

Abstract.—The spawning seasonality, fecundity, and daily egg production of three species of short-lived clupeids, the sardine *Amblygaster sirm*, the herring *Herklotsichthys quadrimaculatus*, and the sprat *Spratelloides delicatulus* were examined in Kiribati to assess whether variable recruitment was related to egg production. All species were multiple spawners, reproducing throughout the year. Periods of increased spawning activity were not related to seasonal changes in the physical environment. Spawning activity and fish fecundity were related to available energy reserves and, hence, food supply. The batch fecundity of *A. sirm* and *S. delicatulus* also varied inversely with hydrated oocyte weight.

The maximum reproductive life span of each species was less than nine months and averaged two to three months. Each species had a similar spawning frequency of three to five days, but this varied more in *A. sirm* and *S. delicatulus*. *Amblygaster sirm* had the highest fecundity and potential lifetime egg production, but the number of eggs produced per kilogram of fish was highest in the small sprat *S. delicatulus*.

Monthly estimates of the daily egg production of each species varied with the proportion of the population that was spawning. Estimates of egg production showed little similarity to the frequency distribution of birthdates back-calculated from length-frequency samples. The distribution of back-calculated birthdates confirmed that fish spawned in all months, but the proportion born each month varied widely from species to species and year to year. The reproductive strategy of these species ensures that successful spawning is likely, and so the level of recruitment is more dependent on post-hatching survival rates than on egg production.

Reproductive biology and egg production of three species of Clupeidae from Kiribati, tropical central Pacific

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The sprat *Spratelloides delicatulus*, the herring *Herklotsichthys quadrimaculatus*, and the sardine *Amblygaster sirm* are the dominant tuna baitfish species in the Republic of Kiribati (Rawlinson et al., 1992). All three species inhabit coral reef lagoons and adjacent waters. Sprats school in shallow water around reefs and adjacent seagrass during the day. Herring also form dense schools in shallow water along the shoreline and among reefs during the day (Williams and Clarke, 1983). Unlike the other species, sardines school near the bottom of the lagoon during the day (Conand, 1988). All species disperse into the mid and upper waters of the lagoon during the night to feed and become available to the commercial fishery.

A major source of lost fishing time by pole-and-line vessels in Kiribati has been irregular baitfish catches (MacInnes, 1990). These important tuna baitfish species have shown large seasonal and interannual fluctuations in abundance since they were first recorded during the 1940's (McCarthy, 1985¹; Rawlinson et al., 1992). Both *A. sirm* and *H. quadrimaculatus* disappear from baitfish catches for variable periods and can be absent for months or years (Kiribati Fisheries Division, 1989²).

Changes in abundance may be related to variable or irregular recruitment, because many clupeoids (especially clupeids and engraulids) have little capacity to compensate for environmental variation during the period of peak spawning and egg production (Cushing, 1967, 1971).

Most clupeids, including some tropical species, are multiple spawners (Alheit, 1989). Multiple spawning should be advantageous for short-lived species because it enables them to maintain relatively stable population sizes in unpredictable environments (Armstrong and Shelton, 1990). Multiple spawning has been established for few tropical clupeids (e.g., *Sardinella brasiliensis*; Isaac-Nahum et al., 1988). Of the three major baitfish species in Kiribati, only *S. delicatulus* has been shown to be a multiple-spawner (Milton and Blaber, 1991). All three species are subject to high natural mortality in Kiribati (Rawlinson et al., 1992), thus lifetime egg production

¹ McCarthy, D. 1985. Fishery dynamics and biology of the major wild baitfish species particularly *Spratelloides delicatulus*, from Tarawa, Kiribati. Kiribati Fisheries Div., Tarawa, Kiribati, 53 p.

² Kiribati Fisheries Division. 1989. Fisheries Division 1989 Annual Rep., Ministry of Natural Resources Development, Tarawa, Kiribati, 38 p.

may be increased if they spawned multiple batches of eggs.

Egg production of multiple spawning species depends on reproductive life span, the time between spawnings, and the age structure of the population (Parrish et al., 1986). Batch fecundity of *S. delicatulus* varies widely between sites, both within and between countries (Milton et al., 1990). In a short-lived species such as *S. delicatulus* (<5 months; Milton et al., 1991), reproductive life span may have an important influence on potential lifetime egg production.

Batch fecundity of *H. quadrimaculatus* does not appear to vary throughout its distribution, and ranges from 4,000 to 10,000 eggs (Marichamy, 1971; Hida and Uchiyama, 1977; Williams and Clarke, 1983; Moussac and Poupon, 1986; Conand, 1988). Fish mature at about 90 mm in length at six months of age (Williams and Clarke, 1983), and they survive for at least one year (Milton et al., 1993). Little is known of fecundity and egg production of *A. sirm.* Fecundity of the species is related to length and weight, with a mean of 20,000 eggs per batch, and individuals probably spawn more than one batch of eggs (Conand, 1988).

Temperate clupeids vary widely in life-history parameters (e.g., *Clupea* spp., Jennings and Beverton, 1991). Food availability and environmental conditions affect the size and number of eggs of Pacific herring (*Clupea pallasii*) (Hay and Brett, 1988). Results of studies of temperate clupeoids suggest that they do not spawn during periods of high food abundance, but store energy as fat for later reproductive activity (Hunter and Leong, 1981; Iles, 1984). There are no similar studies of tropical clupeids. *Encrasicholina heterolobus*, a tropical engraulid, does not deplete energy reserves in the liver or soma during spawning (Wright, 1990). Fish with higher condition factor (*K*) also had higher fecundity.

Stored energy or fish condition that may influence both spawning frequency and batch fecundity have a marked influence on egg production and, hence, affect subsequent recruitment (Ricker, 1954; Beverton and Holt, 1957). Adult reproductive variation should strongly influence recruitment in short-lived tropical species that have short larval phases and rapid growth. An example is *S. delicatulus* which, in the Solomon Islands, live a maximum of five months and mature at about two months of age (Milton and Blaber, 1991; Milton et al., 1991). *Amblygaster sirm* and *H. quadrimaculatus* live less than two years (Milton et al., 1993) and mature in 6–12 months (Williams and Clarke, 1983; Conand, 1988).

In this study, we examined the variability in reproductive biology of the three major baitfishes in Kiribati to determine the influence of adult reproductive variability on subsequent recruitment. Our objective was to test the hypothesis that reproductive biology of short-lived clupeids is adapted to maintaining relatively stable population sizes. We determined potential life-time egg production and whether estimated egg production is related to the frequency distribution of back-calculated birthdates.

Methods and materials

Study areas

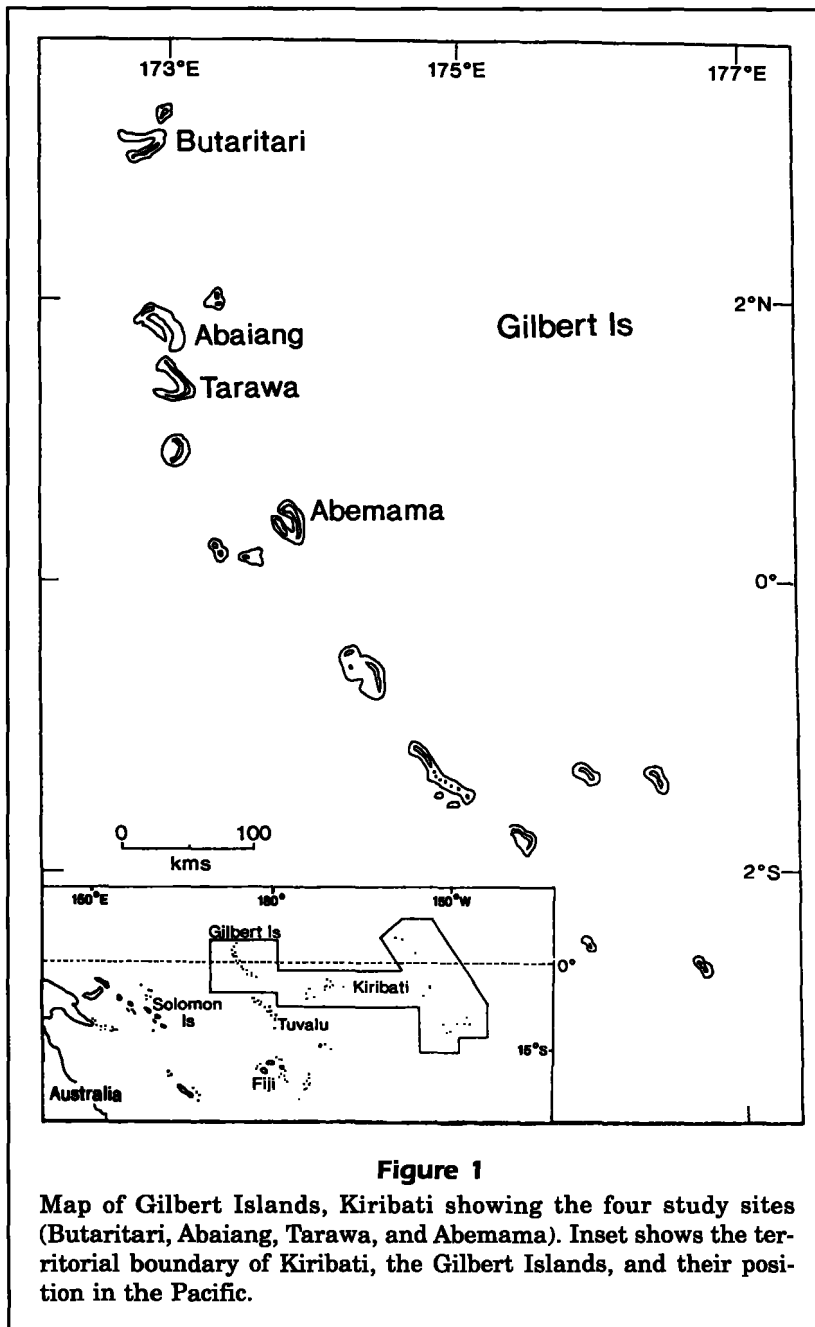
The Republic of Kiribati covers an area of 3×10^6 km² in the central Pacific ocean and comprises three main island groups (Gilbert, Phoenix, and Line Islands) (see Inset Fig. 1). The Gilbert Island group is the most populated, consisting of 16 coral reef islands. All islands in the group have a typical ocean platform coral reef structure and have been built up by scleractinian corals and coralline algae on a submerged mountain (Gilmour and Colman, 1990³). Most atolls consist of small islets lying on the eastern side of a lagoon with an open western side due to the prevailing easterly winds. Most typically have passages between the islets through which water is exchanged.

