
	Vona Vona	1.9	135	8.8	50	24
	Tulagi	1.6	84	10.0	51	31
<i>Spratelloides delicatulus</i>	Munda	2.0	60	5.7	37	34
	Vona Vona	1.0	35	5.9	37	23
	Tulagi	1.2	43	5.5	38	25
<i>Spratelloides lewisi</i>	Munda	1.5	235	13.3	35	210
	Vona Vona	2.8	107	11.2	35	90
	Tulagi	1.0	24	12.5	40	10
<i>Spratelloides gracilis</i>	All	2.0	12	11.9	35	6



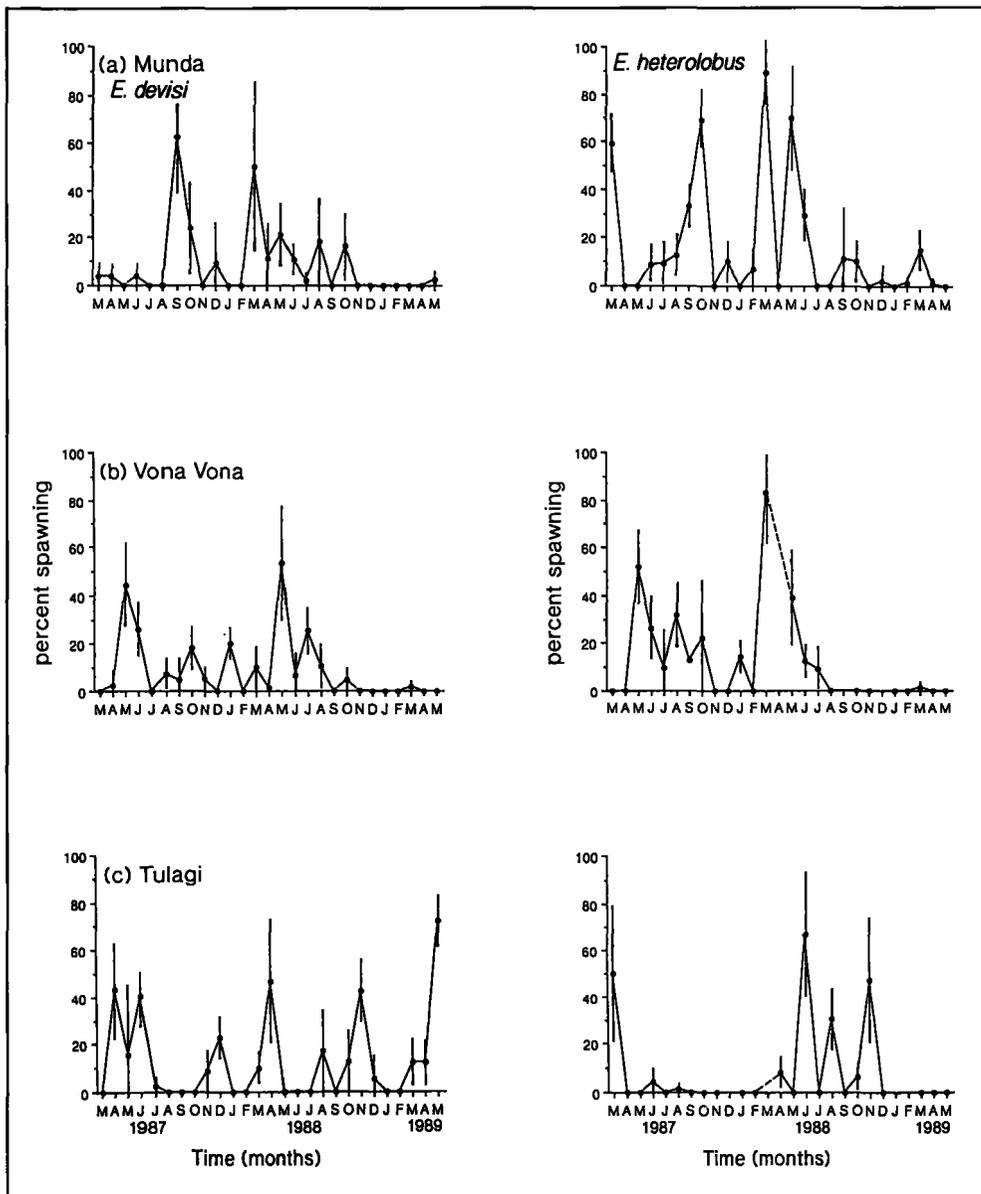


Figure 5

Monthly variation in proportion ($\pm 95\%$ confidence limits) of female *Encrasicholina devisi* and *E. heterolobus* spawning at three sites in the Solomon Islands, March 1987–May 1989.

similar stage of development. Fish with spent ovaries (Stage 6) were observed but were rare ($<1\%$).

Archamia zosterophora This species matured at 37mm and was capable of spawning at this length (Table 2, Fig. 4d). A gonosomatic index value greater than 2.5% corresponded with sexual maturity (Table 2).

