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BREEDING ACTIVITY OF MARINE PHYTAL HARPACTICOID COPEPODS FROM COOK STRAIT

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ABSTRACT

The reproductive status of 20 species of alga-dwelling harpacticoid copepods at Island Bay, Wellington, New Zealand, was investigated from April 1973 to March 1974. These data form the first comprehensive account of the breeding regime in natural populations of truly phytal species.

In most species the breeding season, as defined by the presence of ovigerous females in the population, was either continuous or protracted: distinct maxima occurred at different times in different species, but a large number (40%) reached maximum breeding activity in the autumn. However, the proportion of copepodites appears to be a better indicator of the effects of reproduction, because increases in this index generally lead to the observed maxima in population density. By the relationship between the yearly mean number of eggs per female and the mean percentage of ovigerous females in the population, the 20 species fall into 5 identifiable groups: *Group 1* of 4 species, where 57-78% of the female population are ovigerous, each with a low number of eggs per female (7-13); *Group 2* of 6 species, where 32-42% of the female population is ovigerous, each with 10-19 eggs per female; *Group 3* of 7 species, with a low percentage of ovigerous females (12-30%) carrying 15-25 eggs; *Group 4* of 2 species, with 30-32% of the females ovigerous and carrying a large number of eggs per female (38-45); *Group 5* of 1 species, with a high percentage of ovigerous females (60%) and with a large number of eggs per female (50).

In general, breeding is not correlated with temperature and food supply; continuous breeding is perhaps related to the small summer-winter temperature differential in Cook Strait, and to a suspected unlimited availability of food. Differing physiological responses to temperature and food results in reproductive maxima being reached at different times of the year in various species. Onset of reproduction in the supralittoral pool species *Robertsonia propinqua* (T. Scott) may be determined by a combined temperature/salinity regime of 13-14° c at about 30-35‰.

Sex ratios varied noticeably both within and between species from season to season, probably because of a homeostatic mechanism related to population density. Females predominate during low population densities, but males predominate during high abundance. The most abundant species occurring on *Coralina* have their maxima of reproductive activity temporally separated. Such a succession may reduce competition between them.

The strictly phytal species *Porcellidium dilatatum* Hicks (Porcellidiidae) has longevity and egg maturation rates which are similar to those of level-bottom meiobenthic species. In general, reproductive capacity is higher in alga-dwelling species than in interstitial species.

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INTRODUCTION

Literature on the reproduction of harpacticoid copepods has until recently been concerned mainly with the experimental approach to rearing and larval development (e.g., Nicholls 1935, Bozic 1960, Vilela 1969), reproductive genetics (e.g., Battaglia & Volkmann-Rocco 1973), and calculation of reproductive potential measured by the intrinsic rate of natural increase (r_m) (Heip 1972, Heip & Smol 1976).

Few published accounts of field studies on seasonal reproductive activity exist: Barnett (1970) presented a detailed account of the life cycles of two mudflat-dwelling species of *Platychelipus* (Laophontidae), and Lasker *et al.* (1970) analysed the growth, reproduction, and metabolism of the meioepibenthic sand-dwelling species *Asellopsis intermedia* (T. Scott). The reproduction and growth of *Bulbamphiascus imus* (Brady) and the seasonal reproductive cycle of *Halectinosoma herdmanni* (T. & A. Scott) were described from the fine sand biotope of Marseilles by Dinet (1972); Heip (1973) and Coull & Vernberg (1975) have noted breeding succession in some brackish water and estuarine species. Harris (1972) and Mielke (1976) have each presented comprehensive analyses of seasonal changes in reproductive activity of a number of species from sandy beaches in Cornwall and the North Sea island of Sylt respectively. In a long-term meiofaunal study of Firemore Bay in Loch Ewe, Scotland, McIntyre & Murison (1973) briefly re-examined the breeding cycles of four of the interstitial species studied in Cornwall by Harris (1972), and found only minor differences in breeding maxima between the two sites.