The four study sites (Abaiang, Butaritari, Tarawa, and Abemema) were typical of islands in the Gilbert Island group; all had narrow islets on their southern and eastern sides, except Abaiang (Fig. 1). Lagoons were mainly shallow (20–30 m deep), often with large areas of intertidal seagrass or sand on their eastern sides. Bottom topography of the deeper parts of the lagoon was generally smooth, with some coral outcrops. Our study sites were similar to those described by Hobson and Chess (1978) in the Marshall Islands.

Environmental parameters

On each sampling occasion, we measured the time of collection, sea surface temperature (°C), cloud cover (okters), wind direction and speed, and moon phase because these factors may be related to spawning or recruitment (Dalzell, 1985, 1987; Peterman and Bradford, 1987; Milton and Blaber, 1991). For each site, monthly rainfall data for 1989

³ Gilmour, A. J., and R. Colman. 1990. Report on a consultancy on a pilot environmental study of the outer island development program, Republic of Kiribati. Graduate School of the Environment, Macquarie Univ., Australia, 151 p.



and 1990 were obtained from the Kiribati Government Meteorological Division.

Sampling

Fifty to 1,000 *Amblygaster sirm*, *Herklotsichthys quadrimaculatus*, and *Spratelloides delicatulus* were collected monthly at one or more of four sites in Kiribati (Butaritari, Abaiang, Tarawa, and Abemama; Fig. 1) between August 1989 and May 1991. Additional samples of *A. sirm* and *H. quadrimaculatus* were collected in November 1988

and January 1989 from Tarawa. Fish were caught by several methods at each site. Most samples were collected from the commercial tuna baitfish catches each month at each site. Supplementary samples were obtained by beach-seining (*H. quadrimaculatus* and *S. delicatulus*), cast-netting (*H. quadrimaculatus*) in shallow water during the day, or gill-netting (25- and 38-mm stretched mesh) at night near baitfishing operations. All fish were preserved in 70% ethanol.

Reproductive biology

Laboratory studies All fish collected from commercial baitfish sampling were measured (standard length in millimetres), and a subsample of 20 to 60 specimens weighed (± 0.005 g). Gonads, otoliths, liver, and viscera were removed and the amount of visible fat subjectively estimated. Both ovaries from the first 20 females of each species at each site for each month were dried of surface moisture, weighed (± 0.001 g) and stored in 4% formalin-seawater for histology. Testes, ovaries of other fish, liver, and the soma were dried at 60°C to a constant weight. Otoliths were used to estimate the age (in days) of each fish by methods outlined in Milton et al. (1993). Additional samples of fish caught by other methods were treated separately, but in a similar way. We report only on results of studies of fish collected from commercial samples unless otherwise stated.

For histological preparations, gonads were embedded in paraffin, sectioned at 9 mm, 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), and were similar to those of Moussac and Poupon (1986) for *H. quadrimaculatus* from the Seychelles. We staged each gonad according to the relative numbers of cells at each developmental stage (Young et al., 1987; Table 1), and the presence of any post-ovulatory follicles was noted. The percentage of each histological section that corresponded to each developmental stage was subject-

Table 1

Criteria used for staging female gonads of tropical clupeids stained with haematoxylin and eosin.

Stage	Histology
(1) Immature	Chromatin nucleolar stage — prefollicle cells surround each oocyte
(2) Developing/resting	Perinucleolar stage — uniform staining cytoplasm
(3) Maturing	Yolk vesicle formation; some non-staining yolk (lipid)
(4) Ripe	Vitellogenic stage — red-staining yolk; developed chorion
(5) Running ripe (spawning)	Globular red-staining yolk; oocytes hydrated; development complete
(6) Spent	Presence of post-ovulatory follicles; cortical alveoli present and/or atresia of remaining ripe oocytes

tively estimated. Post-ovulatory follicles were aged according to stages found in other multiple-spawning clupeoids (Hunter and Goldberg, 1980; Goldberg et al., 1984; Isaac-Nahum et al., 1988). Gonosomatic indices (GSI) were calculated as the ratio of wet gonad weight to somatic weight (total weight minus gonad weight), expressed as a percentage. Similarly, we calculated a hepatosomatic index (HSI) as the ratio of liver dry weight to somatic dry weight (total weight minus entire viscera), expressed as a percentage.

Length and age at sexual maturity were defined as the minimum size and age at which fish had ripe oocytes (Stage 4), determined by histological examination. Fish that had running-ripe oocytes (Stage 5) were recorded as in spawning condition. We defined the length and age at first spawning as the smallest size where the proportion of running-ripe oocytes in the section exceeded 85% for more than 50% of the fish of that length or age. We chose this criterion after examining large numbers of histological sections with running-ripe oocytes. In these sections they always represented more than 85% of the section area. Our results were similar to that found in other tropical clupeoids (Milton and Blaber, 1991). The reproductive life span of the population of each species at each site each month was determined from the oldest fish (Milton et al., 1993) in each sample minus the age at first spawning.

We estimated batch fecundity for each species from fish that had been examined histologically and had oocytes that were starting to hydrate (ripe-early running ripe; Stages 4–5; Table 1), but we did not

examine the fecundity of fish with any empty follicles. An advanced modal size group of oocytes could be distinguished in ripe fish. We separated a subsample of between half (*A. sirm*) and all (*S. delicatulus*) of the ovary and weighed it. The number of eggs in the advanced mode was counted and the fecundity was estimated by multiplying the number of eggs in the subsample by the ratio of total gonad weight to subsample weight. Fecundity estimates were made within three to four days after the ovary was removed from the fish to minimize the potential bias of differential absorption of fixative by oocytes and surrounding somatic tissue.

We used hydrated oocytes from fish caught between 2000 and 2330 hours to estimate egg weight. Oocyte weights were estimated from hydrated oocytes in ovaries that were almost ready to spawn (late Stage 5; Table 1). We measured oocyte dry weight by counting 10 samples of 10 oocytes from each ovary, drying the oocytes at 50° C to a constant mass and weighing each subsample separately.

We scored visceral fat on a five-point scale. If a fish had less than 25% of the intestine covered in fat deposits, it was scored as (1); 25–50%, (2); 50–75%, (3); and 75–100%, (4). A fish scored (5) when all intestine was covered with fat and deposits were also present around the stomach (Nikolsky, 1963).

The proportion of females examined histologically each month that had post-ovulatory follicles (POF; Stage 6) was used to evaluate reproductive seasonality. We determined that these fish had spawned within the previous 15–48 hours, because these structures decompose and cannot be recognised after that time (Hunter and Goldberg, 1980; Clarke, 1989). In samples where no fish had POF's, we used the proportion of fish in the histological subsample whose sections had greater than 85% running-ripe oocytes (Milton and Blaber, 1991). We used this proportion to calculate monthly estimates of mean daily oocyte production and the number of batches of oocytes spawned each month (Parrish et al., 1986).

We estimated daily oocyte production (n/kg of adults; egg production index) for samples collected from commercial baitfishing, because these samples were assumed to be most representative of the population. Our methods were similar to those of Parker (1980, 1985), which have been used to estimate the spawning biomass of a number of multiple spawners (Armstrong et al., 1988; Pauly and Palomeres, 1989; Somerton, 1990). However, our methods differed because we used commercial catch per unit of effort (CPUE) as an index of adult abundance.

$$\text{Egg production index} = \left(\sum (f_i p F_i S R_i) / \sum W_i \right) * \text{CPUE} \quad (1)$$

where f_i is the proportion of females in the i th length class, p is the proportion of the sample spawning, F_i is the fecundity of a fish of that length taken from the fecundity-length regression, SR_i is the sex-ratio of the i th length class and W_i is the total weight of fish in the i th sample. CPUE was estimated from the monthly catch returns of the commercial fleet. We chose this method of estimating egg production because *S. delicatulus* have demersal eggs (Leis and Trnski, 1989) and the eggs of *A. sirm* and *H. quadrimaculatus* are difficult to sample adequately in the large areas of suitable habitat in each lagoon.

For comparison with adult spawning data, we back-calculated the distribution of birthdates of fish collected in each length-frequency sample by using the growth equations of Milton et al. (1993). Frequencies in each age class were adjusted for mortality by using the estimates of Rawlinson et al. (1992). The distribution of birthdates was also back-calculated for *H. quadrimaculatus* and *S. delicatulus* length-frequency samples from previous studies at one site (Tarawa) January 1976 to February 1977 (R. Cross, 1978⁴) and May 1983 to April 1984 (McCarthy, 1985¹). We used age distribution in these earlier studies and those of the present study to examine seasonal, annual, and site-related differences in the reproductive life span of each species.

Statistical analyses Inter- and intra-specific differences in fat index, HSI and K were examined with Fisher's t -tests to account for unequal sample sizes. Seasonal and site-related differences in fecundity (expressed as oocytes per gram) were examined by analysis of covariance with weight as the covariate. Hydrated oocyte weight and reproductive life span were examined by one-way analysis of variance.

We examined the relative influence of exogenous and endogenous factors on the fecundity of each species at each site by stepwise regression (Sokal and Rohlf, 1981). We included the following: length, weight, age, sea-surface temperature ($^{\circ}\text{C}$), wind speed (in knots), moon phase (expressed by fitting a sin/cosin curve to the number of days since the last full moon before the sample was taken divided by the number of days in a lunar month (29.5) (Milton and Blaber, 1991), fish condition (K : weight/length³), fat, and HSI(%). We retained only those variables that significantly improved the fit of the model ($P < 0.05$). Because several of these variables were correlated, we did a partial-correlation analysis between these variables and fecundity, and the results

of the two approaches were compared. If the variable most related to fecundity in the stepwise regression was not the one most related to fecundity in the partial-correlation analysis, the stepwise regression model was discarded and no relationship was assumed.