Spawning seasons

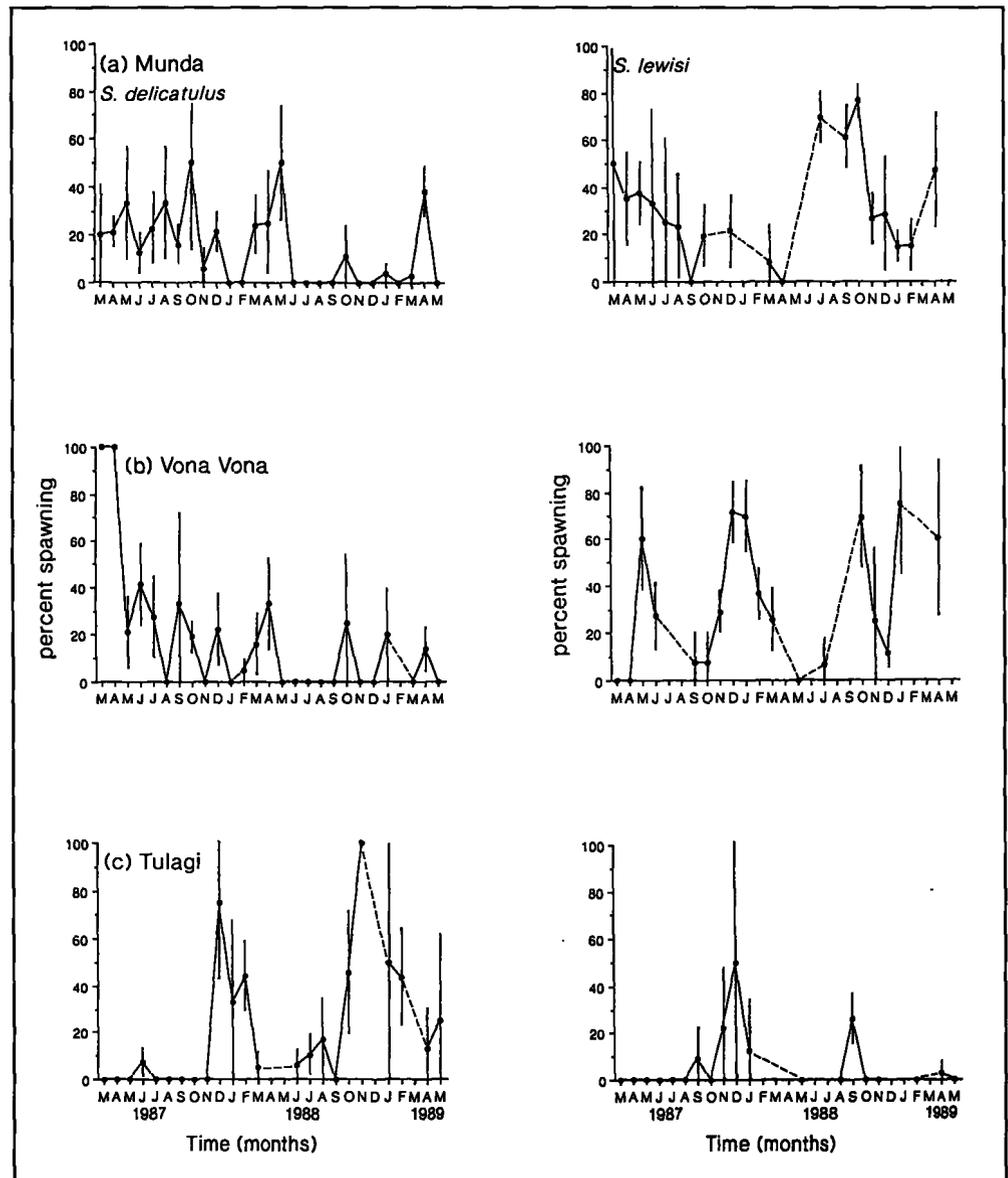
All non-parametric tests showed a significant deviation from random spawning for all species at all sites ($P < 0.05$). The distribution of deviations (plus signs) was either clumped or regular. For no species at any site were there significant positive correlations between the

proportion of larger fish and the proportion spawning ($P > 0.05$).

Encrasichollina Spawning activity by the two *Encrasichollina* species showed both seasonal and interannual variation (Fig. 5). Both species had one or two major peaks in spawning each year. However, the pattern was different each year. Both species had a major peak in spawning activity early in the year (March–May) during 1987 and 1988, except for *E. devisi* at Munda in 1987 when most fish spawned later (Sept.–Oct.). The peak spawning was usually followed by several months when a small proportion of the population was spawning. Patterns of spawning at Munda and Vona Vona were more similar than at Tulagi. *Encrasichollina*

Figure 6

Monthly variation in proportion ($\pm 95\%$ confidence limits) of female *Spratelloides delicatulus* and *S. lewisi* spawning at three sites in the Solomon Islands, March 1987–May 1989.



heterolobus also had fewer, smaller peaks in spawning activity during most of 1987 at Tulagi and at all sites during the first five months of 1989. *Encrasicholina devisi* in Munda and Vona Vona did not have a March–May spawning peak in 1989.

Spratelloides Two *Spratelloides* species also showed inter- and intraspecific differences in spawning activity between sites and between years (Fig. 6). *Spratelloides delicatulus* spawned continuously during 1987 at both Munda and Vona Vona, but the proportion spawning declined in the next 17 months. At Tulagi, the pattern was reversed, with less spawning during 1987 than in 1988–89 when there was a single major protracted spawning season from December to March

(Fig. 6c). *Spratelloides lewisi* showed seasonal spawning activity at all sites. Fish from Vona Vona and Tulagi had a similar pattern during 1987–88, with increased spawning activity from October to May. However, the proportion spawning at Tulagi (50%) was much lower. The spawning activity of *S. lewisi* at Munda showed no seasonal increase during 1987, although during 1988 a higher proportion was spawning during the middle of the year (Fig. 6).

