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Age structure, growth rates, movement patterns and feeding in an estuarine population of the cardinalfish *Apogon rueppellii*

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Abstract

The biology of a population of the cardinalfish *Apogon rueppellii* has been studied over several years (1977–1983) in the Swan Estuary in south-western Australia, using samples collected monthly from the shallows by beach seine and from various depths by otter trawl. While the life cycle of this species typically lasts for one year, at the end of which time the mean length is 50 to 60 mm, some individuals survive for a further year and attain lengths up to 104 mm. *A. rueppellii* shows a marked tendency to move offshore into deeper water during the winter months. This tendency is more pronounced in the 1+ than in the 0+ year class and in larger than smaller 0+ individuals. An inshore movement of *A. rueppellii* in the spring is followed by spawning and by oral brooding by the males, which leads to the recruitment of large numbers of a new 0+ year class on to the banks during the summer. The offshore movement is correlated with changes in salinity and temperature. The larger catches taken by otter trawl during the day than at night indicate that *A. rueppellii* exhibits a diel pattern of activity. Mean fecundity ranged from 70 in the 45 to 49 mm size class to 345 in the 90 to 94 mm size class. Measurements of fecundity and the number of oral-brooded eggs demonstrated that the majority of the eggs released by the female are collected and incubated by the males. Copepods are ingested in relatively greater amounts by small than by large *A. rueppellii*, whereas the reverse situation occurs with larger crustaceans, polychaetes and small fish. The presence of greater amounts of copepods in the diet during the day and of amphipods at night probably reflects the diel activity patterns of the prey.

Introduction

The Apogonidae are small fish that are typically found in the tropics and subtropics of both the Northern and Southern Hemispheres (Lachner, 1953). While many species of these cardinalfishes are found in warm shallow waters and reefs, particularly those of the Indo-Pacific region (Fraser, 1972), some species occur in brackish and even fresh water (Lachner, 1953). This family is characterised by its oral brooding habit, which in most species is restricted to the males (Smith, 1961; Breder and Rosen, 1966; Charney, 1976).

Studies on the biology of apogonids have concentrated almost entirely on marine populations and have placed particular emphasis on space utilisation, reproduction and diel patterns of movement and feeding. It is evident from such investigations that many cardinalfishes brood large numbers of eggs (Ebina, 1932; Garnaud, 1950; Lavett Smith *et al.*, 1971; Allen, 1975; Omori and Takahashi, 1980) and are nocturnally active carnivores whose diet can vary with season and size (see e.g. Livingstone, 1971; Allen, 1975; Vivien, 1975; Chave, 1978; Matallanas, 1982). The work of Kuwamura (1983) indicates that brooding in *Apogon notatus* occurs when the temperature reaches 20 °C, and Allen (1975) has estimated that the period between fertilisation and hatching in *Sphaeramia obicularis* is 8 d. While comparatively little detailed attention has been paid to such features as age structure and growth rates in apogonid populations, the study of Omori and Takahashi (1980) has demonstrated that the life cycle of *Apogon lineatus* in a bay in Japan typically lasts for only one year.

During the last few years, extensive sampling in the marine embayment of Cockburn Sound (Dybdahl, 1979) and in the nearby Peel-Harvey and Swan estuarine systems in south-western Australia has yielded large numbers of *Apogon rueppellii* (Chubb *et al.*, 1979; Potter *et al.*, 1983 b, c). Although *A. rueppellii* is obviously abundant in some ecosystems and has a distribution which extends from Albany (35 °S, 118 °E) in temperate south-western Australia northwards and eastwards to Arnhem Land in the Northern Territory [13 °S; 137 °E (Fig. 1)], there is very little information on the biology of this species.

The present study, which is apparently the first detailed investigation of a strictly estuarine population of cardinalfishes, has determined the age and size structure and growth rates in the population of *Apogon rueppellii* in the Swan Estuary. Particular attention has also been paid to describing seasonal and size-related patterns of movement and to determining whether these movements are correlated with such factors as temperature and salinity. An examination has been made of the relationship between the size of fish and both the fecundity and the numbers of orally brooded eggs. The stomach contents of *A. rueppellii* have been analysed to ascertain the relationship between diet and the size of fish and the time of day.

Materials and methods

Sampling regime 1977–1979

Sampling at Beach Seine Sites 1–14, which are located throughout the lower, middle and upper estuary of the Swan Estuary, south-western Australia (Fig. 1), was carried out twice monthly during the day between February 1977 and December 1978 and once monthly during 1979. The beach seine was 133 m long and 2 m deep, with a stretched mesh of 25 mm in the wings and 9 mm in the pocket.

Two otter trawl samples were collected during the day once monthly between August 1977 and December 1979 from depths of 2 to 16 m at Trawl Sites 1–6 in offshore regions of the lower, middle and upper estuary (Fig. 1). Each sample represented the catch made during a 5 min trawl in daylight at a boat speed of 3 to 4 km h^{-1}. The trawl net, which was 5 m long, had a mouth width of 2.6 m and a depth of 0.5 m. The warp and bridle lengths were 50 and 13 m, respectively. The net was constructed of 51 mm stretched mesh and terminated in a cod end of 25 mm.

The abundance data for *Apogon rueppellii* in Fig. 2 and the length-frequency histograms in Fig. 5 are based on data collected from the main axis of the Swan Estuary in 1977, 1978 and 1979, using samples taken inshore by beach seine at Seine Sites 2, 3, 4 and 5 and in nearby offshore regions by otter trawl at Trawl Sites 1, 2, 4 and 5. The data shown in Fig. 2 for each sampling occasion represents the sum of the fish caught by beach seine and by otter trawl at each of the above sites. The monthly data in Fig. 5 obtained by both beach seines and by otter trawls each correspond to, or were adjusted to correspond to, a monthly collection of two samples from each of the above 4 adjacent seine and trawl sites, which were then summed. The points in the growth curves in Fig. 7 represent the mode in a normal curve fitted by eye to the peaks for the classes hatched in late 1976 and 1977 shown in length-frequency histograms for all beach seine and otter trawl samples.

A two-way ANOVA was used to determine whether the numbers of *Apogon rueppellii* caught in beach seines and in otter trawls differed amongst regions of the estuary and in different seasons of the year. Before analysis, the catch data for all beach seine and otter trawl samples throughout the estuary were transformed using $\log_{10}(N+1)$ (Sokal and Rohlf, 1969).