In order to estimate egg production (Eq. 1), we estimated the proportion of females in each 5-mm length class from the total sample of each species. The variance of these estimates was calculated by using the normal approximation to the binomial distribution (Walpole, 1974). We assessed whether the monthly percentage of annual egg production was related to the proportion of annual recruitment in the same month by rank-correlations (Conover, 1980).

The average age of the potential spawning population in each sample was compared by a nested analysis of variance with month of sampling nested within year. Significant differences between treatments were identified from comparison of the least-squares means of each treatment, as sample sizes differed between cells (Sokal and Rohlf, 1981).

Results

Environmental parameters

Sea-surface temperature in Kiribati varied little throughout the year. During the study period, temperatures varied between 29 $^{\circ}\text{C}$ and 32 $^{\circ}\text{C}$ (Table 2). Rainfall varied along the Gilbert Island group; rainfall was higher in Butaritari than at the other sites. Some rain fell throughout the study period but was more intense during 1990 at all sites. Rainfall during 1989 was below the long-term average at all sites and was 16–50% that of 1990. The highest rainfall fell during the north-east monsoon (December–April) at all sites. Winds were mostly light, and varied in direction seasonally, blowing from the east during the monsoon, but from the south-south-west for the rest of the year (Table 2).

Reproductive biology

Maturation The length and age at first maturity of *A. sirm* varied between sites (Table 3). *Amblygaster sirm* matured younger and smaller in Kiribati than elsewhere. Length and age at first spawning were much greater than the length or age when fish reached sexual maturity, but this size was similar to that of fish from northern Australia (Table 3). *Herklotsichthys quadrimaculatus* matured and were capable of spawning at 70 mm length and 4 months of age (Table 3). The relative size and age at which fish matured (as a proportion of maximum size and

⁴ Cross, R. 1978. Fisheries research notes. Fisheries Division, Ministry of Commerce and Industry, Tarawa, Kiribati, 58 p.

age) did not differ among fish from the four sites. In Kiribati, *S. delicatulus* become sexually mature at 40 mm and two months of age and spawn shortly afterwards. Compared to the other species, the length and age at maturity and first spawning varied less among sites (Table 3). The three species differed in the length and age at sexual maturity and first spawning. However, as a proportion of their maxima, the three species were similar (*t*-test; $P>0.1$). All matured and spawned at about 70% of maximum size and 50% of maximum age (Table 3).

Timing of spawning We identified recent spawning by the presence of post-ovulatory follicles in the ovaries. In *A. sirm*, follicles were detected in samples collected between 0100 to 1630 hours, and new post-ovulatory follicles (identified as day-0 [<24 hr]; Hunter and Goldberg, 1980; Goldberg et al., 1984) were observed in fish collected between 0100 and 0510 hours. Female *H. quadrimaculatus* with post-ovulatory follicles were collected between 2130 and 1630 hours and day-0 follicles were found in samples collected between 2130 to 0300 hours. In female *H. quadrimaculatus* caught after 0300 hours, follicles could not be distinguished from day-1 type POF's, as the follicles degenerated rapidly. Similarly, we detected post-ovulatory follicles in female *S. delicatulus* collected from 2210 to 1930 hours, and follicles of all females collected earlier than 0845 hours were identified as day-0. Those in females of the single sample collected later in the day (1930) were assigned as day-1.

Spawning season There was protracted spawning in *A. sirm* with periods of intense spawning activity (Fig. 2). During both 1989 and 1990, fish spawned August to October and also during May-June in 1990. Condition, fat index, and HSI were less during spawning periods and reached a peak in March-April 1990, i.e., before spawning (Fig. 2). We found less fat deposits in spent fish and the fish were in poorer condition than fish with gonads in other stages of development ($P<0.05$; Table 4). We noted no significant differences in HSI among fish with gonads at the same stage of development.

Herklotsichthys quadrimaculatus spawned throughout the study period: 20 to 50% of the popu-

Table 2
Mean water temperature ($^{\circ}$ C), wind speed (kn), cloud cover, and monthly rainfall (mm) at four sites in Kiribati from November 1988 to May 1991.

Parameter	Butaritari	Abaiang	Tarawa	Abemama
Water temperature ($^{\circ}$ C)	30.2 \pm 0.3	30.2 \pm 0.4	29.5 \pm 0.1	29.9 \pm 0.2
Range	28-32	27-33	29-30	29-31
Wind speed (kn)	2.2 \pm 0.6	4.2 \pm 0.9	5.4 \pm 1.2	2.2 \pm 0.2
Range	0-7	0-10	1-15	1-5
Prevailing direction	East	East	East	East
Cloud cover (okters)	2 \pm 0.6	5 \pm 0.6	3 \pm 0.5	1 \pm 0.4
Range	0-6	1-7	0-7	0-4
Monthly rainfall (mm) (1945-88)	263 \pm 35	181 \pm 35	165 \pm 35	128 \pm 33
Range	7-908	0-761	0-824	0-728
Monthly rainfall 1989 (mm)	184 \pm 29	42 \pm 10	77 \pm 23	36 \pm 10
Range	51-351	0-108	6-235	3-102
Monthly rainfall 1990 (mm)	404 \pm 37	-	298 \pm 51	202 \pm 31
Range	195-614	-	19-643	93-402
Months sampled	14	12	18	13

lation spawned each month (Fig. 3). Female condition, fat index, and HSI all followed a similar pattern during the study but did not appear to be directly related to spawning activity. Fish in spawning condition had the highest HSI, fat, and condition values, but these were only significantly greater than those of spent fish ($P<0.05$; Table 4).

Spratelloides delicatulus spawned almost continuously throughout the study period but spawning varied in intensity (Fig. 4). Peak spawning occurred during different periods in each of the years sampled. Female HSI and fat index showed a similar pattern during the study but monthly changes in these parameters or fish condition did not follow the spawning cycle. We found no significant differences in HSI or fat index for females with ovaries in different stages of development ($P>0.1$; Table 4). Fish condition was lower among spent fish than in ripe or spawning fish ($P<0.05$; Table 4). Females with ripe ovaries had higher mean HSI, fat, and condition than those in other stages of development, but these differences were not significant (Table 4).

Fecundity The relative fecundity of *A. sirm* and *H. quadrimaculatus* did not differ among sites or seasonally within sites in Kiribati (ANCOVA with weight as covariate; overall $P>0.07$; Table 5). However, the relative fecundity of *H. quadrimaculatus* was significantly different between fish from Tarawa and Abemama (*t*-test; $P<0.05$). Batch fecundity of both species did not differ among sites in Kiribati. Within their respective species groups, both species had similar batch fecundities to the other species listed, although their relative fecundities were lower (Table 5).

Table 3

Length and age at sexual maturity and first spawning of *Amblygaster sirm*, *Herklotsichthys quadrimaculatus*, and *Spratelloides delicatulus* from various populations throughout their range. (L_{mat} = length at maturity, L_{fsp} = length at first spawning, L_{max} = maximum size, T_{mat} = age at maturity, T_{fsp} = age at first spawning, T_{max} = maximum age, K = Kiribati, I = India, SI = Solomon Islands).

Species	Site	Length at maturity (mm) (L_{mat}/L_{max})	Length at first spawning (mm) (L_{fsp}/L_{max})	Age at maturity(d) (T_{mat}/T_{max})	Age at first spawning (d) (T_{fsp}/T_{max})	Source ¹
<i>A. sirm</i>	Kiribati	110 (0.50)	180 (0.80)	150 (0.29)	330 (0.65)	(1)
	New Caledonia	132 (0.72)	—	295 (0.40)	—	(2)
	N. Australia	174 (0.79)	193 (0.88)	—	—	(3)
	Sri Lanka	166 (0.88)	—	~330 (0.80)	—	(4)
Mean	146 (0.72)	—	—	—		
<i>H. quadrimaculatus</i>	Hawaii	80 (0.63)	90 (0.70)	160 (0.53)	190 (0.63)	(5)
	Marshall Is.	90 (0.82)	—	190 (0.72)	—	(6)
	Fiji	95 (0.78)	98 (0.80)	275 (—)	294 (—)	(7), (8)
	Butaritari (K)	65 (0.68)	70 (0.74)	125 (0.50)	135 (0.53)	(1)
	Abaiang (K)	70 (0.74)	70 (0.74)	125 (0.37)	125 (0.37)	(1)
	Tarawa (K)	69 (0.72)	70 (0.73)	138 (0.45)	150 (0.48)	(1)
	Abemama (K)	70 (0.64)	72 (0.65)	140 (0.34)	150 (0.36)	(1)
	New Caledonia	91 (0.64)	—	244 (—)	—	(9)
	Andaman Is. (I)	99 (0.81)	104 (0.85)	—	—	(10)
	Seychelles	97 (0.71)	—	150 (0.30)	—	(11)
	Mean	83 (0.72)	82 (0.74)	172 (0.46)	174 (0.47)	
<i>S. delicatulus</i>	Fiji	35 (0.56)	39 (0.63)	52 (0.43)	61 (0.51)	(7), (8)
	Butaritari (K)	40 (0.68)	40 (0.68)	65 (0.51)	68 (0.54)	(1)
	Abaiang (K)	45 (0.75)	53 (0.88)	62 (0.51)	80 (0.64)	(1)
	Tarawa (K)	45 (0.68)	50 (0.76)	77 (0.50)	90 (0.57)	(1)
	Munda (SI)	37 (0.58)	37 (0.58)	72 (0.47)	78 (0.51)	(12), (13)
	Vona Vona (SI)	37 (0.66)	37 (0.66)	68 (0.53)	72 (0.56)	(12), (13)
	Tulagi (SI)	38 (0.60)	38 (0.60)	73 (0.55)	75 (0.57)	(12), (13)
	Maldives	38 (0.69)	40 (0.73)	90 (0.60)	97 (0.65)	(13), (14)
	India	42 (0.71)	—	—	—	(15)
Mean	40 (0.66)	42 (0.69)	70 (0.51)	78 (0.57)		

¹ Sources: (1) present study, (2) Conand (1991), (3) Okera (1982), (4) Dayaratne and Gjosaeter (1986), (5) Williams and Clarke (1983), (6) Hida and Uchiyama (1977), (7) Lewis et al. (1983), (8) Dalzell et al. (1987), (9) Conand (1988), (10) Marichamy (1971), (11) Moussac and Poupon (1986), (12) Milton and Blaber (1991), (13) Milton et al. (1991), (14) Milton et al. (1990), (15) Mohan and Kunhikoya (1986).