Too few *S. gracilis* and *A. zosterophora* could be obtained to determine their spawning seasons. However, a proportion of the fish sampled of both species was in spawning condition for several months of the year (Fig. 7). *Archamia zosterophora* data from Munda showed that some spawning activity occurred through-

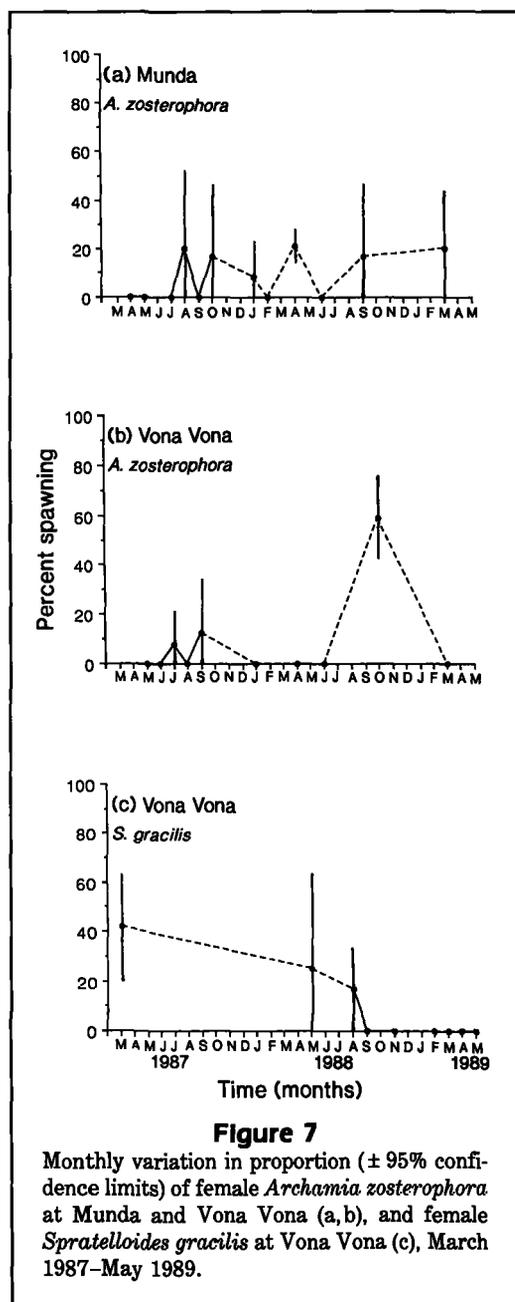


Figure 7

Monthly variation in proportion (\pm 95% confidence limits) of female *Archamia zosterophora* at Munda and Vona Vona (a,b), and female *Spratelloides gracilis* at Vona Vona (c), March 1987–May 1989.

out the year. At Vona Vona, however, there was a peak in spawning activity in samples taken in October 1988. The spawning data for *S. gracilis* are consistent with data for other *Spratelloides* at Vona Vona, with a decline in spawning activity during late 1988 and 1989 (Fig. 7).

Eggs and larvae *Encrasicholina* eggs were present in the zooplankton at each site most months of the sampling period (Fig. 8). The abundance of eggs did not vary greatly at each site during the period, al-

though the samples from Vona Vona had fewer eggs than the other sites. Overall, the mean *Encrasicholina* egg density for the entire sampling period varied from $0.08 \pm 0.03/\text{m}^3$ at Vona Vona to 0.43 ± 0.10 at Munda. The overall mean teleost egg density was also lower at Vona Vona ($1.34 \pm 0.21/\text{m}^3$) and highest at Munda ($4.98 \pm 0.10/\text{m}^3$). *Encrasicholina* egg density did not correlate with total egg density at any site ($P > 0.3$) or with the proportion of spawning *E. devisi* or *E. heterolobus* ($P > 0.5$). No *Spratelloides* larvae were found, although apogonid larvae were present but could not be identified to species.