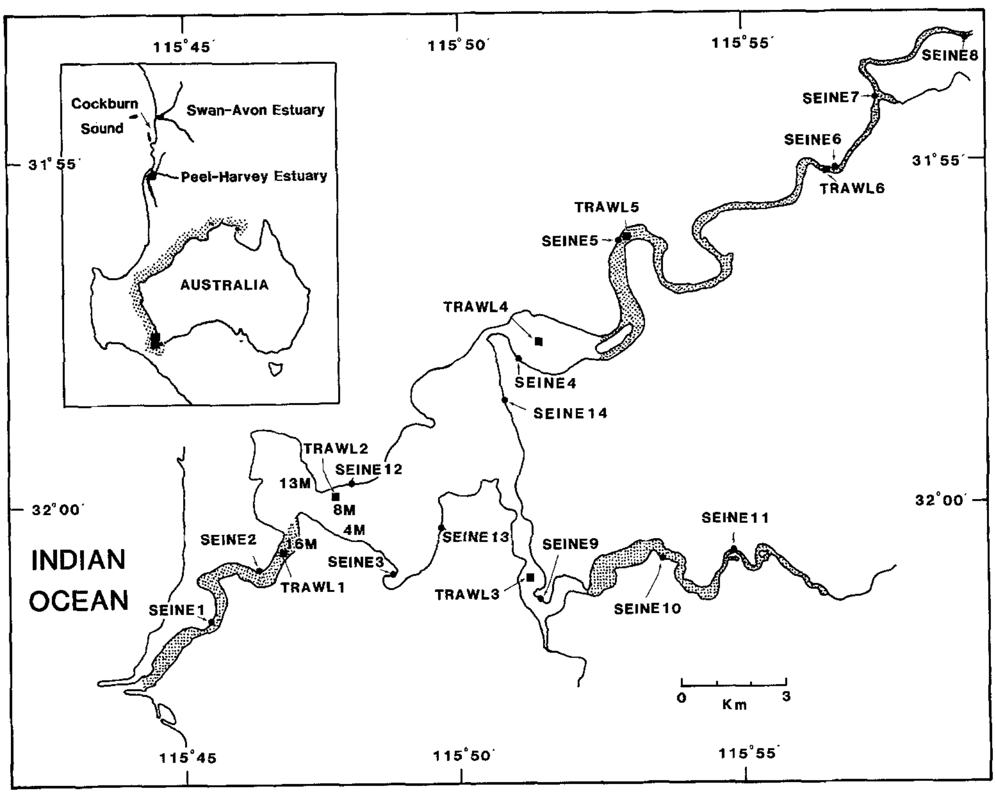

Fig. 1. Map showing sites in Swan Estuary where sampling was carried out by beach seine (Seine Sites 1–14) and by otter trawl using a 25 mm mesh cod end (Trawl Sites 1–6) and a 9 mm mesh cod end (sites where depth was 4, 8, 13, 16 m). Lower and upper estuary and distribution of *Apogon rueppellii* in Australia are stippled. Black rectangle on map of Australia shows region illustrated in inset

Sampling regime 1981–1983

Apogon rueppellii were collected monthly between May 1981 and March 1982 by beach seine from several sites and by otter trawl at water depths of 4, 8, 13 and 16 m (Fig. 1). These fish were used to obtain data on the relationship between gonadal development, oral brooding and the time of recruitment of the 0+ year class.

Two otter trawl samples of 5 min duration were made at 4, 8, 13 and 16 m (Fig. 1) during both the day and night between May 1982 and March 1983 to provide data on the abundance and size of *Apogon rueppellii* at different depths and times of day. Comparisons were made with beach seine samples collected at Seine Sites 12–14 in four different months during this period (May, August, November 1982, February 1983). While all other aspects of the otter trawl sampling regime in May and June 1982 were the same as that described above for the 1977–1979 sampling period, the cod end on the otter trawl was changed to the same size as that of the beach seine pocket, i.e., 9 mm, for the samples taken from July 1982 onwards.

Length, weight and environmental measurements

The total length and weight of all fish caught by beach seine and by otter trawl were recorded to the nearest 1 mm and 0.1 g, except in the case of very large samples when the measurements were restricted to a random subsample of at least 100 fish. When random subsamples were taken, the total number of fish was either counted, or estimated from the ratio of the weight of the subsample to the total sample.

Surface and bottom salinities and temperatures were measured at the time of both beach seine and otter trawl sampling.

Gonadal data

The weight of the ovary and testis of *Apogon rueppellii* in large representative subsamples of late 0+ and 1+ year-class fish taken between May 1981 and March 1982 were recorded to the nearest 0.1 g. The gonadosomic indices (GSIs) for both males and females were calculated from the equation $W_1 / W_2 \times 100$, where W_1 = weight of the gonad and W_2 = total body weight. The number of eggs in the ovary and in the mouth of males were recorded (sample sizes are shown in Fig. 9). The measurements of the diameters of Formalin-preserved mature and fertilised eggs are based on a total of ten eggs from each of ten individuals. An estimate of the time oral brooding takes in *A. rueppellii* was obtained by recording the time taken to hatch by eggs which were clearly in the early states of development. The results are based on 20 oral brooding males placed in aquaria containing water at a salinity (29‰) and ambient temperatures (24° to 28 °C) similar to those in their natural habitat at the time of capture. Because of the need to "handle" the oral brooding males carefully, it was undesirable to remove a sample of eggs from the mouth to determine their precise stage of development. The lengths of 100 newly-hatched larvae collected during this aquaria study were measured.

Analysis of diet

The stomach contents of *Apogon rueppellii*, which were taken from fish collected in otter trawls during the day and night between May 1982 and March 1983 at the 4, 8 and 13 m sites (Fig. 1), were analysed using the points method (Hynes, 1950; Ball, 1961). The stomach of each fish which contained food was given a fullness value between 1 (only a trace of food) and 10 (fully distended). The fullness value for each stomach was then divided amongst each of the identifiable food items according to their relative volume. The resultant value for each food item in the stomach of each *A. rueppellii* was then used to determine the mean for that item in the whole sample, this subsequently being referred to as mean percentage volume. After subjecting the data to angular transformation (Zar, 1974), ANOVA was used to determine whether the major categories of prey were ingested in significantly different proportions by fish of different sizes, by fish during the day and night and by fish in different seasons. The relative frequency of occurrence of each food item in the stomachs was also determined.

Results

Distribution

A two-way ANOVA showed that there was a significant difference ($P < 0.001$) between the mean numbers of *Apogon rueppellii* caught in beach seines in different regions of the estuary during 1977, 1978 and 1979. The numbers in seines were greatest in the middle estuary, followed by the lower estuary. While large catches were taken at Seine Site 5 at the bottom end of the upper estuary, a total of only 33 individuals were taken further upriver at Seine Sites 6, 7 and 8 throughout the whole of the above three years. ANOVA also demonstrated that the numbers in beach seines varied significantly with season ($P < 0.001$), with the greatest numbers in each region always being taken in the summer (December–February) and the lowest numbers occurring in the winter (June–August). There was, however, a significant season/region interaction ($P = 0.03$), a feature attributable to variations between the abundance of fish in different regions in the spring and autumn. A two-way ANOVA for the 1978 and 1979 data showed that the numbers in otter trawls also differed significantly between seasons ($P < 0.001$), but in this case the greatest numbers were found in the autumn and winter and the lowest were recorded during the summer. Unlike the situation with beach seines, there was no significant season/region interaction evident in the data collected by otter trawl ($P > 0.05$).

Annual and seasonal changes in abundance

The numbers of *Apogon rueppellii* caught in beach seines during the day showed marked seasonal variation (Fig. 2). The very high numbers taken in February and March of 1977, January and February of 1978 and March and April of 1979 almost entirely reflect a large influx of the 0+ recruits (cf. Figs. 2 and 5). The abundance of these young fish varied considerably among years. For example, four samples of between approximately 1 200 and 2 300 were obtained in early 1978, whereas the maximum single catches in 1977 and 1979 were 791 and 468, respectively.