In all these studies distinct reproductive periods were observed, with most species breeding most actively in the late boreal spring and summer. However, in some other investigations, species have been observed to breed throughout the year, or to reach breeding maxima in the autumn and winter (Bodin 1972a, b, c; Heip 1973, Mielke 1976).

Harpacticoid copepods associated with marine algae at Island Bay, Wellington, New Zealand, all showed pronounced seasonal changes in population density (Hicks 1977b). To help explain such variability, quantitative data on the reproductive state of the most abundant species were obtained, and information on the population structure was collected and analysed for seasonal breeding activity of 20 species. Apart from a paper by Lepez (1974) on reproduction in *Porcellidium rubrum* Pallares from Chilean *Ulva lactuca*, this account represents the first comprehensive research on reproductive activity of truly alga-dwelling harpacticoids. The data cover 12 months only; they are applicable only to the site studied and to the year of the study. The composition of the fauna, its occurrence, species associations, and seasonal population densities have been described by Hicks (1977a, b), where detailed accounts of the study area, physical variation in the environment, seaweed habitats, and sampling methods are also given.

METHODS

Seaweed samples were collected in the last week of each month from April 1973 to March 1974. Sublittoral samples were obtained by scuba-diving with a portable sample-cutter measuring 10×10 cm.

Copepods were narcotised in the laboratory with an isotonic solution of magnesium chloride and then fixed in 10% formalin. Those from sublittoral algae were hand sorted, and specimens from *Corallina officinalis* in intertidal pools were collected by the swirling/decantation method (see Uhlig *et al.* 1973). Hand sorting was completed under a binocular microscope, and the extracted samples were stored in a 2 : 1 mixture of 5% formalin and 50% monoethylene glycol. Mean numbers of copepods extracted from the seaweeds were normally calculated from two or sometimes three samples. The mean, variance, and standard deviation were each calculated from pooled sample data to indicate the degree of sampling error for quantitative values. Analyses had a S.D. of about 5%, and most trends in data presented in the results were therefore considered meaningful. The efficiency of the sorting procedures was tested and estimated at over 90% (Hicks 1977a).

Adults and copepodites were collected. On the 0.1 mm sieve used, many of the nauplii were not retained, but nauplii were not included in the analysis because their identification is difficult. Copepodites were counted as a group, without separation into stages; adults were easily sexed in the present species, the males being distinguished by their modified haplocer or sub-chirocerate antennules and/or by the reduced fifth leg. The number of females carrying ovisacs and the number of eggs in each sac were counted; mean number of eggs per female was derived from aliquots of all ovigerous females (Motoda's subsampling technique, see Wiborg 1962), usually based on over 30 individuals. The number of mating pairs (males grasping females) could be counted in five species. Vigorous swirling and decantation during extraction, however, probably reduced their numbers. Also, couples often disengaged on the addition of preservative; thus only those species with tenacious coupling remained intact, and therefore the copular data are minimum values.

RESULTS

Most species studied apparently breed continuously throughout the year, with distinct maxima of activity at different times. For each of the 20 species, diagrams (Figs 1-5) show total population density, sex ratio, the proportion of females carrying ovisacs expressed as the percentage of the total female population, percentage of copepodites per total population, and number of eggs per female. Where applicable, the percentage of mating couples is also included.