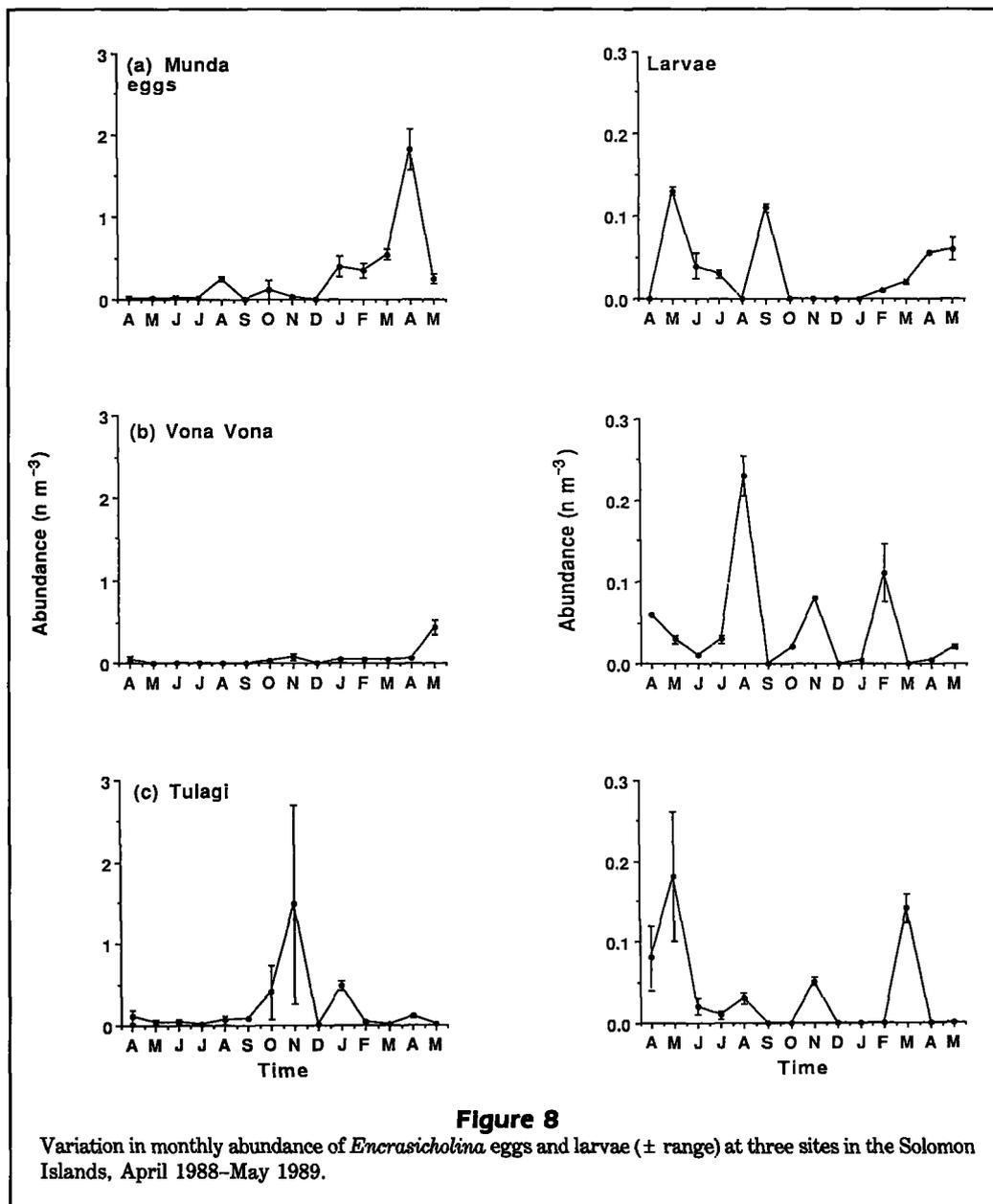
The density of *Encrasicholina* larvae followed a similar pattern at all sites (Fig. 8): larvae were present in most months, increasing every three or four months. In contrast to egg densities, *Encrasicholina* larvae reached higher densities at Vona Vona ($0.05 \pm 0.01/\text{m}^3$) than at Munda ($0.03 \pm 0.006/\text{m}^3$). Other fish larvae were also in higher densities at Vona Vona (1.15 ± 0.27) than at the other sites (Munda 0.93 ± 0.26 and Tulagi 0.60 ± 0.22). The density of *Encrasicholina* larvae was significantly correlated with the density of other fish larvae at Munda (r^2 0.62, $P < 0.05$), but not at other sites.

Proximate spawning stimuli

To assess the independence of the 11 proximate stimuli, all variables were correlated with one another (Table 3). At all sites, most measures of rainfall were significantly correlated ($P < 0.05$). Total rainfall was negatively correlated with moon phase at Vona Vona and Tulagi, and with zooplankton biomass at Tulagi. Cloud cover was correlated with total rain and days of rain at Tulagi ($P < 0.05$). Zooplankton biomass and density were correlated at Munda and Tulagi. However, there were no consistent correlations at all sites between non-rainfall variables (Table 3).

Principal component analysis was also performed separately on the proximate variables from each site. Rainfall variables at each site had loadings on the first three factors that were similar in magnitude and direction. Zooplankton density and biomass also covaried at each site. Temperature, moon phase, tide, and wind had loadings that varied independently for the first three factors at each site. These variables, zooplankton density, and the number of days of rain (which covaried least with other rainfall variables) were used in a separate stepwise regression analysis.

Encrasicholina Analysis of the relationships between all 11 environmental parameters and the proportion of each sample spawning showed no consistent pattern for either species of *Encrasicholina* (Table 4). At Munda, spawning of *E. devisi* positively correlated



with wind and time since rain. At Vona Vona there was a negative correlation with wind strength and positive correlation with zooplankton biomass and tide range. Spawning at Tulagi correlated most strongly with time since heavy rainfall (>25 mm), temperature, and zooplankton biomass (Table 4). When all data were included, time since heavy rain was the only significant correlate.

Stepwise regression analysis of the six independent proximate stimuli (Table 5) showed a much poorer fit. The only site that showed a significant relationship was Vona Vona, where full moon, greater tidal range, and

low wind accounted for 40% of the variation in spawning of *E. devisi*. Although not significant, days of rain had a similar coefficient in the equations of best fit at both Munda and Tulagi (Table 5), which suggests that rainfall had a similar effect on spawning at these sites.

The significant proximate stimuli for *E. heterolobus* differed between sites (Table 4). The best fit was obtained at Vona Vona (r^2 0.44, $P < 0.01$) where greater spawning occurred when cloud cover was low and moon phase approached full. Spawning was negatively related to total rainfall and days since rain at Munda (r^2 0.3, $P < 0.05$), and there was a negative

Table 3Correlations between independent environmental variables. * $P < 0.05$. See "Data analyses" section for explanation of variables.