The low numbers in most beach seine samples between March and September of 1977 and between June and mid-September of 1978 corresponded to increased catches of both 0+ and 1+ year-class fish by otter trawl in the deeper water (cf. Figs. 2 and 5). During these periods, marked haloclines were present in deeper water, with differences of 20 and 10‰ S being common between the surface and bottom in the winters of 1978 and 1979, respectively. During the heavy rainfall and cooler periods of the year, the temperatures on the bottom were higher than they were on the surface and in the shallows.

The numbers of *Apogon rueppellii* in otter trawls, when large catches were taken, was always greater during the day than the night (Fig. 3). This provides a very strong indication that this cardinalfish shows a tendency to move away from the bottom at night. As was the case for the daytime data obtained in 1977, 1978 and 1979 (Fig. 2), the numbers in the day and night otter trawl samples taken

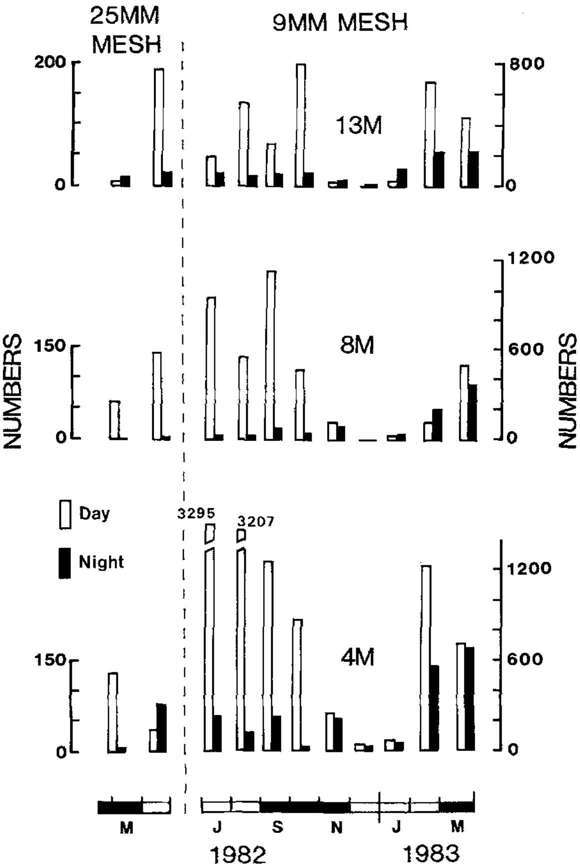

Fig. 3. *Apogon rueppellii.* Numbers caught by otter trawl during day and night at depths of 4, 8 and 13 m using cod ends with 25 mm mesh (May and June 1982) and 9 mm mesh (July 1982 to March 1983)

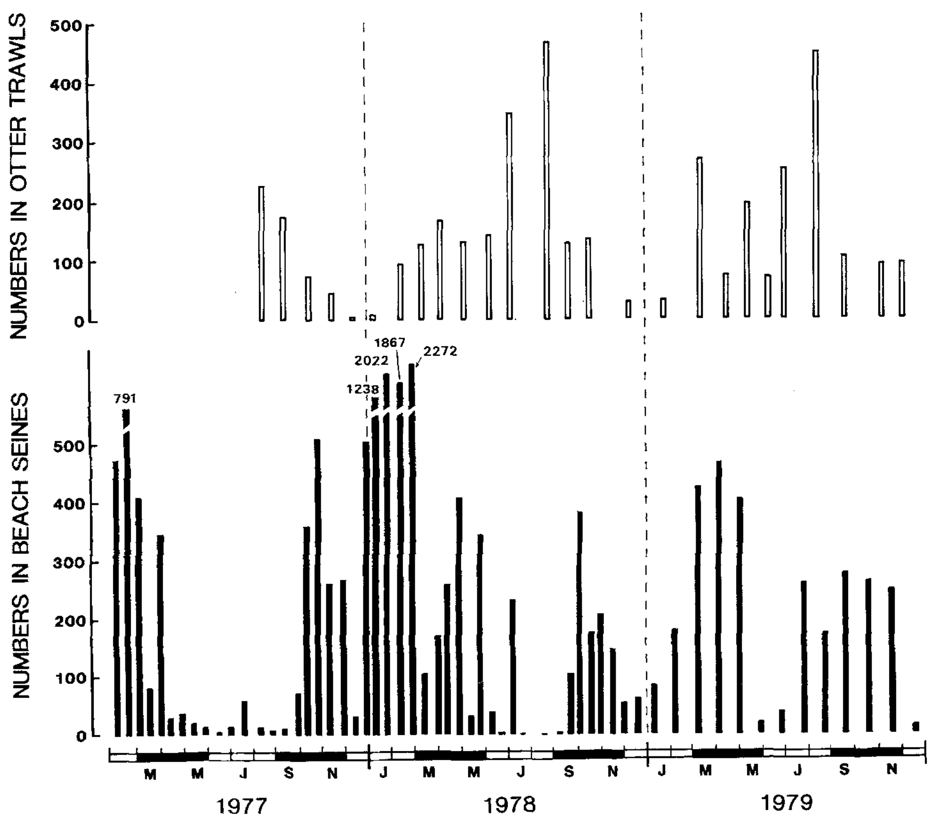

Fig. 2. *Apogon rueppellii.* Numbers caught during the day at Beach Seine Sites 2, 3, 4 and 5 and at Otter Trawl Sites 1, 2, 4 and 5 using the 25 mm mesh. In this and Figs. 3, 7 and 8, the autumn (March–May) and spring (September–November) months are denoted by black rectangles

between May 1982 and March 1983 were greater during the winter than the summer (Fig. 3).

In an attempt to ascertain whether the movement of *Apogon rueppellii* off the banks was correlated with such environmental factors as salinity and temperature, an investigation was made of the relationship between the catches in beach seines with these two parameters. The data were fitted to two models constructed with GLIM (Baker and Nelder, 1978), the first using untransformed abundance data and a Poisson error term and the second employing log-transformed abundance data with a normal error. An examination of the residuals (see Draper and Smith, 1966) indicated, however, that the data did not satisfy the assumptions of either of these models. The catches were therefore separated into those occurring in sequential, equal salinity (0 to 4.9‰, 5 to 9.9‰, etc.) and temperature intervals (10° to 14.9 °C, 15° to 19.9 °C, etc.) (see also Fig. 4) and then compared using the non-parametric Kruskal-Wallis test (Siegel, 1956). The significance of the interaction term between salinity and temperature was calculated using the procedure outlined by Bradley (1968: p. 140).

The mean numbers of *Apogon rueppellii* caught by beach seines differed in the salinity categories ($\chi^2_7 = 67.92$, $P < 0.001$). Beach seines caught no fish below 5‰ S and the mean catches of less than 38 fish for each 5‰ salinity interval below 25‰ S were much lower than those recorded above this salinity (Fig. 4). The mean catches also differed amongst temperature groups ($\chi^2_4 = 46.13$, $P < 0.001$). A sequential increase in mean numbers was recorded from the 10 fish in the 10° to 14.9 °C temperature category to 215 fish in the 30° to 34.9 °C group, with a particularly sharp rise occurring above 25 °C (Fig. 4). The salinity–temperature interaction term was significant ($\chi^2_{28} = 66$, $P < 0.001$). While catches by otter trawl were consistently much greater above 20‰ S, thereby paralleling quite closely the trends shown by beach seine samples, the trends shown by the relationship between catches and temperature were quite different for the two methods (Fig. 4).