Annual mean sex ratio, mean percentage of ovigerous females, mean number of eggs per female, and the reproductive capacity of each species appear in Table 1. Reproductive capacities are derived for each species

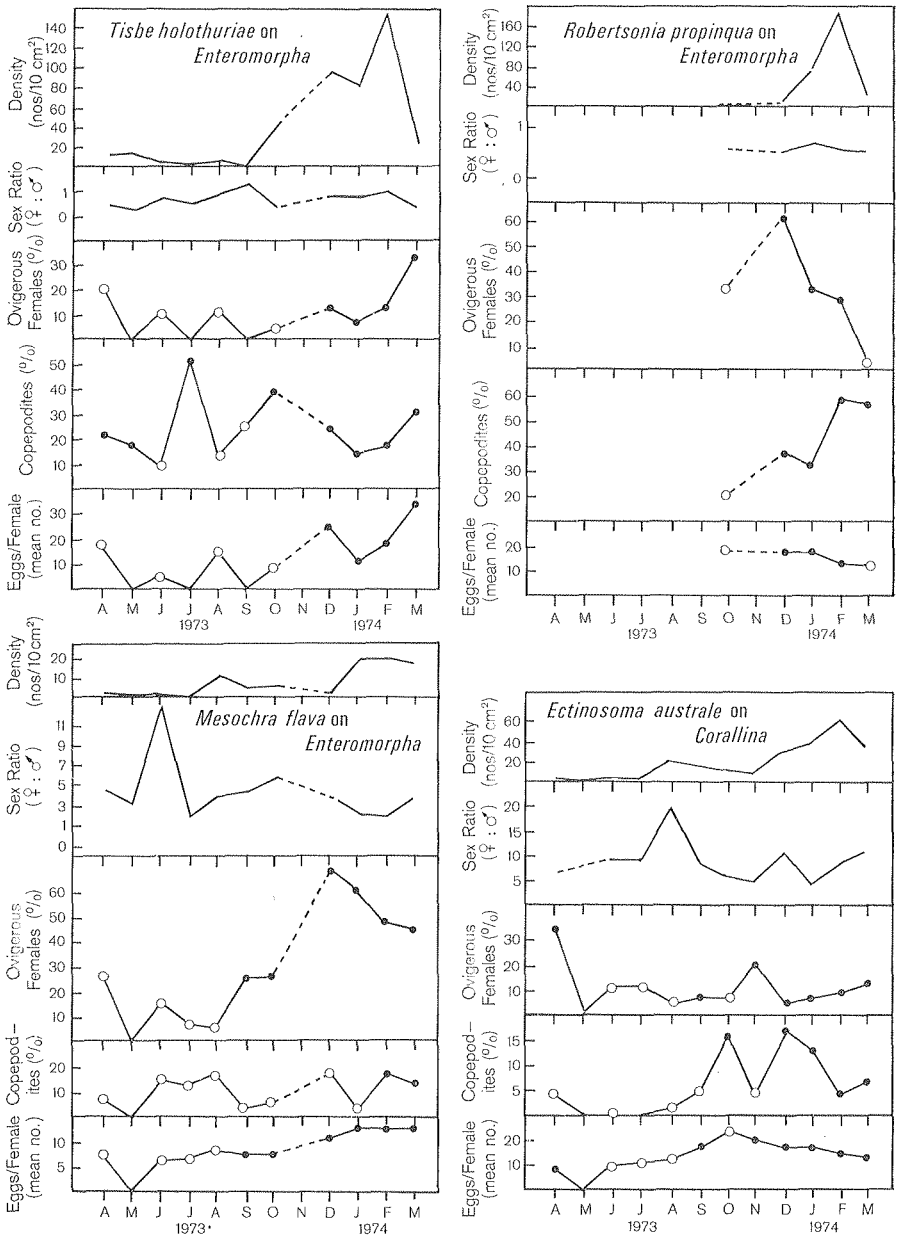
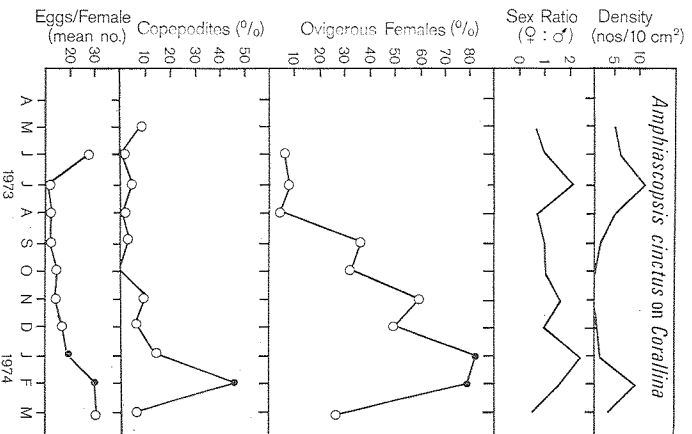
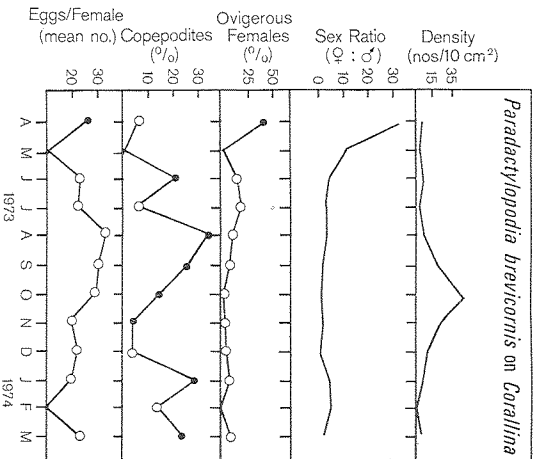
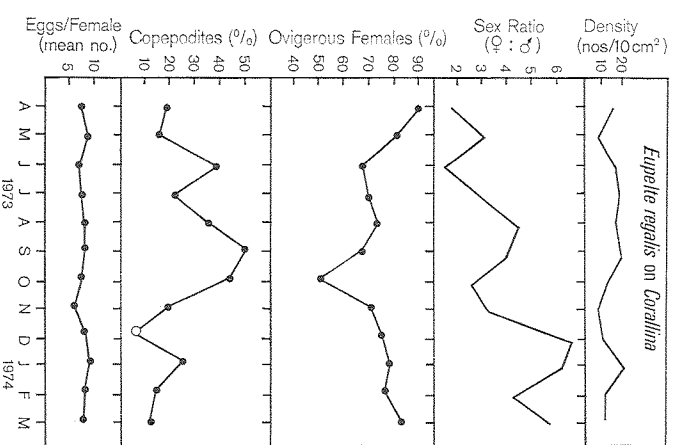
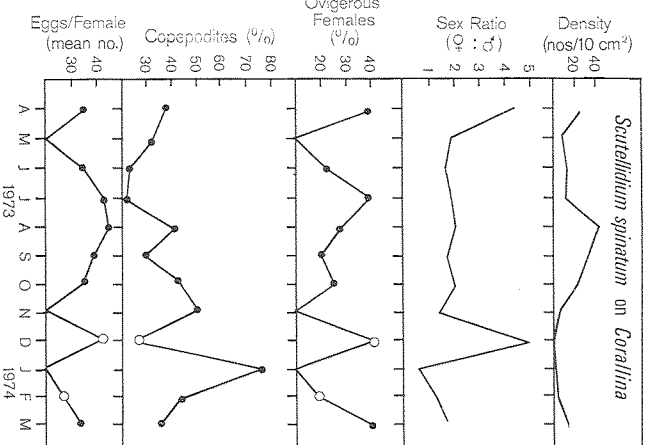