Variable	Temp.	Biomass	Density	Moon phase	Tide range	Cloud cover	Wind speed	Rain*			
								Total	Days	Days 25 mm	Rain
Munda											
Temperature	x	-0.02	-0.12	-0.32	-0.20	0.41	0.18	0.46*	0.04	-0.19	0.37
Biomass		x	0.73*	-0.21	-0.08	0.21	-0.38	0.08	-0.36	0.00	0.30
Density			x	0.05	0.23	0.29	-0.23	-0.03	-0.22	0.05	-0.01
Moon phase				x	0.06	0.01	0.50*	-0.29	0.3	0.51*	-0.29
Tide range					x	-0.07	0.07	-0.09	0.47*	0.12	-0.05
Cloud cover						x	0.25	0.30	0.01	0.11	0.17
Wind speed							x	0.16	0.33	0.23	-0.11
Total*								x	-0.21	-0.62*	0.69*
Days									x	0.52*	-0.31
Days 25 mm										x	-0.54*
Rain											x
Vona Vona											
Temperature	x	-0.05	-0.46*	-0.25	0.08	0.38	0.06	0.25	-0.19	0.10	0.24
Biomass		x	0.31	-0.03	-0.32	0.21	0.39	-0.09	-0.15	-0.41	0.08
Density			x	0.19	-0.27	-0.15	0.26	-0.19	-0.03	-0.25	0.04
Moon phase				x	0.08	-0.29	-0.09	-0.55*	0.26	0.42*	-0.36
Tide range					x	-0.05	-0.34	-0.30	0.28	0.46*	-0.34
Cloud cover						x	0.49*	0.10	-0.21	0.03	0.25
Wind speed							x	0.16	-0.06	-0.28	0.12
Total*								x	-0.49*	-0.56*	0.62*
Days									x	0.33	-0.83*
Days 25 mm										x	-0.44*
Rain											x
Tulagi											
Temperature	x	-0.22	-0.20	-0.22	-0.33	0.10	-0.11	0.33	-0.40	-0.21	0.11
Biomass		x	0.70*	0.41*	0.24	-0.33	-0.15	-0.45*	0.14	0.09	-0.44*
Density			x	0.19	0.22	-0.45*	-0.45*	-0.40*	0.49	-0.05	-0.52*
Moon phase				x	0.22	-0.38	0.04	-0.51*	-0.00	0.10	-0.35
Tide range					x	-0.18	-0.19	-0.18	0.28	-0.13	-0.26
Cloud cover						x	0.39	0.52*	-0.33	-0.25	0.72*
Wind speed							x	0.06	-0.24	0.10	0.21
Total*								x	-0.36	-0.42*	0.67*
Days									x	0.15	-0.44*
Days 25 mm										x	-0.29
Rain											x

* Total = Total rainfall since previous sample
 Days = No. days since rain
 Days 25 mm = No. days since rain > 25 mm
 Rain = No. days of rain since previous sample.

relationship with tide range at Tulagi. Overall, the most significant variable was total rainfall. The results of the regression analysis of the independent stimuli (Table 5) were similar, except at Vona Vona where a four-variable model including zooplankton density, wind, and days of rain gave the best fit.

Spratelloides For *S. delicatulus*, moon phase was highly correlated with spawning and accounted for at least 26% of the variation in spawning periodicity at all sites (Table 4). Increased cloud cover and reduced tidal range were also correlated with spawning at Vona Vona and Tulagi. However, when data from all sites were combined, the most significant correlates were

Table 4

Stepwise multiple regression of best fit of 11 proximate variables related to the proportion of each species spawning at each site. Maximum number of variables allowed was three. Negative sign preceding a variable indicates negative correlation; r_p^2 = partial correlation coefficient, r^2 = overall correlation coefficient, P = significance level, N = sample size.

Species	Site	Environmental parameter	r_p^2	r^2	P	N
<i>Encrasicholina devisi</i>	Munda	Days since 25 mm rain	0.16	0.35	<0.05	22
		— Days since rain	0.10			
		— Wind speed	0.09			
	Vona Vona	— Wind speed	0.33	0.50	<0.01	21
		Zooplankton biomass	0.11			
		Tide range	0.06			
	Tulagi	Days since 25 mm rain	0.31	0.59	<0.005	19
		Temperature	0.25			
		Zooplankton biomass	0.03			
	Overall	Days since 25 mm rain	0.12	0.14	<0.01	62
— Days since rain		0.02				
<i>Encrasicholina heterolobus</i>	Munda	— Total rainfall	0.19	0.30	<0.05	22
		— Days since rain	0.11			
	Vona Vona	— Cloud cover	0.32	0.44	<0.01	21
		— Moon phase	0.12			
	Tulagi	— Tide range	0.24	0.24	<0.05	16
	Overall	— Total rainfall	0.11	0.14	<0.05	59
			Temperature	0.03		
<i>Spratelloides delicatulus</i>	Munda	Moon phase	0.28	0.28	<0.01	22
	Vona Vona	Moon phase	0.26	0.50	<0.01	22
		— Tide range	0.13			
	Tulagi	Cloud cover	0.11	0.60	<0.005	17
		— Moon phase	0.51			
	Overall	— Cloud cover	0.09	0.13	<0.05	61
		— Tide range	0.05			
— Zooplankton biomass		0.04				
		Cloud cover	0.04			
<i>Spratelloides lewisi</i>	Munda	Zooplankton biomass	0.22	0.41	<0.05	18
		Days since rain	0.10			
		Cloud cover	0.09			
	Vona Vona	Cloud cover	0.29	0.62	<0.01	15
		— Wind speed	0.19			
		— Moon phase	0.14			
	Tulagi	— Temperature	0.39	0.66	<0.01	14
		— Zooplankton biomass	0.16			
Overall	— Days since rain	0.11	0.20	<0.01	47	
	Temperature	0.13				
	Zooplankton biomass	0.07				
<i>Spratelloides gracilis</i>	Vona Vona	Moon phase	0.62	0.32	<0.05	8
		Temperature	0.10			
		Zooplankton biomass	0.10			
<i>Archamia zosterophora</i>	Munda	— Days since 25 mm rain	0.49	0.65	<0.01	11
		— Days since rain	0.16			
	Vona Vona	Zooplankton biomass	0.42	0.42	<0.05	10
	Overall	— Days since 25 mm rain	0.30	0.41	<0.05	21
		Zooplankton biomass	0.11			

negative tide range, cloud cover, and negative zooplankton biomass. When the number of variables were reduced (Table 5), wind and days of rain at Vona Vona and temperature at Tulagi were also significant ($P < 0.05$). Among samples from months where spawning

had been detected, moon phase and days of rain showed the best fit.