Length-frequency data for inshore and offshore samples

The length-frequency histograms for August 1977, which were the first that were based on both beach seine and otter trawl samples, showed a pronounced modal length class at 60 to 64 mm (Fig. 5). While 88.2% of the cardinalfish contributing to this standardised composite sample (see "Materials and methods – Sampling regime 1977–1979") came from otter trawls in August, the number obtained by this sampling technique declined in subsequent months, with the result that by November the percentage contribution had fallen to 8.2%.

The length-frequency data for August to November 1977 were compared with monthly length-frequency histograms for the previous six months which were based solely on samples collected by beach seines. (N.B. Only the February data for this latter period are shown in Fig. 5). These comparisons demonstrated that the group corresponding to that which produces the modal length class of 55 to 59 mm in October and November corresponds to the one which, in February, yielded a well-defined modal length class at 35 to 39 mm (Fig. 5). Since this group is the product of spawning in late 1976, the pronounced modal length class exhibited in all samples between February and November represents the 0+ year class. The decline in the proportion of larger fish between August and November could be due to their earlier spawning and death. The view that breeding might occur earlier in larger individuals would be consistent with our observation that many of the very high GSIs at the beginning of the breeding season were found amongst this size category.

The appearance of the new 0+ recruits in December 1977, when they ranged in length from 16 to 37 mm, coincided with a marked decrease in the numbers of the previous 0+ year class as they reached the end of their first year of life (Fig. 5). This latter year class, now 1+, was well represented in several samples taken during 1978. Thus, modal length classes could be followed through the beach seine and more particularly the otter trawl samples until September 1978, when the modal length class was 80

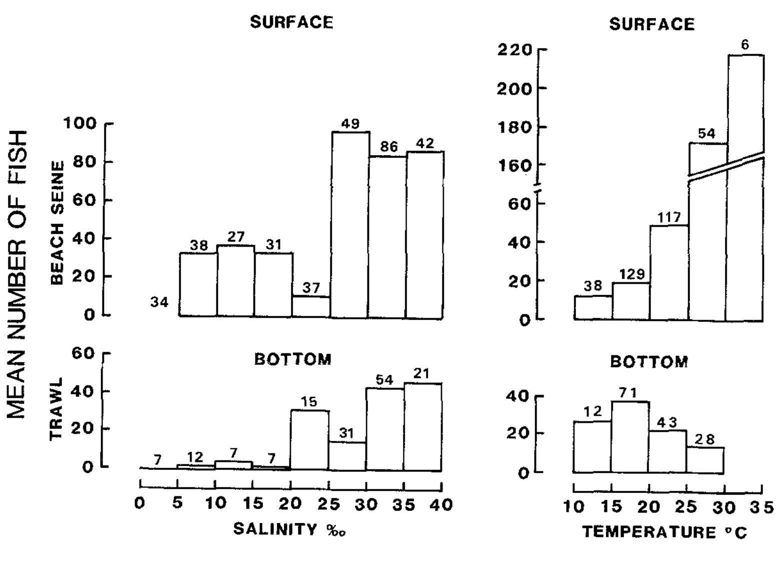

Fig. 4. *Apogon rueppellii.* Mean catch taken in beach seines and otter trawls at different salinities and temperatures. Number of samples is given above each histogram

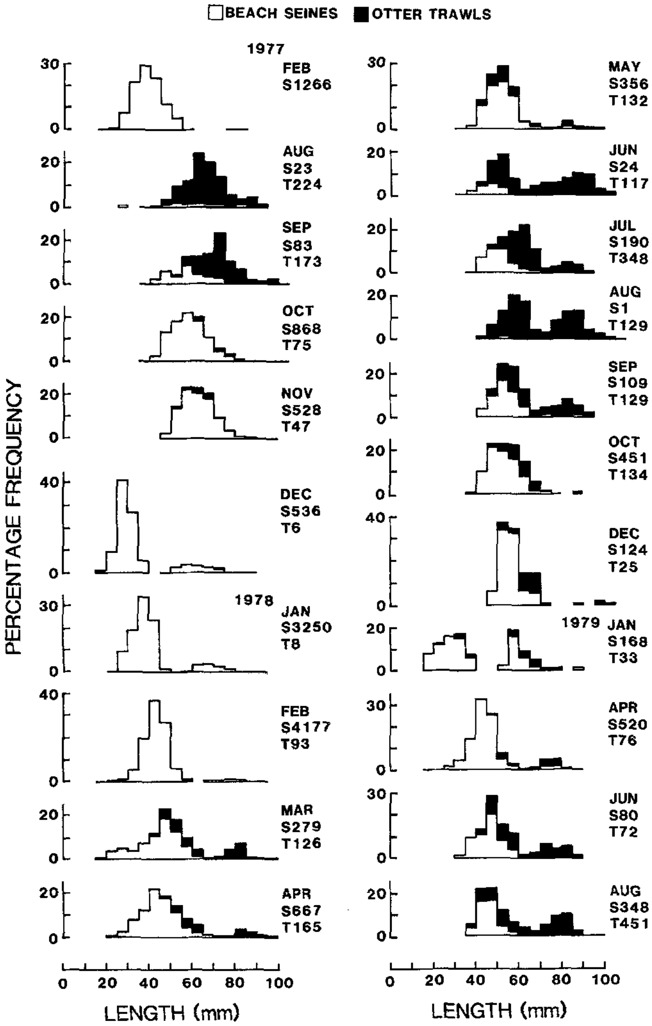

Fig. 5. *Apogon rueppellii.* Length-frequency histograms for fish caught by beach seine and by otter trawl using a 25 mm mesh cod end. Data for monthly beach seine and otter trawl samples have each been standardised to a common effort of two samples per month. S and T = standardised beach seine and otter trawl numbers, respectively

to 84 mm. An examination of scale annuli of a subsample of 30 large *Apogon rueppellii* (> 75 mm) in May confirmed the view that these fish were in their second year of life.

The 0+ year class, hatched in late 1977, increased from a modal length of 25 to 29 mm in December 1977 to 50 to 54 mm in December 1978, at which time spawning had already commenced. Representatives of this year class, now 1+, were present between January and August of 1979 (Fig. 5). The modal length-class for 1+ year class *Apogon rueppellii* in August 1979 was identical to that for 1+ fish in August 1978. A decline in the 1+ year class after August may be due to an earlier spawning of these larger individuals, as apparently occurred in the previous year. The new 0+ year class in 1979 produced modal length classes of 30 to 34 mm in January, 40 to 44 mm in April and 45 to 49 mm in June and August.

The proportion of the total standardised monthly catch in otter trawls was greatest during the winter (June to August) in both 1978 and 1979 (Fig. 5). Although otter trawling was not undertaken prior to August 1977, the marked decline in the contribution made by the otter trawls between August and November provide very strong indications that the same situation existed in the winter of 1977. Moreover, in the winter of each year, the modal lengths of the 0+ year class were frequently greater in otter trawls and the larger fish were almost entirely restricted to these offshore samples.