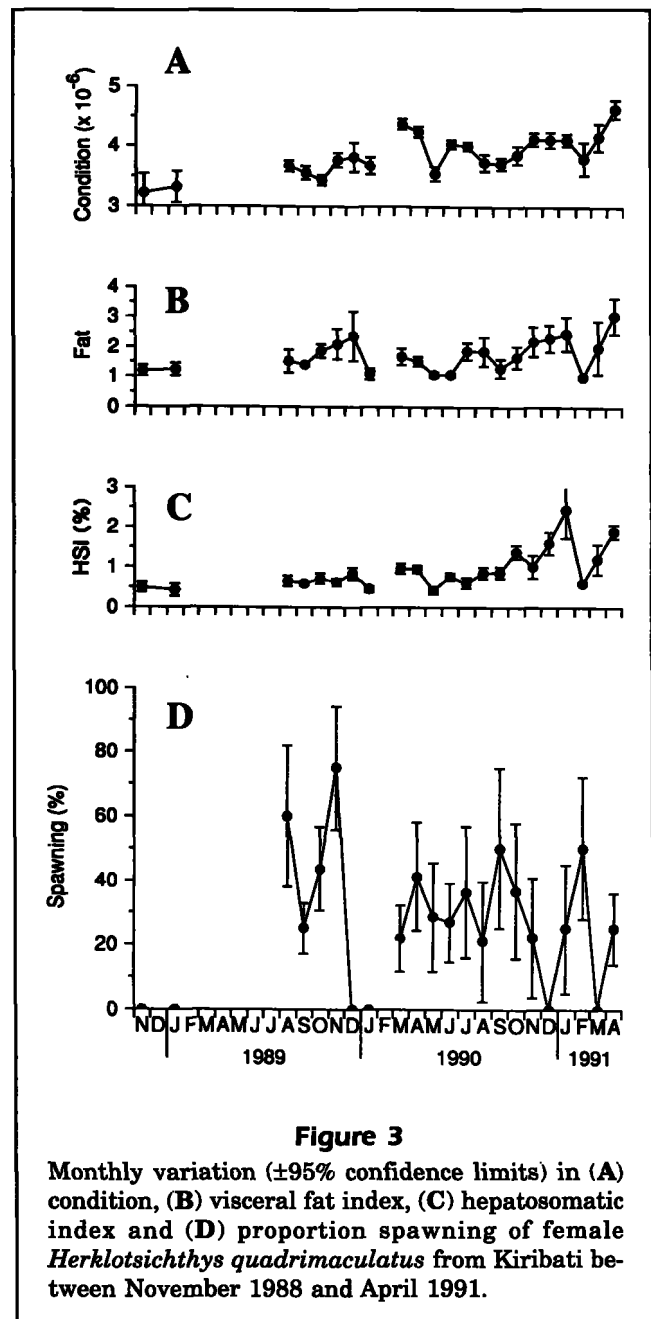
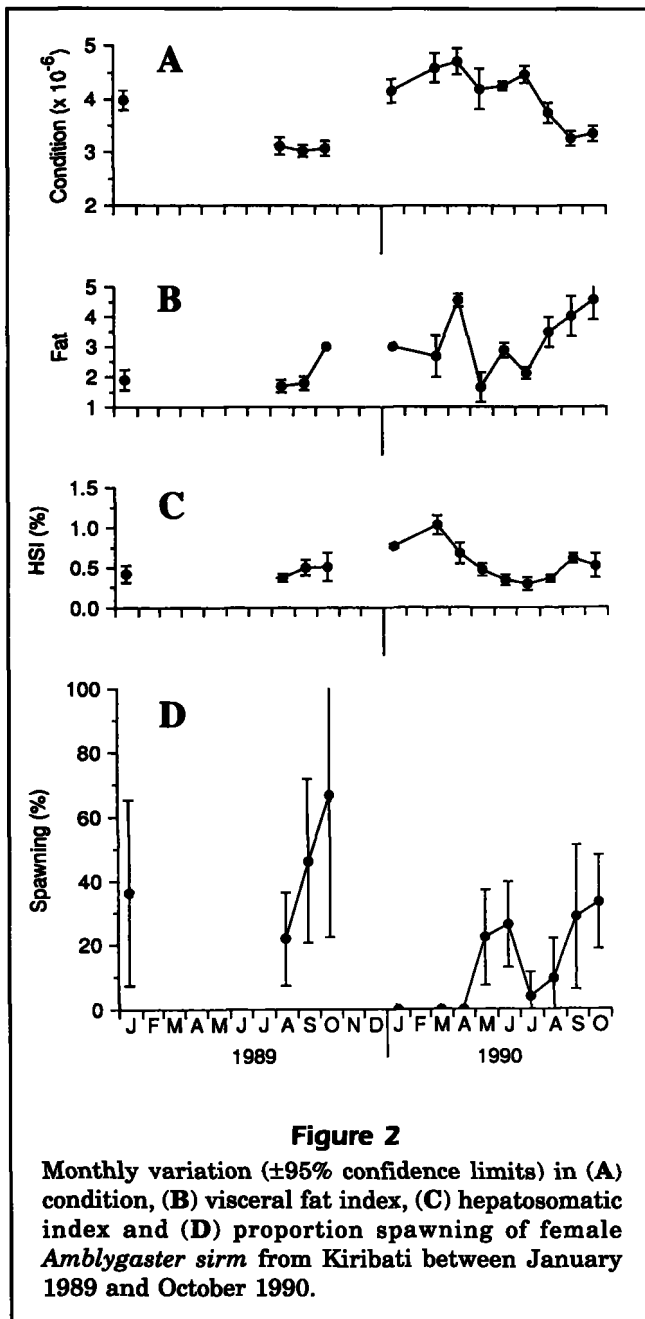
Using stepwise linear regression, we found that fecundity was related to weight in all species (Table 6; Fig. 5). Fecundity of *A. sirm* was significantly correlated with HSI and fish condition. Fish condition, HSI, and fat index were all correlated with fecundity in *H. quadrimaculatus* (Table 6). Fecundity was significantly correlated with weight and condition at two of the four sites. Although, when data from all sites were combined, weight and fat index were the only significant correlates.

Fecundity of *S. delicatulus* varied widely among sites, both within Kiribati and among countries (Table 5). In Kiribati, relative fecundity was higher at Butaritari than at Abaiang ($P < 0.05$), but differed less than among sites in the Solomon Islands. Fecundity did not vary seasonally at any site. Relative

fecundity of *S. delicatulus* was highest in New Caledonia — significantly higher than at all other sites except Butaritari in Kiribati (Table 5). However, the relative fecundity of *S. delicatulus* was lower than its congeners, *S. gracilis* and *S. lewisi*, at sites where they co-occurred (Table 5).

We found that the fecundity of *S. delicatulus* correlated strongly with fish weight (Fig. 5). The only other factor related to fecundity in *S. delicatulus* was HSI. There was a significant relationship between fecundity and HSI at Butaritari and Tarawa and when all data were combined. Spawning fish had a higher HSI at Butaritari than at other sites (2.24 ± 0.13 vs. 1.41 ± 0.08 ; $P < 0.001$).

The HSI of male *S. delicatulus* that had a GSI similar to that of spawning females (>5%) was also



higher at Butaritari (1.41 ± 0.06 ; $N=57$) than at other sites (Abaiang $HSI=1.07 \pm 0.11$; $N=7$; Tarawa $HSI=0.81 \pm 0.09$; $N=14$). The proportion of male *S. delicatulus* that had GSI greater than 5% was also higher at Butaritari (36%) than at other sites (Abaiang 17.5%; Tarawa 20%).

Oocyte weights of *A. sirm* and *S. delicatulus* differed significantly from site to site (Table 7). In *S. delicatulus*, we found the greatest oocyte weight at Abemama and Abaiang — significantly higher than at Butaritari and Tarawa ($P<0.01$). Oocyte weights in *A. sirm* were also higher at Abaiang ($P<0.001$;

Table 7). We found no significant differences among sites for oocyte weights of *H. quadrimaculatus*.

Sex ratio The sex-ratio of *A. sirm*, *H. quadrimaculatus*, and *S. delicatulus* changed as fish grew but only among the largest length classes of each species were there significant deviations from a ratio of 1:1. In all three species, females dominate the largest length classes (Fig. 6). In our samples, we found significantly more female *A. sirm* and *S. delicatulus* among fish larger than the length at first spawning (180 and 45 mm respectively). With *H.*

Table 4

Mean hepatosomatic index (HSI: %), visceral fat index (Fat) and condition (K : dry weight/length³) of *Amblygaster sirm*, *Herklotsichthys quadrimaculatus* and *Spratelloides delicatulus* at different stages of gonadal development (SE = standard error \pm N = number of females examined).

Species	Stage	HSI \pm SE	Fat \pm SE	K ($\times 10^{-6}$) \pm SE	N
<i>A. sirm</i>	maturing	0.38 \pm 0.06	3.4 \pm 0.6	4.05 \pm 0.25	8
	ripe	0.43 \pm 0.04	3.2 \pm 0.3	4.14 \pm 0.07	30
	spawning	0.39 \pm 0.06	2.6 \pm 0.4	4.03 \pm 0.13	16
	spent	0.42 \pm 0.05	1.7 \pm 0.2	2.77 \pm 0.13	6
<i>H. quadrimaculatus</i>	maturing	0.87 \pm 0.08	1.4 \pm 0.1	3.89 \pm 0.05	45
	ripe	0.96 \pm 0.06	1.6 \pm 0.1	3.81 \pm 0.05	127
	spawning	1.04 \pm 0.07	1.8 \pm 0.1	3.91 \pm 0.05	95
	spent	0.69 \pm 0.04	1.7 \pm 0.1	3.53 \pm 0.06	40
<i>S. delicatulus</i>	maturing	1.41 \pm 0.19	1.3 \pm 0.2	2.36 \pm 0.06	15
	ripe	1.98 \pm 0.10	1.6 \pm 0.1	2.51 \pm 0.04	41
	spawning	1.84 \pm 0.15	1.3 \pm 0.1	2.46 \pm 0.04	35
	spent	1.46 \pm 0.10	1.2 \pm 0.1	2.28 \pm 0.04	55

quadrimaculatus, females dominated among fish over 80 mm (Fig. 6).