There was significant positive correlation between spawning of *S. lewisi* and zooplankton biomass and days since rain at Munda (Table 4). Lower temperature,

Table 5

Stepwise linear regression models of best fit for six independent proximate stimuli. y = percent spawning; t = temperature; d = zooplankton density; m = moon phase; ti = tidal range; w = wind speed; r = days of rain between samples; r^2 = multiple regression coefficient; P = significance level; N = sample size. Overall includes all samples; spawning includes only months when spawning was detected.

Species	Site	Model	r^2	P	N
<i>Encrasicholina devisi</i>	Munda	$y = 0.53 - 0.02r$	0.14	<0.08	22
	Vona Vona	$y = 3480m + 0.29ti - 0.15w - 3479$	0.40	<0.05	21
	Tulagi	$y = 0.14t - 0.0003d - 0.18r - 2.89$	0.33	<0.07	19
	Spawning	$y = 0.52 - 0.006r$	0.02	<0.44	40
	Overall	$y = 0.50 - 0.0001d - 0.01r$	0.07	<0.10	62
<i>Encrasicholina heterolobus</i>	Munda	$y = 0.92 - 0.15r$	0.08	<0.22	22
	Vona Vona	$y = 3741m + 0.0001d - 0.26w - 0.08r - 3742$	0.50	<0.05	21
	Tulagi	$y = 0.79 - 0.92ti$	0.24	<0.05	16
	Spawning	$y = 0.10t - 0.57ti - 0.02r - 1.73$	0.27	<0.05	33
	Overall	$y = 2459m - 0.42ti - 0.02w - 0.01r - 2458$	0.16	<0.05	59
<i>Spratelloides delicatulus</i>	Munda	$y = 7084m - 0.0001d - 0.37ti - 7083$	0.38	<0.05	22
	Vona Vona	$y = 10759m + 0.27w + 0.13r - 10759$	0.49	<0.01	22
	Tulagi	$y = 8825 + 0.11t - 8828m$	0.51	<0.005	17
	Spawning	$y = 3510m + 0.02r - 3510$	0.16	<0.05	38
	Overall	$y = 0.57 - 0.36ti$	0.05	<0.11	61
<i>Spratelloides lewisi</i>	Munda	$y = 0.0003d + 0.17r - 0.39$	0.24	<0.13	18
	Vona Vona	$y = 5217 - 5216m$	0.15	<0.15	15
	Tulagi	$y = 1.40 - 0.04t - 0.25ti$	0.26	<0.17	14
	Spawning	$y = 0.02r - 0.0001d + 0.34$	0.30	<0.01	29
	Overall	$y = 0.08t - 0.03w + 0.01r - 2.34$	0.23	<0.01	47
<i>Spratelloides gracilis</i>	Vona Vona	$y = 12588m + 0.56ti - 12587$	0.86	<0.05	8
<i>Archamia zosterophora</i>	Munda	$y = 4262 - 4262m - 0.49ti$	0.50	<0.06	11
	Vona Vona	$y = 0.08t - 1.98ti - 0.80$	0.94	<0.001	10
	Spawning	$y = 3957 - 3956m$	0.30	<0.16	8
	Overall	$y = 0.72 - 0.79ti$	0.46	<0.001	21

low zooplankton biomass, and recent rain explained 66% of the variation in spawning periodicity at Tulagi ($P < 0.01$). Cloudy conditions, light winds, and waning moon phases were the variables most correlated with spawning in *S. lewisi* at Vona Vona (Table 4). However, the combined data showed that temperature and zooplankton biomass were the most significant stimuli. These conflicting results were reflected in the second analysis, where the stimuli chosen could not explain a significant amount of the variation in spawning at any site (Table 5).

Correlations between environmental stimuli and the spawning periodicity of *S. gracilis* could only be analysed for fish from Vona Vona. Most variation could be explained by moon phase, temperature, tide, and zooplankton biomass (Tables 4, 5). Most fish spawned at full moon and when temperature, tidal range, and prey biomass were high.

Archamia zosterophora This species was most frequently caught at Munda and Vona Vona where it

spawned most often during periods of high rainfall (at Munda), and when zooplankton biomass was high (at Vona Vona) (Table 4). These variables were also the most significant when all data were combined. When these variables were excluded from the analysis (Table 5), lower tidal range and higher temperatures (Vona Vona) were the only significant stimuli.

Discussion

Size-at-sexual-maturity of some *Encrasicholina* and *Spratelloides* species from the Solomon Islands varied both locally and compared with other studies elsewhere in the South Pacific.

Encrasicholina heterolobus and *S. gracilis* reached sexual maturity at smaller lengths than previously reported (Tham 1965; Tiews et al. 1971; Dalzell and Wankowski 1980; Conand 1985; Dalzell 1985, 1987b). Such differences may be partly an artifact of the different sexual maturity criteria used. The present study,

unlike others, used histological examination of gonads to verify macroscopic stages.

In the Solomon Islands, *Encrasicholina devisi* reached sexual maturity at 45 mm, and some fish at this size were in spawning condition. This is consistent with results from Papua New Guinea (Dalzell and Wankowski 1980), New Caledonia (Conand 1985), and southern India (Luther 1979). *Spratelloides delicatulus* also showed little difference throughout the region in length-at-sexual-maturity (Lewis et al. 1983, Conand 1985, McCarthy 1985).

Spratelloides lewisi showed local variation in length-at-sexual-maturity. Fish from Tulagi were not sexually mature at less than 40 mm (compared with 35 mm at other sites) and they also grew to a greater size than fish from the other sites (unpubl. data).