Length-frequency data for different water depths

Comparisons were made between the length-frequency data for samples of *Apogon rueppellii* collected in four different months by beach seine with those obtained by otter trawls operating in the same months with a 9 mm cod mesh at depths of 4, 8, 13 and 16 m. These comparisons showed that the modal length class of the 0+ year class in samples from shallow water and from a depth of 4 m were similar, but that these differed from the similar modal length classes displayed by the 0+ year class in samples from 8, 13 and 16 m. For convenience, the length-frequency histograms for different water depths have been restricted to the data obtained by otter trawl samples from 4, 8 and 13 m (Fig. 6).

The length-frequency histograms for May and June 1982, based on samples collected at 4 m with the 25 mm cod end mesh, showed 0+ and 1+ year class *Apogon rueppellii* at modal length classes of 40 to 44 and 70 to 74 mm, respectively (Fig. 6). The markedly higher numbers in the period between July and September is probably in part due to the rise in abundance that has already been shown typically to occur in otter trawls in the winter (Figs. 2, 5). However, the major factor producing the larger numbers is almost certainly the greater efficiency of the 9 mm cod-end mesh in capturing the smaller individuals. This view is supported by data collected from a series of trawls made at various depths in May 1984 with the 9 mm mesh net placed outside the 25 mm mesh net. Thus, while only 54% of the fish less than 60 mm were retained by the 25 mm mesh, the comparable value for fish greater than 60 mm was 97%. Despite differences in the numbers of the two size classes taken by these different mesh sizes, the modal length class of the 0+ and 1+ year class fish was identical in the 25 and 9 mm samples. This result means that, in spite of some differential selectivity in favour of the capture of the 1+ year class used for the length-frequency histograms shown in Fig. 5, the description of patterns of change in size based on modal length classes is valid. Moreover, since the mesh of both the beach seine and the otter trawl during 1977, 1978 and 1979 was not altered, the vast seasonal changes in the catches in the shallows and offshore regions shown in Fig. 5 reflect the type of changes in abundance that are occurring in these regions.

The greater total numbers and proportion of the 0+ year class in collections from 8 and 13 m between July and October than in the previous two months parallels the situation just described for 4 m (Fig. 6). However, the

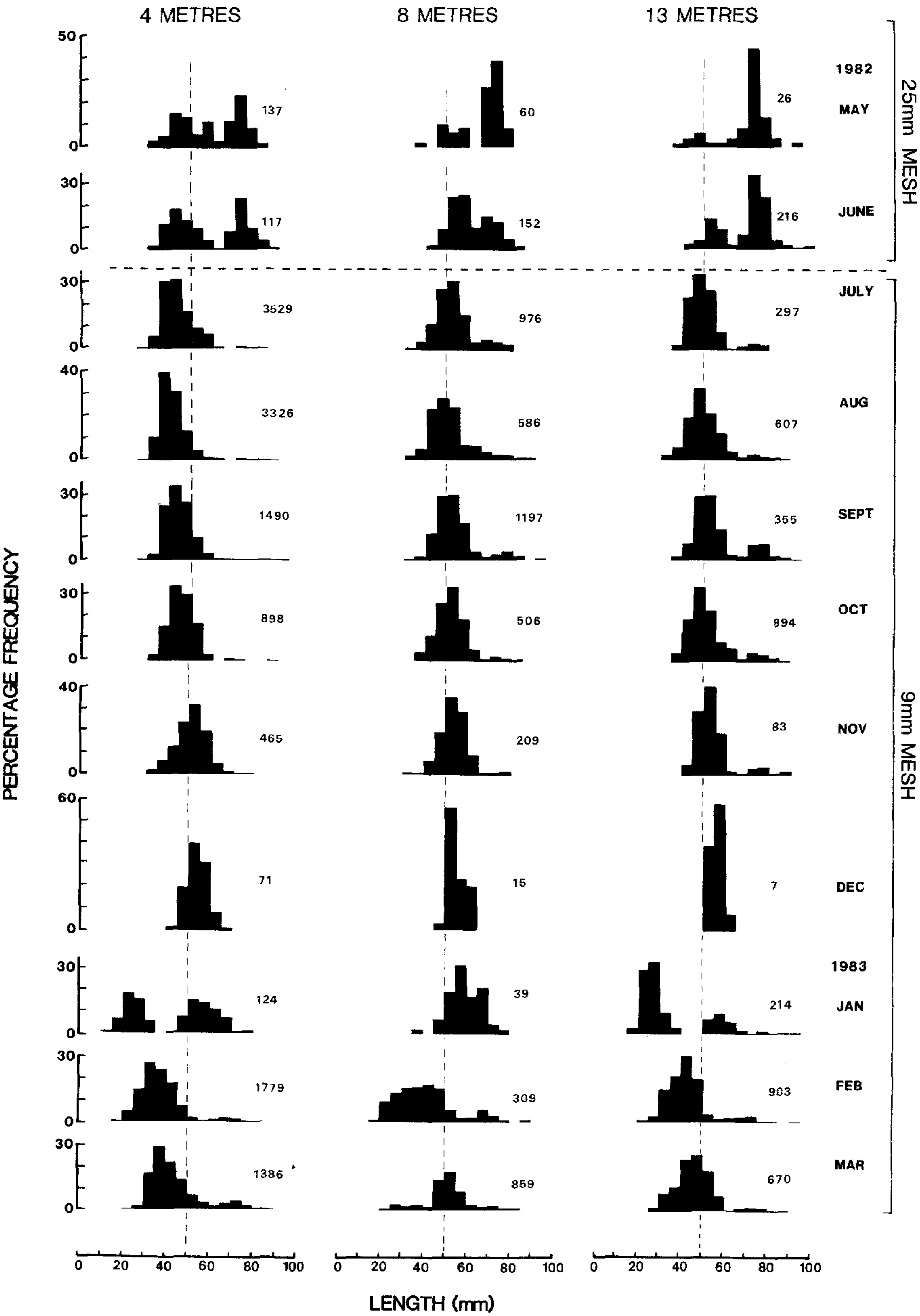

Fig. 6. *Apogon rueppellii*. Lenght-frequency histograms for fish caught by otter trawl using a 25 mm and a 9 mm mesh cod end at depths of 4, 8 and 13 m. Data for monthly samples have been standardised to a common effort of 5 min trawls on one day and one night per month. Numbers beside histograms indicate sample sizes

modal length class of the 0+ year class in all samples taken at 8 and 13 m between May and October was always 5 or 10 mm greater than those in the data for 4 m. Furthermore, the proportion of 1+ fish was in general greater in samples at 8, 13 and also 16 m than at 4 m. The first appearance of appreciable numbers of 0+ recruits in 1983 took place at the 4 and 13 m site in January and at the 8 m site in February. However, in both February and March, the numbers of these new recruits was far greater at 4 m than at either 8, 13 or 16 m.