Egg production The number of spawnings per month and the daily egg production of all species generally followed the pattern of the proportion spawning (Fig. 7). We found lower daily egg production in *A. sirm* than in the other species. During the period of maximum spawning activity, *A. sirm* and *H. quadrimaculatus* spawned up to 20 times per month (Fig. 7), and *S. delicatulus* spawned daily.

Reproductive life span The reproductive life span of *A. sirm* was significantly longer in Tarawa (60.1 \pm 15.4 days) than at the other sites during 1989–90 ($P < 0.01$; Table 8). Similarly, we found *H. quadrimaculatus* had a longer reproductive life span at Abemama (141.8 \pm 30.9 days) than at other sites during 1989–91 ($P < 0.01$; Table 8). During the same period, the reproductive life span of *S. delicatulus* was similar at all sites (57.5 \pm 4.6 days). However, the reproductive life span of *S. delicatulus* at Tarawa varied significantly between years; fish caught during 1990–91 were not as old as those in previous years ($P < 0.05$; Table 8). No corresponding pattern was observed in *H. quadrimaculatus* from Tarawa. *Herklotsichthys quadrimaculatus* and *S. delicatulus* lived significantly longer after maturity than *A. sirm* ($P < 0.01$).

Our estimates of maximum lifetime egg production of *A. sirm* were similar at the two sites (Abaiang and Tarawa). *Herklotsichthys quadrimaculatus* had

higher lifetime egg production at all sites than did co-occurring *S. delicatulus*. The number of days between successive spawnings influenced estimates of lifetime egg production. Although longer in *A. sirm*, the difference was not significant (Table 8).

Recruitment *Amblygaster sirm* recruited from a single protracted period in Kiribati during 1989 (March to October; Fig. 8). We found a greater proportion of survivors had been born between March and July than in all other months except September ($P < 0.05$). There were insufficient data to compare monthly egg production with recruitment, but the pe-

riod of highest recruitment corresponded with the times of greatest spawning activity. However, this did not appear to be directly related to the absolute number of oocytes produced (Fig. 7).

The proportion of *H. quadrimaculatus* born each month differed over the four years ($P < 0.05$; Fig. 9). In 1976, the greater proportion were born from November to March, while in 1983 over 40% were born during July. Fish caught during 1989–90 showed a different pattern. The highest proportion in 1989 were born in May, whereas in 1990 the highest proportion were born in January. Over all 4 years' data, December (15.4%) and July (13.7%) had the greatest mean proportion of births ($P < 0.05$), but the July value may be biased by the large value in 1983 (Fig. 10). Where data were comparable, we found no relationship between proportion of annual recruitment and monthly egg production ($r_s = 0.70$, $P < 0.10$, $N = 6$ in 1989; $r_s = -0.15$, $P > 0.5$, $N = 11$ in 1990).

The proportion of *S. delicatulus* born each month varied considerably among the four years examined (Fig. 10). December had the highest proportion of births in 1976. In 1983, most fish were born between May and August, and a similar pattern was found in 1989. By comparison, the distribution of birthdates was more evenly spread in 1990 (Fig. 10). The months with the largest mean proportion across the four years were May (11.2%), June (14.9%), July (15.8%), and December (11.9%). We found a negative relationship between the proportion of births and egg production in 1990 ($r_s = -0.58$; $P < 0.05$, $N = 10$).

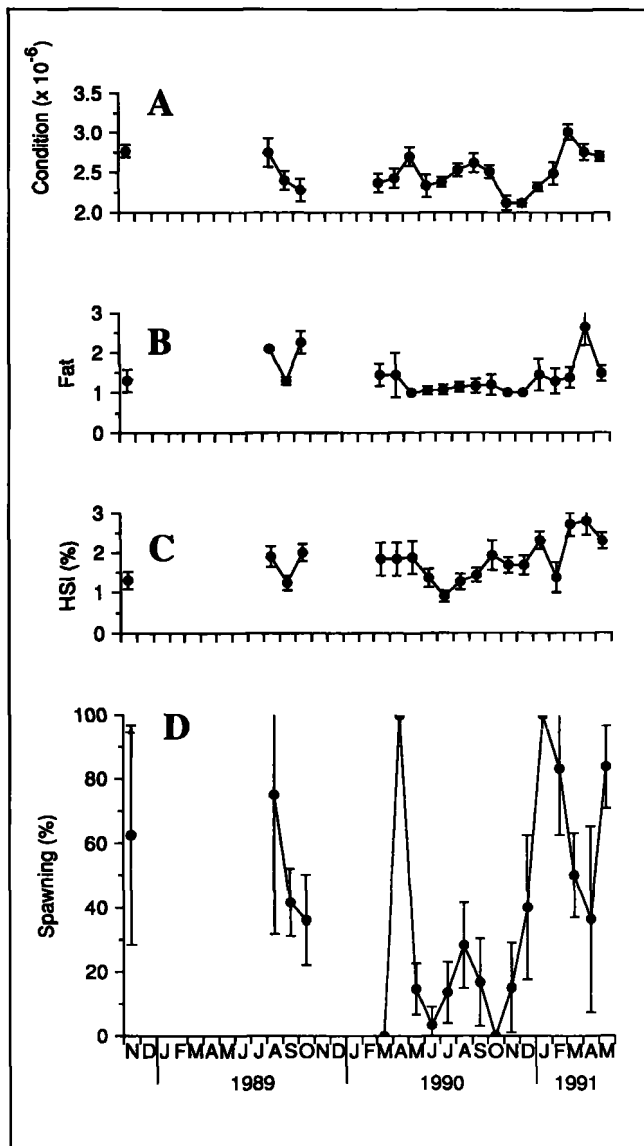


Figure 4

Monthly variation ($\pm 95\%$ confidence limits) in (A) condition, (B) visceral fat index, (C) hepatosomatic index and (D) proportion spawning of female *Spratelloides delicatulus* from Kiribati between November 1988 and May 1991.

Discussion

The reproductive cycles of *A. sirm*, *H. quadrimaculatus*, and *S. delicatulus* in Kiribati are similar to that reported for temperate multiple-spawning clupeoids (Hunter and Goldberg, 1980; Gil and Lee, 1986; Shelton, 1987; Alheit, 1989). Most studies on multiple spawning clupeoids have been on engraulids; these species spawn many batches of eggs each year and have variable batch fecundity (Alheit, 1989). Our results for *H. quadrimaculatus*

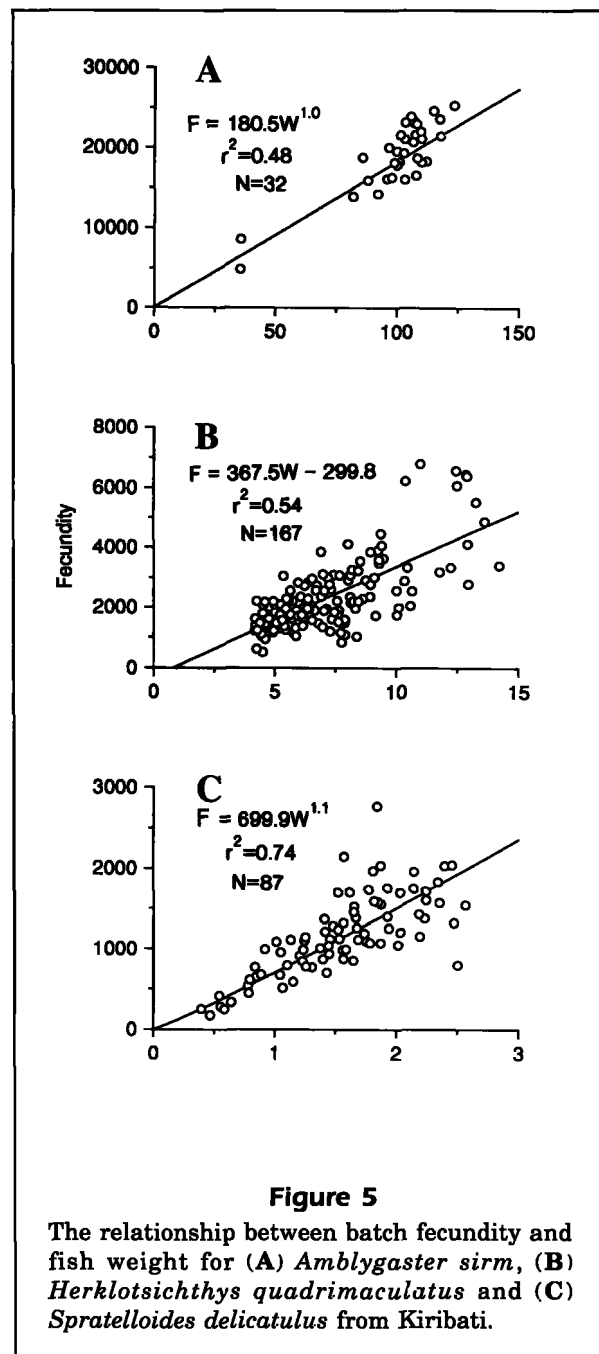


Figure 5

The relationship between batch fecundity and fish weight for (A) *Amblygaster sirm*, (B) *Herklotsichthys quadrimaculatus* and (C) *Spratelloides delicatulus* from Kiribati.

and *S. delicatulus* from Kiribati agree with previous reproductive studies of these species in tropical areas (McCarthy, 1985¹; Moussac and Poupon, 1986; Milton and Blaber, 1991). In the tropics, both species spawn throughout the year, but have periods when spawning activity is greater. In more temperate parts of their range, the reproductive season of both *H. quadrimaculatus* and *S. delicatulus* is shorter and coincides with increases in water temperature in early summer (Williams and Clarke, 1983; Lewis et al., 1983; Conand, 1988).

Table 5

Mean length (mm), age (years), fecundity, relative fecundity (eggs g^{-1}) of *Amblygaster sirm*, *Herklotsichthys quadrimaculatus*, and *Spratelloides delicatulus* and other tropical and subtropical clupeids (sardines, herrings, and sprats) (K = Kiribati, SI = Solomon Islands, I = India, P.N.G. = Papua New Guinea, UK = United Kingdom, SU = Soviet Union, G = Germany).