Length-at-first-spawning, however, was similar for both *Encrasicholina* species and *S. delicatulus* throughout the region (Dalzell and Wankowski 1980, Lewis et al. 1983, Conand 1985), except for *E. heterolobus* at Munda, where fish were in spawning condition at a smaller length than at the other sites in the Solomon Islands.

Both *Spratelloides lewisi* and *S. gracilis* showed variation in length-at-first-spawning between sites. At Tulagi, *S. lewisi* did not spawn until a much greater length was attained. These results are consistent with those of Dalzell (1987), who found a difference of 9 mm in the length-at-first-spawning in two populations of *S. lewisi* in Papua New Guinea waters. Dalzell (1985) also found that Papua New Guinea *S. gracilis* did not develop ripe eggs until 44 mm, which was much larger than the length-at-first-spawning of fish from the Solomon Islands (35 mm). Unfavorable conditions for reproduction may delay the onset of gonadal development in these species at some sites to help offset reproductive uncertainty (Mann and Mills 1979).

No comparative data on length-at-sexual-maturity of *A. zosterophora* are available, and there are few data for other similar-sized apogonids. However, this species matures at almost 80% of maximum size, which is larger than in the clupeoids (70%). The subtropical Australian species *Apogon fasciatus* also matures at about 70% of maximum size (90 mm) near Brisbane (K. Warburton, Zool. Dep., Univ. Queensland, Brisbane, Australia, unpubl. data).

The relationship between length-at-first-spawning and maximum length of the Solomon Islands baitfish closely fits that found for other clupeoids (Beverton 1963). Beverton (1963) showed that length-at-first-spawning among clupeoids is closely proportional to maximum length, with smaller species spawning at a smaller size (relative to their maximum) than larger ones (Blaxter and Hunter 1982). Longhurst and Pauly (1987) hypothesize that length-at-sexual-maturity and

maximum length are determined by the interactions of oxygen supply and demand. Any species of fish living in cold water should grow to a greater size and mature at a larger size than the same species in warm water, given similar food supplies. Water temperature at Tulagi was consistently 1–2°C colder than at the other sites, and this may account for differences in these parameters in *S. lewisi* at this site. The regional differences seen in *E. heterolobus* and *S. gracilis* also support this idea, with fish from higher latitudes maturing at greater lengths. However, similar patterns were not found in the other species. Availability of food also must play an important role by affecting growth rates.

Many clupeoids, including most engraulids, are multiple spawners (Blaxter and Hunter 1982), and studies of other engraulids suggest they spawn batches of eggs every 2–10 days (Hunter and Goldberg 1980, Alheit et al. 1984, Clarke 1987). Smaller species (e.g., *Encrasicholina purpureus*) spawn more frequently during the peak spawning period (as often as every 2 days; Clarke 1987). The spawning frequency of multiple spawning fish can be determined by the presence or absence of postvitellogenic follicles in the ovaries; their presence indicates that a fish has spawned within the previous 24–48 hours (Hunter and Goldberg 1980). Clarke (1987) reported that postvitellogenic follicles were distinguishable in *Encrasicholina purpureus* up to 16 hours after spawning. In our study, we did not find either postvitellogenic follicles or a continuous egg-size distribution indicative of multiple spawning (Blaxter and Hunter 1982). However, the similarity in reproductive behavior of *Encrasicholina* species and the presence of eggs in the plankton throughout most of the year suggest that *E. devisi* and *E. heterolobus* are also multiple spawners. Our data on *Encrasicholina devisi* and *E. heterolobus* were consistent with that of Leary et al. (1975) on *Encrasicholina purpureus*. We found, as had Leary et al., only two egg sizes: one advanced and one with all eggs at the yolk-precursor stage of development. Leary et al. (1975) interpreted these results to indicate that *E. purpureus* spawned once in its lifetime. However, Clarke (1987) found that *E. purpureus* eggs could mature very rapidly, and hence timing of sampling was critical. Running-ripe eggs were only present shortly before spawning, which occurred one or two hours after sunset. If *E. devisi* and *E. heterolobus* are batch spawners similar to *E. purpureus*, then we would expect to collect only fish about to spawn in our samples, as the postvitellogenic follicles of fish that spawned the previous night would have degraded (Clarke 1987). However, spawning is probably less frequent than in the smaller *E. purpureus* because greater energy is required by larger fish to maintain continuous spawning (Hunter and Leong 1981).

Ovaries of the three species of *Spratelloides* and *A. zosterophora* all contained only a single size-group of developing oocytes, which suggests that they spawn all the eggs in the ovaries at once. Whether a female develops another batch of eggs after spawning was not determined. However, given the high proportion of female *Spratelloides* spawning at any time, it seems probable that each female produces more than one batch of eggs. Most apogonids are mouth-brooders (Thresher 1984), and other species have been found with eggs in their buccal cavity that are at more than one stage of development, which suggests that they are multiple spawners (Thresher 1982).

Flexibility in reproduction is well documented among a range of animals and usually involves a direct physiological response to nutrient level or some associated environmental cue (Giesel 1976). Extended breeding seasons are a common phenomenon among tropical fishes, particularly coral reef fish (Munro et al. 1973, Russell et al. 1977, Johannes 1978, Lowe-McConnell 1979, Walsh 1987). The present work, and other studies of *Encrasicholina*, *Spratelloides*, and apogonid reproduction (Leary et al. 1975; Russell et al. 1977; Dalzell and Wankowski 1980; Dalzell 1985, 1987ab; Conand 1985; McCarthy 1985; Clarke 1987), found that the spawning season of these fish is protracted, with some individuals in the population spawning at any time during the year. There are also periods when most of the population is spawning. If reproduction were controlled only by endogenous cycles and females spawned as soon as they were physiologically capable, then as the proportion of larger fish increased there should be a greater proportion of spawning fish in the population. Examination of our data failed to find any significant relationship between the proportion of larger fish and the proportion spawning for any species at any site. Non-parametric tests also showed that the frequency of major spawnings was not random. Hence it is unlikely that spawning periodicities shown by baitfish are a result of intrinsic mechanisms. The timing and intensity of periods of increased spawning activity appear to be highly variable, linked to exogenous stimuli and with no endogenous rhythms.