The growth curves shown in Fig. 7 help to emphasise some of the points exhibited by the length-frequency data for beach seines and otter trawls. The points corresponding to the 0+ year class caught in beach seines between late May and late August of 1977, and generally also between early March and late June of 1978, fell below the line fitted by eye to the whole data set. This implies that the tendency for larger individuals to move out into deeper water becomes even more accentuated during the late autumn and winter, thereby paralleling the situation described for 0-group flatfish in Scottish waters (Poxton *et al.*, 1983). The trends exhibited by the curves show that growth is seasonal, with little increase in length occurring between the late autumn and mid-spring. The group which spawned in late 1976 attained mean lengths of 58 and 84 mm after approximately one and two years, respectively. The 1977 year class reached 52 mm after one year.

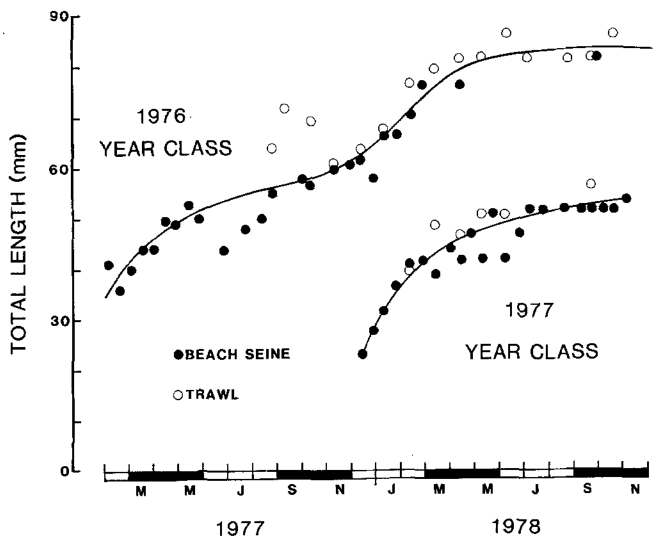

Fig. 7. *Apogon rueppellii*. Growth curves fitted by eye to mid-point of the mode in length-frequency data obtained from beach seine and otter trawl samples between February 1977 and November 1978

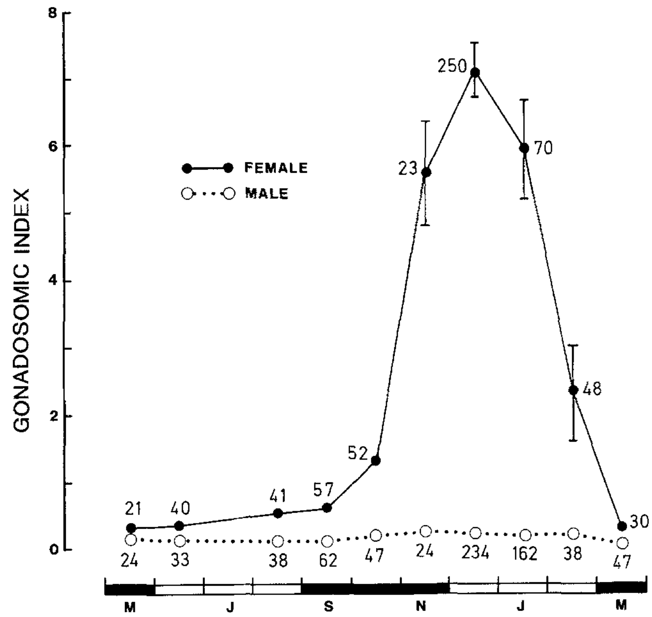

Fig. 8. *Apogon rueppellii*. Mean gonadosomic index (± 1 standard error) for males and females caught between May 1981 and March 1982. Number of fish examined is given beside each data point

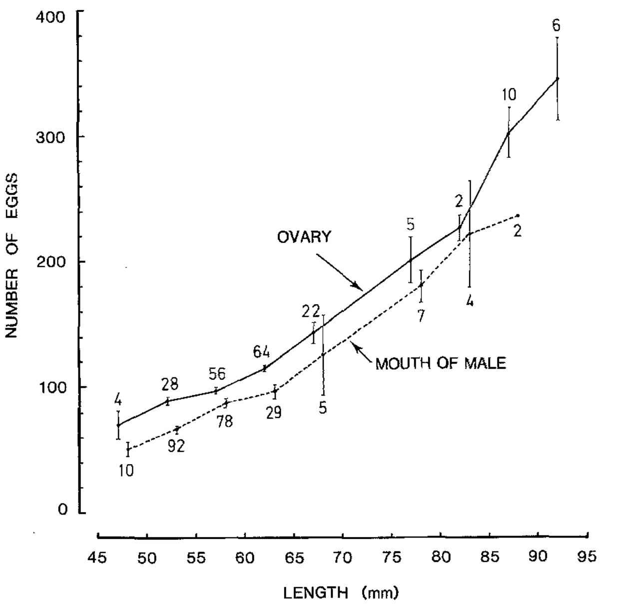

Fig. 9. *Apogon rueppellii*. Mean value (±1 standard error) for the fecundity (mature eggs per female) of females and number of oral brooding eggs in males of sequential 5 mm size groups. Number of fish examined is given beside each data point

Gonadosomic indices, fecundity and egg development

The GSI for females in 1981 increased sharply from 0.6 in September to 5.6 in November and reached a peak of 7.1 in December (Fig. 8). It subsequently fell to 2.3 in February and 0.3 in March of 1982. The GSIs for males, which reached a maximum in November, did not show such pronounced seasonal changes. The GSI data imply that breeding occurs in November, December and January. This view is consistent with the fact that oral brooding males were abundant between December and February and particularly in January, when the mouths of 81% of the 281 males examined contained eggs. While a few new recruits appeared in January, the first real influx of the young of the year occurred in February, at which time they produced a sharp modal length class at 30 to 34 mm.

The mean fecundity of *Apogon rueppellii* increased from 70 mature eggs per female in the 45 to 49 mm length class to 345 in the 90 to 94 mm length class (Fig. 9). Minimum and maximum fecundities of 51 and 457 were obtained for fish of 48 mm (=2.0 g) and 91 mm (=14.0 g), respectively. The mean number of eggs in the mouths of males was always greater than 70% of the values for the fecundity of the same size group of females. For example, in the 55 to 59 mm size group, the mean number of eggs incubated by males (88) represents a value corresponding to 90% of the mean number of mature eggs in the ovary (97).

A comparison of the logarithmic and linear regressions for the relationship between the fecundity (F) and the body weight (W) and the total length (L) showed that these relationships were best expressed as

$$F=58.062+20.23\ W \qquad (r=0.92,\ N=61,\ P<0.001)$$

$$\log F=\log 0.027+2.08 \log L \quad (r=0.90,\ N=61,\ P<0.001).$$

The mean diameter (± 1 standard error) of mature unfertilised eggs was 2.67 ± 0.133 mm, while the comparable measurements for eggs recently fertilised and just prior to hatching were 2.46 ± 0.021 and 2.41 ± 0.041 mm, respectively.

In the experiments with oral brooding males in the laboratory, the eggs, which initially corresponded to early stages in development, took 10 to 16 d to hatch. Since the latter time probably corresponds to the eggs which were in the very earliest stage of development at the beginning of this experiment, oral brooding probably lasts for just over two weeks in the Swan Estuary. The mean length of 100 larvae immediately after hatching was 7.80 ± 0.252 mm.