Species	Site	Length ± SE	Age ± SE	Fecundity ± SE	Rel. fecundity ± SE	N	Source	
Sardines								
<i>Amblygaster sirm</i>	Abaiang (K)	189 ± 5	0.97 ± 0.03	18789 ± 2757	187.1 ± 25.3	7	(1)	
	Tarawa (K)	194 ± 1	1.04 ± 0.03	20327 ± 1391	192.0 ± 12.0	25	(1)	
	New Caledonia	139–177	0.90–2.2	8000–27780	300.0 ± 16.9	24	(2), (3)	
<i>Sardinella brasiliensis</i>	Brazil	162 ± 2	—	23318 ± 2065	356 ± 37	23	(4)	
<i>S. marquesensis</i>	Marquesas Is.	109 ± 6	—	4150 ± 1000	—	6	(5)	
<i>S. zunasi</i>	Korea	75–142	1–3	8800–58800	—	31	(6)	
Herrings								
<i>Herklotsichthys uadrimaculatus</i>	Hawaii	80–121	—	1155–6296	160–311	46	(7)	
	Marshall Is.	100 ± 2	0.59 ± 0.02	4755 ± 380	—	7	(8)	
	Butaritari (K)	75 ± 1	0.45 ± 0.01	1844 ± 108	295.5 ± 12.1	44	(1)	
	Abaiang (K)	75 ± 1	0.45 ± 0.02	1975 ± 133	317.4 ± 19.3	27	(1)	
	Tarawa (K)	76 ± 1	0.44 ± 0.02	2353 ± 110	344.1 ± 10.2	63	(1)	
	Abemama (K)	84 ± 2	0.61 ± 0.04	3008 ± 207	319.1 ± 22.7	33	(1)	
	Andaman Is. (I)	95–115	—	8353 ± —	—	19	(9)	
	Seychelles	88–127	—	4500–8000	—	24	(10)	
	<i>Opisthonema libertate</i>	Mexico	142 ± 1	—	57125 ± 1850	553 ± 14	115	(11)
	Sprats							
<i>Spratelloides delicatulus</i>	Butaritari (K)	52 ± 2	0.27 ± 0.01	1359 ± 143	867 ± 55	19	(1)	
	Abaiang (K)	52 ± 1	0.21 ± 0.02	973 ± 43	667 ± 35	7	(1)	
	Tarawa (K)	54 ± 1	0.29 ± 0.01	1255 ± 54	735 ± 25	49	(1)	
	Abemama (K)	41 ± 1	0.20 ± 0.02	524 ± 95	702 ± 75	12	(1)	
	Munda (SI)	48 ± 1	0.26 ± 0.01	799 ± 45	554 ± 25	57	(12)	
	Vona Vona (SI)	49 ± 1	0.26 ± 0.01	925 ± 102	717 ± 45	28	(12)	
	Tulagi (SI)	46 ± 1	0.21 ± 0.01	926 ± 93	567 ± 49	28	(12)	
	New Caledonia	45	—	710	883 ± 14	20	(2)	
	India	40 ± 3	—	608 ± 54	—	15	(13)	
	<i>S. gracilis</i>	Munda (SI)	50	0.19	514	504	1	(14)
	Vona Vona (SI)	37 ± 1	0.15 ± 0.01	505 ± 51	882 ± 68	13	(12)	
	P.N.G.	53 ± 2	—	2592 ± 313	1690 ± 96	18	(15)	
	Maldives	59 ± 1	0.29 ± 0.02	1998 ± 137	1073 ± 54	33	(12)	
India	40 ± 5	—	790 ± 71	962 ± 53	15	(13)		
<i>S. lewisi</i>	Munda (SI)	44 ± 1	0.18 ± 0.01	887 ± 20	925 ± 16	219	(14)	
Vona Vona (SI)	42 ± 1	0.14 ± 0.01	930 ± 51	1032 ± 36	62	(14)		
Tulagi (SI)	49 ± 1	0.28 ± 0.02	1290 ± 84	1230 ± 69	29	(14)		
<i>Sprattus sprattus</i>	Scotland (UK)	108	3	2729	187	64	(16)	
	Baltic Sea (SU)	121	1.9	2174	232	46	(17)	
	North Sea (G)	—	2	—	413	—	(17)	

Sources: (1) present study, (2) Conand (1988), (3) Conand (1991), (4) Isaac-Nahum et al. (1988), (5) Nakamura and Wilson (1970), (6) Gil and Lee (1986), (7) Williams and Clarke (1983), (8) Hida and Uchiyama (1977), (9) Marichamy (1971), (10) Moussac and Poupon (1986), (11) Torres-Villegas and Perezgomez (1988), (12) Milton et al. (1990), (13) Mohan and Kunhikoya (1986), (14) Milton unpubl. data, (15) Dalzell (1985), (16) De Silva (1973), (17) Alheit (1988).

Although we found *A. sirm* also had an extended spawning season in Kiribati, the species may not spawn throughout the year. Our result differs from previous studies that found the spawning season

lasted two to five months during early summer (Conand, 1991) or the monsoon period (Rosa and Laevastu, 1960; Dayaratne and Gjosaeter, 1986). Neither temperature nor rainfall appear to be the

proximate stimuli for spawning of *A. sirm* in Kiribati. Temperature was constant throughout the year and rainfall was higher at all sites in Kiribati between December and April, when spawning activity was lowest. Most spawning activity in this species occurred during the second half of the year when the prevailing wind direction changed from east to west, associated with the north-west monsoon that starts at this time (Burgess, 1987⁵). Our limited wind and rainfall data did not indicate that increased spawning activity in *A. sirm* was related to the shift in weather pattern.

Gonad maturation and spawning were also linked to changes in fish liver-weight (HSI), visceral fat, and condition of each species. Either HSI or fat index and condition were all significantly reduced in postspawning fish. *Amblygaster sirm* stores energy in the viscera rather than in the liver. Other multiple-spawning clupeoids also transfer energy from stored fat to reproductive tissue (Dahlberg, 1969; Okera, 1974; Hunter and Leong, 1981).

In contrast, spent *H. quadrimaculatus* and *S. delicatulus* had reduced HSI, which suggests that the liver is the energy store utilized during reproduction (Diana and MacKay, 1979; Smith et al., 1990). Energy stored in this organ would be readily available for rapid assimilation; hence, fish could spawn multiple batches of eggs rapidly.

Studies of temperate herring, *Clupea harengus*, have shown that gonad maturation is linked to food availability and fat storage (Linko et al., 1985; Henderson and Almatar, 1989; Rajasilta, 1992). Ovaries of all three species in Kiribati and of *S. delicatulus* in the Solomon Islands (Milton and Blaber, 1991) vary in a similar way to herring. Milton and Blaber (1991) did not find a direct relation between spawning and prey availability. This suggests that while gonad maturation in these clu-

⁵ Burgess, S. M. 1987. The climate of western Kiribati. New Zealand Meteorological Service, Wellington, NZ. Miscellaneous publ. 188, part 7.

Table 6

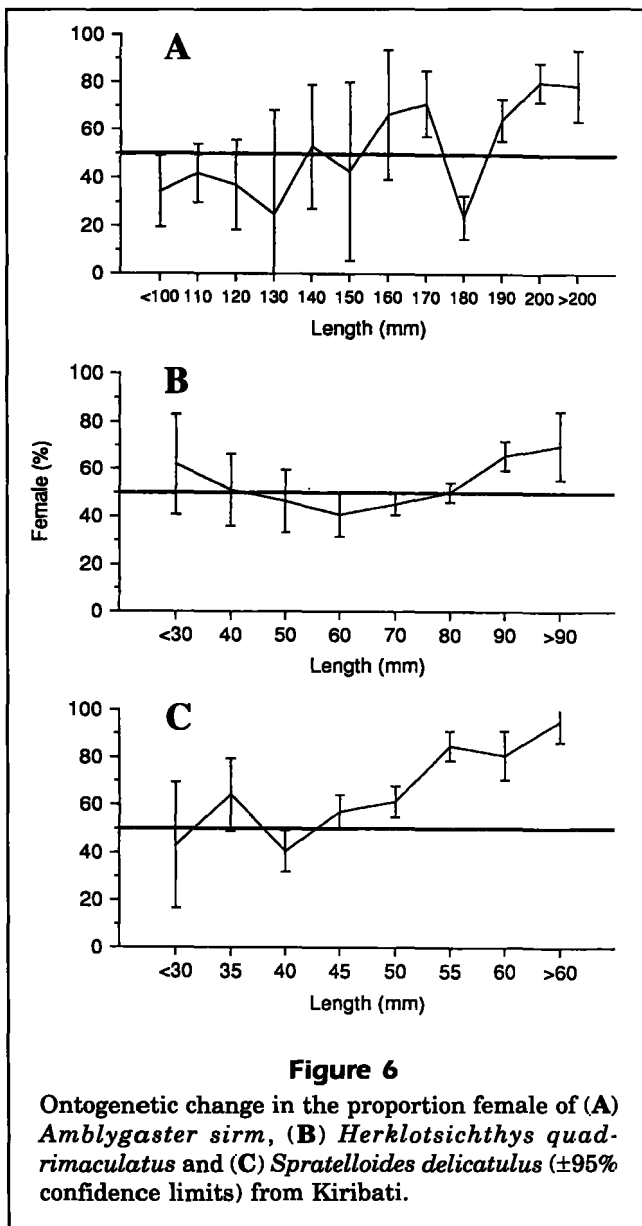
Stepwise regression of the relationship between various endogenous factors and fish fecundity from sites in Kiribati. (Cr_p^2 = partial correlation coefficient; r^2 = overall correlation coefficient; P = significance level; N = sample size; HSI = hepatosomatic index; All = data from each site combined).