Of the several hypotheses put forward to explain the timing of fish reproduction, one of the more widely accepted is the "match-mismatch" hypothesis of Cushing (1967). This proposes that if the timing of reproduction coincides with peaks in the plankton cycle, larval survival is enhanced. Timing of peak plankton production does not necessarily occur at exactly the same time each year, so if fish are serial spawners they can exploit the plankton cycle well (e.g., California sardine) by spawning during any of the months of spring or summer when food becomes superabundant (Cushing 1975). Much of the data to support this hypothesis comes from

temperate waters, but data on the reproduction of tropical clupeoids from open oceans also support this hypothesis (Longhurst 1971, Roy et al. 1989).

Johannes (1978) proposed that coastal tropical fish tend to spawn at times and locations that will reduce predation on larvae by transporting them out of the adult habitat, while enabling them to return to suitable areas for postlarval settlement. At many sites, periods of major spawning coincide with low winds and full moon. The baitfish species studied here spawn in lagoons fringed by coral reefs, where water currents are negligible. Both adults and larvae are pelagic and live in the deeper waters of the lagoon. When the larvae are abundant, adults prey on them (Milton et al. 1990). If deeper waters of the lagoon are the favored habitat, then according to Johannes' hypothesis (1978) adults should spawn when local flushing is greatest (spring tides) but regional flushing is least (low winds) to ensure larvae develop in the same area.

Although baitfish spawn throughout the year, with no consistent seasonal pattern, there appears to be some regularity in their spawning. At each site, certain proximate factors were significant for more than one species. This suggests that if these fish are responding to exogenous spawning stimuli, their influence must be interposed by local hydrography and topography. At Vona Vona, spawning by five of the six species examined was correlated with moon phase. Both *Encrasicholina* and two *Spratelloides* species spawned around the full moon, while *S. lewisi* spawned around the new moon. Both *Encrasicholina* species also spawned when wind strength was reduced. The spawning around phases of the moon has often been assumed to be related to increased tidal exchange during spring tides (e.g., Johannes 1978, Walsh 1987). However, in this study greater tidal range at any site was not directly correlated with moon phase (Table 3). Vona Vona is an enclosed lagoon with many islands and patch reefs. In this habitat, spawning around the full or new moon does not appear to be related to the potential to flush eggs and larvae to more favorable habitats by tidal water movement (Johannes 1978). Possibly, spawning around the full moon when the wind is reduced may increase spawning success by increasing visibility at night (during spawning) and reducing the dispersal of eggs, and hence increasing the chances of fertilization. This hypothesis would also explain the strong negative relationship between spawning by *A. zosterophora* and tidal range at this site.

Moon phase was the single variable most often correlated with spawning in this study, both for five species at one site (Vona Vona) and for one species at different sites (*S. delicatulus*). However, our data do not indicate a strong relationship with moon phase for either *Encrasicholina* species at Munda or Tulagi. This

suggests that either local conditions exert a strong influence on the timing of reproduction in these species or that at these sites reproduction is not strongly linked to particular environmental events. Wright (1989) also found no relationship between spawning by *E. heterolobus* in Indonesia and temperature, rainfall, or tidal phase, and suggested that these factors were not influencing spawning.

However, among the other species, temperature and reduced tidal range appear to be more important at Tulagi. Higher temperatures should allow increased growth under favorable conditions, and reduced tidal exchange would reduce egg movement away from favorable habitats.

While rainfall has been suggested as a proximate factor influencing spawning by *Encrasicholina* species in Papua New Guinea (Dalzell and Wankowski 1980; Dalzell 1984, 1987b), in our study rainfall was only weakly correlated with spawning of *Encrasicholina* at Munda (Tables 4, 5). Spawning appeared to be greater during periods of lower rainfall. Positive relationships between spawning and time since rain or less rain may be indirectly linked to phytoplankton production, which is determined by light or the depth of mixing (Wyatt 1980). Variations in wind strength and cloudiness will cause major variations in the onset and end of the phytoplankton production cycle (Blaxter and Hunter 1982). If rainfall at Munda is linked to the phytoplankton cycle, spawning during periods of low rainfall would be consistent with Cushing's (1967) hypothesis. Some previous studies in southeast Asia and Papua New Guinea (Tiews et al. 1971, Sitthichockpan 1972, Dalzell 1987b) have suggested that *Encrasicholina* spawned more intensively during the months of peak zooplankton production.

The variation in spawning frequency observed among the species in this study suggests that each responds differently to local conditions, reacting to those variables most appropriate to maximize reproductive success in the immediate environment (Bye 1984). No obvious differences were detected in baitfish spawning patterns between the exploited fishing grounds and the unexploited site. If baitfish numbers are higher at the unexploited site, this suggests, in turn, that differences in the observed spawning patterns were not density-dependent. Lack of clear proximate stimuli for spawning among the six species examined makes it difficult to predict the timing of major spawning events by these species.

However, protracted spawning and the baitfish population's adaptation to local conditions suggests that these species should be resilient to increased fishing mortality. Factors affecting larval survival and growth may be more important in determining recruitment to the fishery.

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