The relationship between the number of eggs in the mouth (N) and the body weight (W) and total length (L) of males can be described as

$$N=40.56+14.96\ W \qquad (r=0.74,\ N=119,\ P<0.001)$$

$$\log N=\log 0.019+2.16 \log L \quad (r=0.62,\ N=119,\ P<0.001).$$

Diet

The diet of *Apogon rueppellii* consisted mainly of crustaceans and polychaetes, which in many instances could be classified to the species level (Table 1). However, the data have occasionally been left at the family or genus level when the item belonged to a group whose nomenclature at the species level has not been resolved (B. Nott and J. Just, personal communication).

ANOVA showed that several of the different major food categories, e.g. copepods, amphipods, polychaetes, etc., were ingested in significantly different amounts by fish of different sizes and by fish feeding during the day and night ($P < 0.05$ to 0.001). Some significant seasonal differences in the amounts of the different food categories ingested were also found. The most marked of these was the greatly increased incidence of mollusc siphons taken in the winter.

Table 1. Species and other items found in stomachs of *Apogon rueppellii*

Amphipods	Polychaetes
Caprella sp.	*Capitella capitata*
Corophium sp.	*Ceratonereis erythraeensis*
Melita matilda	*Harmothoe waahli*
Melita spp.	*Marphysa sanguinea*
Ericthonius sp.	*Nereis oxypoda*
Neomicrodeutopus sp.	*Scoloplos simplex*
Paracorophium sp.	
	Teleosts
Tanaids	*Apogon rueppellii*
Paratanais sp.	*Atherinosoma elongata*
	Hyperlophus vittatus
Isopods	
Anthuridae sp.	Other categories
Cymothoidae sp.	Mollusc siphons
Sphaeromatidae sp.	Ascidian larvae
	Eggs – various types including *A. rueppellii* eggs
Copepods	Weed
Sulcanus conflictus	Sand
Gladioferens inermis	
Oithona sp.	
Harpaticoid copepod	
Mysids	
Gasterostraccus sp.	
Decapods	
Palaemonetes australis	
Alpheus richardsoni	
Halicarcinus australis	
Halicarcinus bedfordii	
Halicarcinus ovatus	
Heteropanope serratifrons	

The data in Fig. 10 show that copepods made a very important contribution to the total volume of food ingested by the 20 to 39 mm fish, but none to the 60 to 92 mm category. Conversely, shrimps, crabs, polychaetes and small teleosts, including *Apogon rueppellii* less than 25 mm in length, were more important to larger fish. Copepods and polychaetes were ingested in greater amounts during the day, while amphipods were eaten in larger quantities at night. The trends shown by the data for percentage frequency of occurrence were very similar to those shown in Fig. 10 for mean percentage volume.

Discussion

Life cycle duration and movement patterns

Our data demonstrate that the life cycle of a considerable proportion of the population of *Apogon rueppellii* in the Swan Estuary lasts for only a year. This view is based on the fact that the size group corresponding to the 0+ year class dominates samples taken both by beach seine in the shallows and by otter trawls using the 9 mm cod-end mesh in deeper water. The relative numbers of the 1+ year class varied amongst years. Thus, this group was more conspicuous in length-frequency histograms for samples in 1978

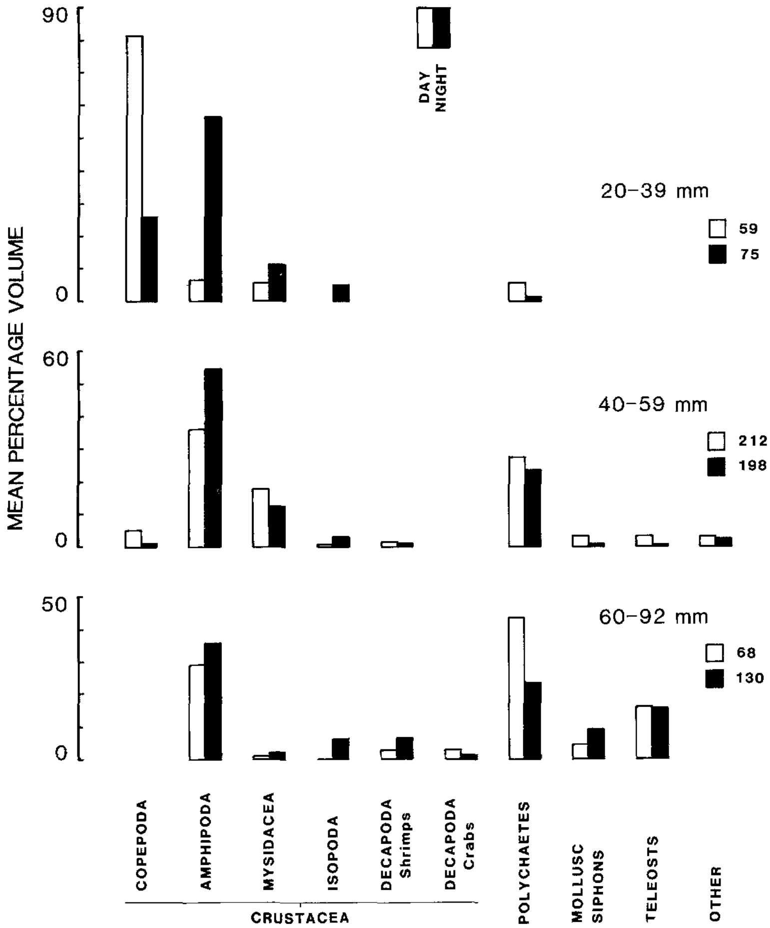

Fig. 10. *Apogon rueppellii.* Mean percentage volume of various food categories in stomachs of three different size groups during day and night. Numbers beside day and night symbols on far right represent number of fish examined

and, to a lesser extent, 1979 than it was in those for 1977. Our finding that *A. rueppellii* typically has a one-year life cycle parallels the situation described for *A. lineatus* in a bay in Japan (Omori and Takahashi, 1980).

From the abundance data (Fig. 2) and the length-frequency histograms (Fig. 5), it is evident that the increase in numbers in the shallows in October and November of both 1977 and 1978 was almost exclusively due to the appearance in the shallows of late 0+ fish. These sexually mature and oral brooding fish belong to the group whose progeny would give rise to the 0+ recruits in the early part of the following year. Likewise, the decline in numbers in December of 1977, 1978 and 1979, prior to the 0+ recruitment, reflects the relative absence of many fish after spawning, presumably due to mortality.

A comparison between the length-frequency data for beach seines and otter trawls taken during the day also demonstrates that the water depth occupied by *Apogon rueppellii* varies with age and size. Thus, in most months of the year, the 1+ year class showed a far greater tendency to occur in relatively greater numbers in otter trawls with the 25 mm cod-end mesh than in beach seines taken at the same time. While this feature can be partly attributed to the larger mesh size of the cod end than that of the beach seine pocket (9 mm) there can be no doubt that the incidence of older fish in deeper water is generally greater. This view is supported by the fact that the proportion of 1+ year class fish was greater in otter trawls taken with a 9 mm cod end mesh at depths of 8, 13 and 16 m than by the same method at 4 m or by beach seine (9 mm mesh pocket) in the shallows. Since the modal length classes in length-frequency histograms for the 0+ fish were greater at 8, 13 and 16 m than at 4 m and in the shallows, it is also evident that the large representatives of this age class show a relatively greater tendency to move out into deeper water.