Species	Site	Factor	r_p^2	r^2	P	N
<i>Amblygaster sirm</i>	Tarawa	Weight	0.24	0.44	<0.05	25
		HSI	0.20			
	All	Weight	0.38	0.64	<0.001	32
		Condition	0.28			
<i>Herklotsichthys quadrimaculatus</i>	Butaritari	Weight	0.36	0.43	<0.001	44
		Condition	0.07			
	Abaiang	Weight	0.28	0.39	<0.01	27
		HSI	0.11			
	Tarawa	Length	0.58	0.63	<0.001	63
		Condition	0.03			
		Age	0.02			
	Abemama	Weight	0.62	0.72	<0.001	33
		Fat	0.10			
	All	Weight	0.54	0.57	<0.001	167
		Fat	0.03			
<i>Spratelloides delicatulus</i>	Butaritari	Weight	0.70	0.76	<0.001	19
		HSI	0.06			
	Abaiang	no factor				7
	Tarawa	Weight	0.37	0.52	<0.001	49
		HSI	0.15			
	Abemama	Weight	0.87	0.87	<0.001	12
		Weight	0.59			
	All	HSI	0.07			

Table 7

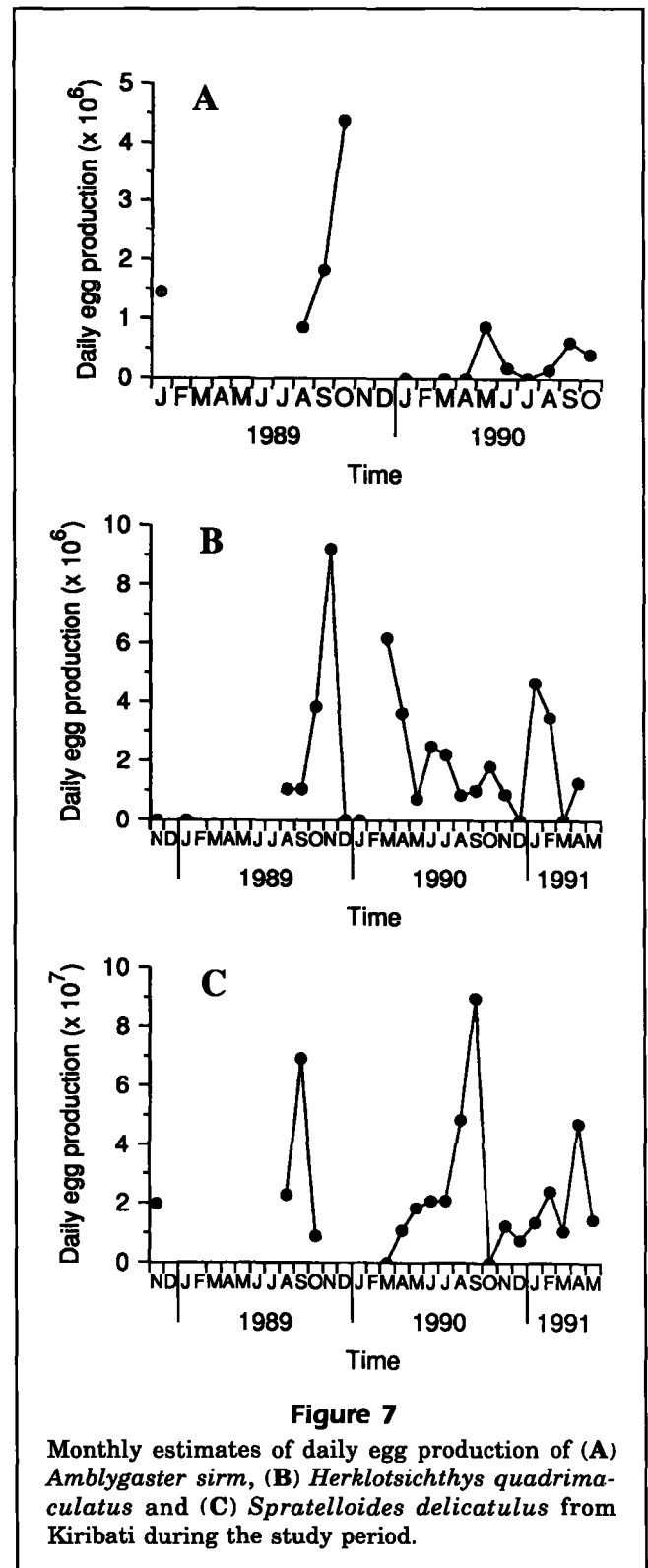
Mean hydrated oocyte dry weight of *Amblygaster sirm*, *Herklotsichthys quadrimaculatus*, and *Spratelloides delicatulus* from four sites in Kiribati (N = number of females examined).

Species	Site	Hydrated oocyte weight \pm SE ($\times 10^{-4}$ g)	N
<i>A. sirm</i>	Abaiang	4.4 \pm 0.5	7
	Tarawa	1.5 \pm 0.1	16
<i>H. quadrimaculatus</i>	Butaritari	2.0 \pm 0.2	36
	Abaiang	1.8 \pm 0.1	12
	Tarawa	1.6 \pm 0.2	19
	Abemama	1.9 \pm 0.2	26
<i>S. delicatulus</i>	Butaritari	0.7 \pm 0.1	11
	Abaiang	1.4 \pm 0.2	12
	Tarawa	0.8 \pm 0.04	27
	Abemama	2.2 \pm 0.2	10



peids is probably linked to cycles in prey abundance, fat storage may reduce the effects of short-term fluctuations in prey abundance on reproduction.

Diel timing of spawning events was similar for all species. We found new post-ovulatory follicles (day-0) in females collected from 2130 hours onwards with the greatest proportion detected after 0100. This indicates that these species spawn during the early part of the night, probably prior to midnight. Our results are consistent with previous studies that found high densities of *A. sirm* eggs in the plankton after midnight (Delsman, 1926; Lazarus, 1987). Studies of other sardines (Goldberg et al., 1984; Isaac-Nahum et al., 1988; Re et al., 1988) and tropi-



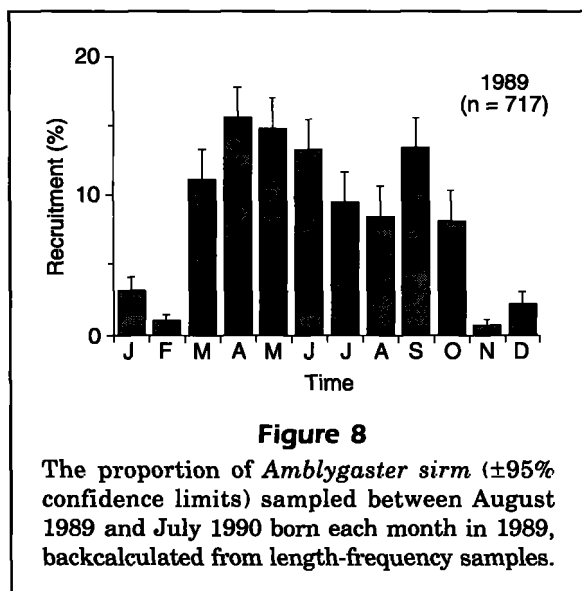
cal clupeoids (Clarke, 1987) also showed that spawning peaked before midnight.

Length and age at sexual maturity of *A. sirm* and *H. quadrimaculatus* in Kiribati differed from those

Table 8

Mean reproductive life span (in days) and days between spawning of *Amblygaster sirm*, *Herklotsichthys quadrimaculatus*, and *Spratelloides delicatulus* from four sites in Kiribati (N = number of length-frequency samples; No. = number of months examined).

Species	Site	Year	Reproductive life span \pm SE	Range	N	Days between spawning	Range	No.	Max. lifetime egg production ($\times 10^4$)
<i>A. sirm</i>	Abaiang	1989–1990	19.0 \pm 6.4	0–66	12				20.0
	Tarawa	1989–1990	60.1 \pm 15.4	0–127	7				41.6
	Abemama	1989–1990	3.2 \pm 3.1	0–19	6				
Overall	1989–1990	26.7 \pm 6.8	0–127	25	6.2 \pm 2.3	1.5–25.9	10	38.7	
<i>H. quadrimaculatus</i>	Butaritari	1989–1991	47.3 \pm 15.0	0–201	14				11.9
	Abaiang	1989–1991	73.9 \pm 15.6	0–201	17				12.8
	Tarawa	1976/83/89–91	84.1 \pm 7.8	0–254	64				19.3
	Abemama	1989–1991	141.8 \pm 30.9	0–286	12				27.7
	Overall	1989–1991	80.6 \pm 8.6	0–286	74	3.1 \pm 0.3	1.3–4.7	15	21.1
	<i>S. delicatulus</i>	Butaritari	1989–1991	53.6 \pm 4.6	24–74	15			
	Abaiang	1989–1991	49.2 \pm 5.1	21–80	11				1.5
	Tarawa	1989–1991	66.9 \pm 10.6	0–144	16				3.5
	Tarawa	1976	76.6 \pm 10.5	45–129	7				3.1
	Tarawa	1983/84	84.3 \pm 9.5	34–152	16				3.7
	all	1989	90.0 \pm 13.4	53–144	7				3.2
	all	1990/91	51.0 \pm 4.1	0–109	35				2.5
	Overall	1989–1991	57.5 \pm 4.6	0–144	42	5.2 \pm 1.8	1–30	16	3.2



in other parts of their range (Table 3). We found few differences within Kiribati, but both species became sexually mature and spawned at much shorter body lengths than at other locations. *Herklotsichthys quadrimaculatus* did not grow as large in Kiribati as elsewhere (Milton et al., 1993), but the proportion of maximum size at which this species matured was similar throughout its range. Milton and Blaber (1991) found regional differences in length at sexual maturity in other small tropical clupeoids; they sug-

gested these differences were consistent with the hypothesis of Longhurst and Pauly (1987) that fish of any species living in cooler water will grow to and mature at a larger size through the interaction of oxygen supply and demand. Our data on *H. quadrimaculatus* is consistent with this hypothesis — the other studies were all at sites at higher latitudes than Kiribati, where the water temperature is lower. Also, the proportion of maximum size at which fish matured was similar at all locations, despite the absolute differences in size at maturity in Kiribati.

By comparison, *A. sirm* matured at a smaller size and grew to a larger size in Kiribati than at other locations (Milton et al., 1993). The proportion of maximum size at which fish matured was also lower than found in previous studies and was less than the proportion common to a wide range of clupeoids (70%; Beverton, 1963). In response to severe fishing pressure, the size and age at sexual maturity of several sardine species have been found to decline (Murphy, 1977). Presumably, this is because any density-dependent effects are reduced during early growth (Beverton and Holt, 1957; Ware, 1980). *Amblygaster sirm* can have high or variable adult mortality in Kiribati (Rawlinson et al., 1992), favouring early maturation (Stearns and Crandall, 1984).

Length at first spawning was a similar proportion of maximum size for the three species and was con-

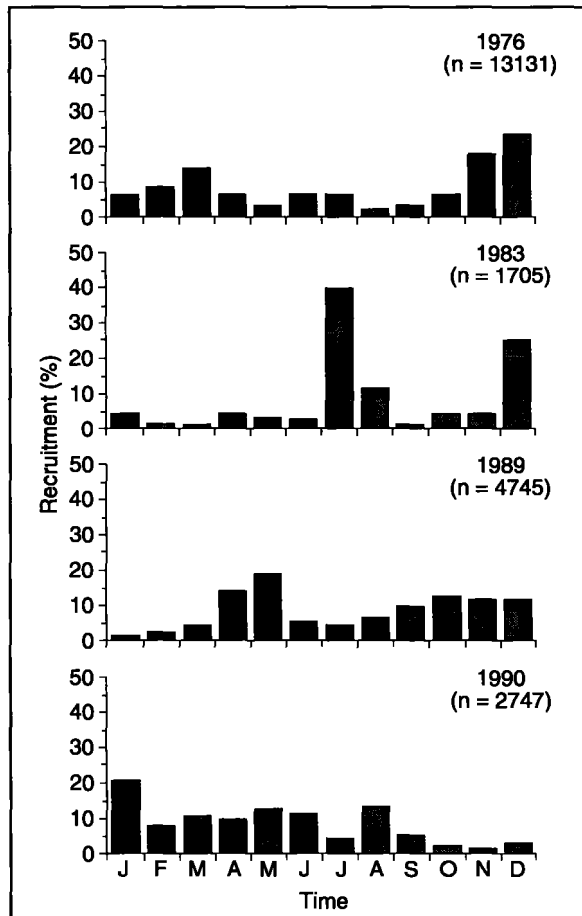


Figure 9

The proportion of *Herklotsichthys quadrimaculatus* born each month in 1976, 1983, 1989, and 1990, back-calculated from length-frequency samples (95% confidence limits of all proportions are all less than 1.5%).

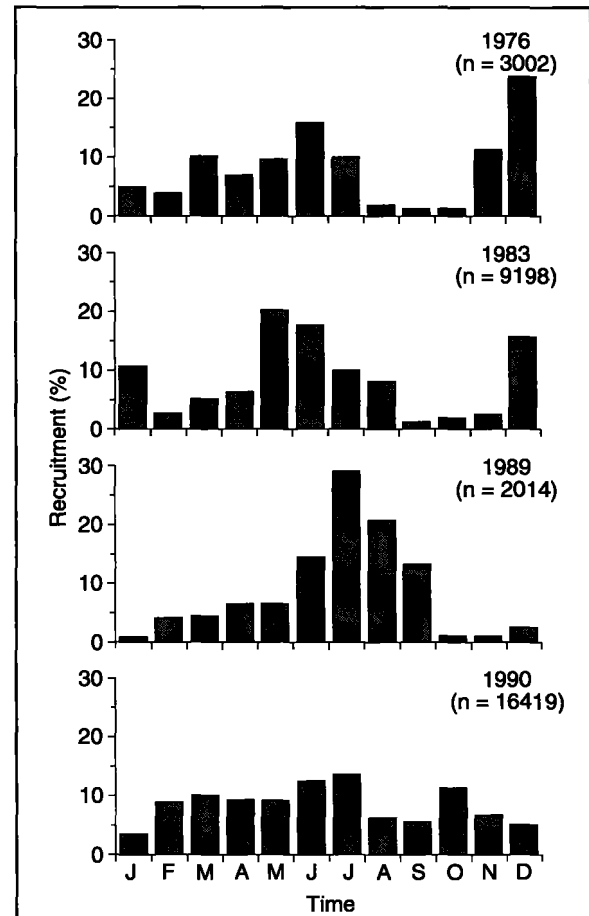


Figure 10

The proportion of *Spratelloides delicatulus* born each month in 1976, 1983, 1989, and 1990, back-calculated from length-frequency samples (95% confidence limits of all proportions are all less than 1.5%).

sistent with the close relation with maximum size found by Blaxter and Hunter (1982) for other clupeoids. These authors also noted a latitudinal effect; fish from lower latitudes spawned at a smaller proportion of maximum size.

Temperate clupeids (especially herrings, *Clupea* spp.) show a great plasticity in the number and size of eggs produced; many species show seasonal, and inter-annual, as well as geographic, variation in their reproductive outputs (Alheit, 1989; Jennings and Beverton, 1991) reflecting energetic resources and environmental conditions (Hay and Brett, 1988; Henderson and Almaraz, 1989). By comparison, the tropical herring, *H. quadrimaculatus*, spawned throughout the year and showed negligible temporal or spatial variation in fecundity, egg weight, or inter-spawning interval. This indicates that egg production was almost constant throughout the

study period and suggests that adult food resources and larval survival are predictable or relatively constant (Sibly and Calow, 1983).

In comparison to other species, *S. delicatulus* had a higher relative fecundity that was also correlated with HSI. Females in spawning condition also had a higher HSI at Butaritari. Commercial CPUE was highest at this site (Rawlinson et al., 1992) and *S. delicatulus* spawned more, smaller eggs than at other sites where relative fecundity was lower. These data suggest that the fecundity of *S. delicatulus* may be influenced by the amount of energy stored in the liver. This energy store would be important in a small multiple-spawning species; it would enable the fish to continue spawning during short periods of reduced food supply (Hay and Brett, 1988). The length of the inter-spawning interval has been shown experimentally to be related

to food supply in other fish species (Townshend and Wootton, 1984). Fish at Butaritari may experience a more predictable environment that enables them to produce more eggs of smaller size than fish in more variable environments.

In contrast, *A. sirm* delayed spawning beyond the size and age at sexual maturity and did not spawn until one year old. As fecundity was related to weight, delayed spawning enabled *A. sirm* to grow faster than the other species (Milton et al., 1993) and have a higher batch fecundity when spawning started. Murphy (1968) hypothesized that delayed spawning and longer reproductive life span would evolve in response to variable reproductive success. However, Armstrong and Shelton (1990) demonstrated that, even with a short reproductive life span, multiple spawners had a high probability of successful reproduction when subject to random environmental fluctuations over time. Thus, delaying spawning would be of adaptive advantage if mortality was low (Roff, 1984) because batch fecundity and lifetime egg production would be increased.

Our estimates of the reproductive lifespan of *A. sirm* indicate that this species spawns fewer times in their lifetime than other species and thus would also have less chance of successful spawning than other species. Given that this is the longest-lived of the species examined, our estimate of overall mean lifespan may be biased by the small number of months sampled. Large fish may be under-represented in small catches and may contribute to underestimating the reproductive potential of *A. sirm*.

Herklotsichthys quadrimaculatus had a longer reproductive life span and spawned more frequently than did the other species. Reproductive life span varied little among sites (except Abemama) and there was no significant temporal variation, which suggests that survival rates of large adult *H. quadrimaculatus* are fairly constant in Kiribati. This is reflected in their life-history parameters, which varied little among sites or over time. In contrast, the frequency distribution of back-calculated birthdates indicated that overall survival was variable both between and within years, and was not related to monthly egg production. We have no estimates of adult abundance during the study period, and so population egg production could not be assessed. However, the annual CPUE and abundance of *H. quadrimaculatus* in the baitfishery were similar in the three years for which both data sets were available (Rawlinson et al., 1992). This suggests that population size was relatively constant during this period. If so, then variation in post-hatching survival probably has an important influence on recruitment in this species (Smith, 1985).

The reproductive life span of the smallest species, *S. delicatulus*, was intermediate between the other species and varied little among sites during 1989 and 1990. Unlike *H. quadrimaculatus*, the reproductive life span of *S. delicatulus* varied between years, which suggests that survival rates are not as constant or as predictable as those of *H. quadrimaculatus*. Potential lifetime egg production of each female was only one tenth that of other species, but, because of the larger number of females, monthly estimates of daily egg production were higher. The distribution of back-calculated birthdates varied between years, but a greater proportion of births fell in May-August, irrespective of the pattern of egg production. Annual CPUE of *S. delicatulus* (Rawlinson et al., 1992) was similar in 1989 and 1990, which suggests that fishing mortality had not contributed to the increased mortality that reduced the reproductive life span in 1990.

The reproduction and abundance of *S. delicatulus* may be more directly influenced by its environment than are the other species. Adult survival is variable and low (Tiroba et al., 1990); egg production varies, probably in response to food supply, and survival to recruitment is unpredictable. Yet the potential for successful reproduction with this strategy may still be relatively high (Armstrong and Shelton, 1990). In contrast, *H. quadrimaculatus* appears to be able to offset environmental variability to produce a relatively constant supply of eggs.

The distribution pattern of back-calculated birthdates of each species was not consistent among species. Months when a higher proportion survived differed for each species during all years; months with highest mean survival were not the same for any species. This suggests that the effects of environmental conditions such as seasonal food availability or favorable physical conditions are not the same for each species. Alternatively, other factors such as predation (Rawlinson et al., 1992) may have greater influence on survival to recruitment. Egg production by *S. delicatulus* was positively correlated to survival rates in 1989 and negatively correlated in 1990. This seems unrelated to fish abundance as catch rates were higher in 1989 than in 1990 (Rawlinson et al., 1992).

Large variations in recruitment, reflected in catch rates of the main baitfishes do not appear to be directly linked with variations in egg production. All spawn in the lagoon for most of the year, and distribution of birthdates indicated recruitment in most months. Although the absolute level of recruitment varied throughout the year, multiple spawning reduces fluctuations in population size due to environmental variability and should ensure that relatively

stable population sizes are maintained. Earlier studies of *A. sirm* and *H. quadrimaculatus* in Tarawa lagoon suggested that these species spend at least part of their life outside the lagoon (R. Cross, 1978⁴; McCarthy, 1985¹). If this is the case, fluctuations in the relative abundances of these species may be related to migrations; a better understanding of the factors causing large-scale movements is necessary before predicting the potential yield of this fishery.

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