The far greater number of fish taken by otter trawl than by beach seine during many of the months between autumn and mid-spring emphasises that, in addition to age and size, the offshore movements have a seasonal component. Our data show that water temperatures in the winter did not fall as low in deeper water as in the shallows. Thus, the occupation of the deeper waters at these times has the advantage of exposing the fish to less extreme minimum temperatures. Higher minimum temperatures in the deep water may be of selective advantage to a species which, throughout much of its distribution, occurs in warmer waters than those found in the shallows of the Swan Estuary in the winter. While the offshore movements into deeper water were correlated with salinity, it should be noted that a population of *Apogon rueppellii* in a local protected marine embayment undertakes similar seasonal migration (Dybdahl, personal communication). Since this implies that salinity does not exert a major influence on the seasonal movements of *A. rueppellii,* and there was a significant interaction between salinity and temperature in our data, care must be taken in assigning a possible role for this environmental parameter. However, a seasonal movement out under the pronounced haloclines that frequently characterise parts of the Swan Estuary in the winter (Spencer, 1956; Hodgkin, 1974) would enable this species to remain in higher salinities than those prevailing in the shallows. Recent studies in the nearby Peel-Harvey estuary have provided strong evidence that the blue manna crab *Portunus pelagicus* has a preference for similar higher salinity regimes and moves under the halocline during periods of low inshore and surface salinities (Potter *et al.*, 1983a). It is also possible that the winter movement into deeper water is of advantage in providing a relatively poor swimmer such as *A. rueppellii* with refuge from the turbulent inshore winter conditions caused by storms in marine environments and by freshwater discharge in estuarine environments.

Fecundity and oral brooding

The mean fecundity of approximately 210 determined for *Apogon rueppellii* measuring 70 to 90 mm is far lower than the values of between 4 900 and 21 000 recorded for comparable sized representatives of the apogonids *Cheilodipterus affinis* (Lavett Smith *et al.,* 1971), *Sphaeramia orbicularis* (Allen, 1975) and *Apogon lineatus* (Omori and Takahashi, 1980). The much lower egg number in *A. rueppellii,* than for example in *S. orbicularis,* is related to much larger egg diameters (2.4 vs 0.6 to 0.7 mm) and to a larger size at hatching (7.5 vs 3.3 mm). Mean egg diameters of only 0.24 mm have been recorded for the apogonids *Phaeoptyx conklini* and *Apogon maculatus* (Charney, 1976). The large eggs and large size at hatching in *A. rueppellii* may be of advantage to a species which breeds in estuaries where, even in the case of the Swan, the environment is less stable than that of the marine regions where apogonids are more typically found.

Our results show that the males of *Apogon rueppellii* incubate a number of eggs that is proportional to their body size. From our observations that the mouths of males tend to be full of eggs, it is apparent that the size of the buccal cavity is a major factor limiting the number of eggs brooded by males. A similar conclusion was reached by Omori and Takahashi (1980) on the basis of their work with *A. lineatus.* The comparisons between the number of eggs in oral brooding males with those in the ovary of mature females of comparable size show that, on average, the males of *A. rueppellii* succeed in collecting at least 70% of the eggs spawned by females. Moreover, since oral brooding fish occasionally contained eggs in their stomachs and probably lose some to the environment during development, and as a few eggs were sometimes released on capture, the above percentage values are almost certainly an underestimate. The very high retrieval rate of eggs, which may thus approach 100%, is mainly due to the fact that apogonid eggs are collected immediately after spawning (Kuwamura, 1983) and possess connecting threads which ensure that they remain clumped together after discharge from the female (Ebina, 1932; Breder and Rosen, 1966; Charney, 1976).

Since the modal length class of the new 0+ recruits in February, March and April of 1977, 1979 and 1983 were similar to that of February 1982, the main spawning period in 1976/1977, 1978/1979 and 1982/1983 presumably occupied similar time periods as in 1981/1982, i.e., November–January. The recruitment of considerable numbers of 0+ year-class fish in December 1977 and the presence of a modal length class of 40 to 44 mm in February 1978 implies that spawning peaked earlier than usual in 1977/1978, probably in November 1977. This view is consistent with the larger size of fish in January and February of 1978 than in the same months of 1979. It would appear from our temperature data that spawning is initiated at approximately 23 °C, which is slightly greater than that at which oral brooding commences in *Apogon notatus* (Omori and Takahashi, 1980).

Diet

Stomach analyses demonstrate that *Apogon rueppellii* is a carnivore which feeds to a large extent on crustaceans, polychaetes, mollusc siphons and small teleosts. However, the diet does change markedly with increasing size, with a shift from copepods towards larger crustaceans, polychaetes and fish. These results parallel quite closely those recorded for other apogonids. For example, in the western Mediterranean, smaller *Epigonus denticulatus* feed predominantly on mysids and copepods, whereas the largest size category rely to a large extent on teleosts (Matallanas, 1982). The change in diet of *A. rueppellii* with increasing size almost certainly reflects the ability of the larger fish to ingest larger prey items. In this context, Chave (1978) has shown that the size of prey items was related to the body size of the fish in the case of six species of cardinalfishes.

The decline in the relative amounts of copepods ingested at night by small *Apogon rueppellii* is probably due to a movement of these crustaceans towards the water surface and thus out of the main foraging area. By contrast, the increase in the relative amount of amphipods at night presumably reflects their movement into the water column at this time. These views are based on the diel movements of copepods and amphipods in an eelgrass community in eastern Australia which Robertson and Howard (1978) considered would influence their availability as prey for fish. Diel patterns of prey availability have also been invoked for diel differences in the composition of the diet of several species of reef apogonids (Vivien, 1975).

The evolution of an estuarine mode of life

The population of *Apogon rueppellii* in the Swan River passes through the whole of its life cycle within the estuary, which parallels the situation recorded for the atherinid *Allanetta mugiloides* (Prince *et al.*, 1982; Prince and Potter, 1983) and the teraponid *Amniataba caudavittatus* (Chubb *et al.* 1979). Although populations of all three species are found in the marine environment, which is presumably where they each originated, only *Apogon rueppellii* is found in large numbers in inshore coastal regions near the Swan (Chubb *et al.*, 1979; Dybdahl, 1979; Prince *et al.*, 1982; Prince and Potter, 1983). Some other species which live in the Swan Estuary, such as the atherinids *Atherinosoma elongata* and *Atherinosoma wallacei,* have rarely or never been found in marine habitats (Prince *et al.*, 1982), and several marine species spend much of their life cycle in the Swan Estuary (Chubb *et al.*, 1979, 1981; Chubb and Potter, 1984). From the above data, it would appear that the environment in the Swan Estuary is particularly favourable for permanent or extended colonisation by marine species. In this context, it is important to note that the hydrology of the estuary of the Swan River is relatively stable. For example, tidal action is small, high salinities are maintained in the low and middle estuary for much of the year, and heavy freshwater discharge is generally restricted to the winter months (Spencer, 1956; Hodgkin, 1974; Prince *et al.*, 1982). Moreover, the marked haloclines that form in the deeper parts of the estuary during periods of heavy freshwater discharge provide regions into which species with a preference for higher salinities and reduced turbulence can move at such times.

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