FIG. 1—Seasonal breeding pattern of four species of alga-dwelling harpacticoid copepods at Island Bay, Wellington, New Zealand. Open circles represent data derived from 10 or fewer individuals in the population; broken lines indicate loss of the November sample from *Enteromorpha*; that for sex ratio of *Ectinosoma australe* represents no data, as the species was absent from collections.



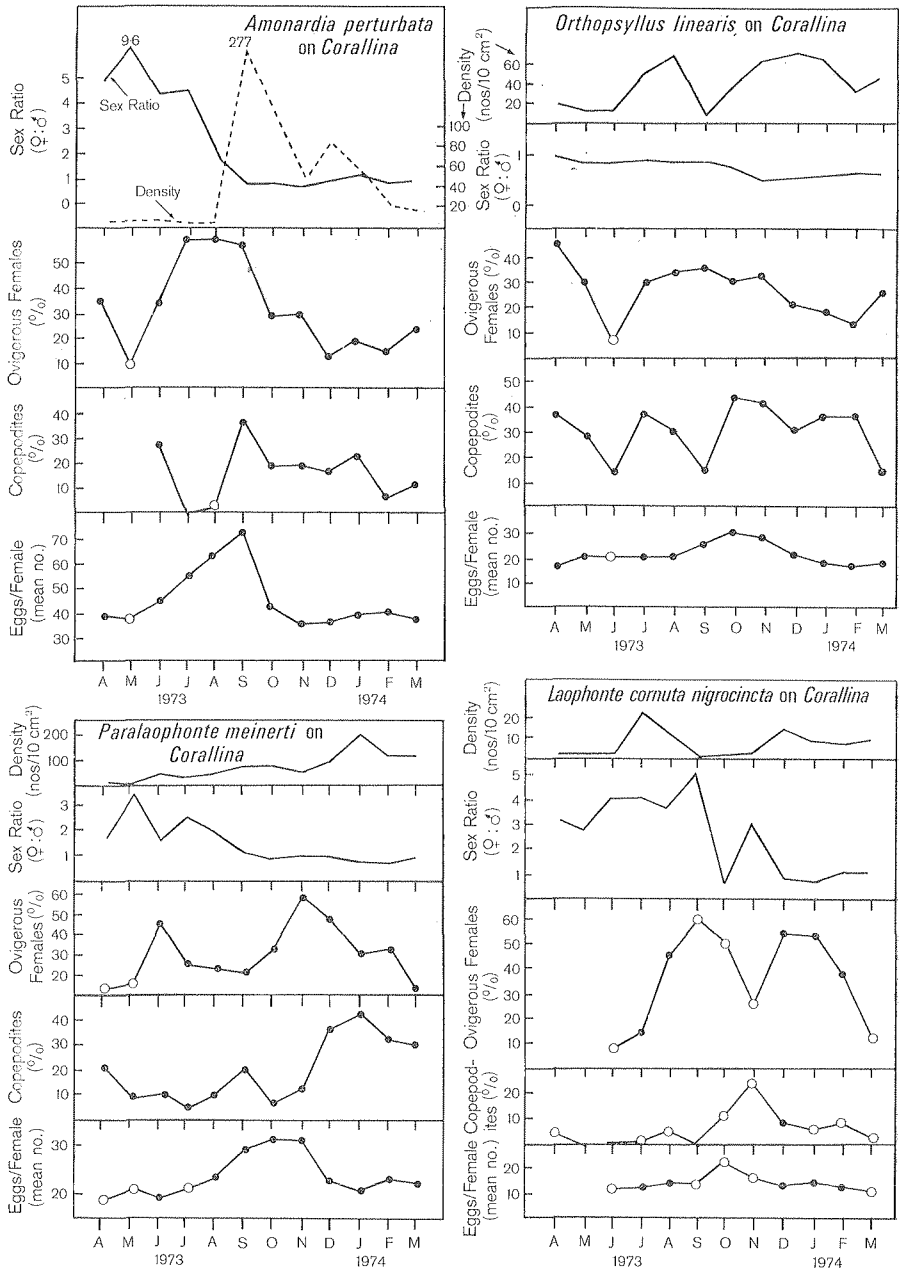


FIG. 3.—Seasonal breeding pattern of four species of alga-dwelling harpacticoid copepods at Island Bay, Wellington, New Zealand. Open circles represent data derived from 10 or fewer individuals in the population.

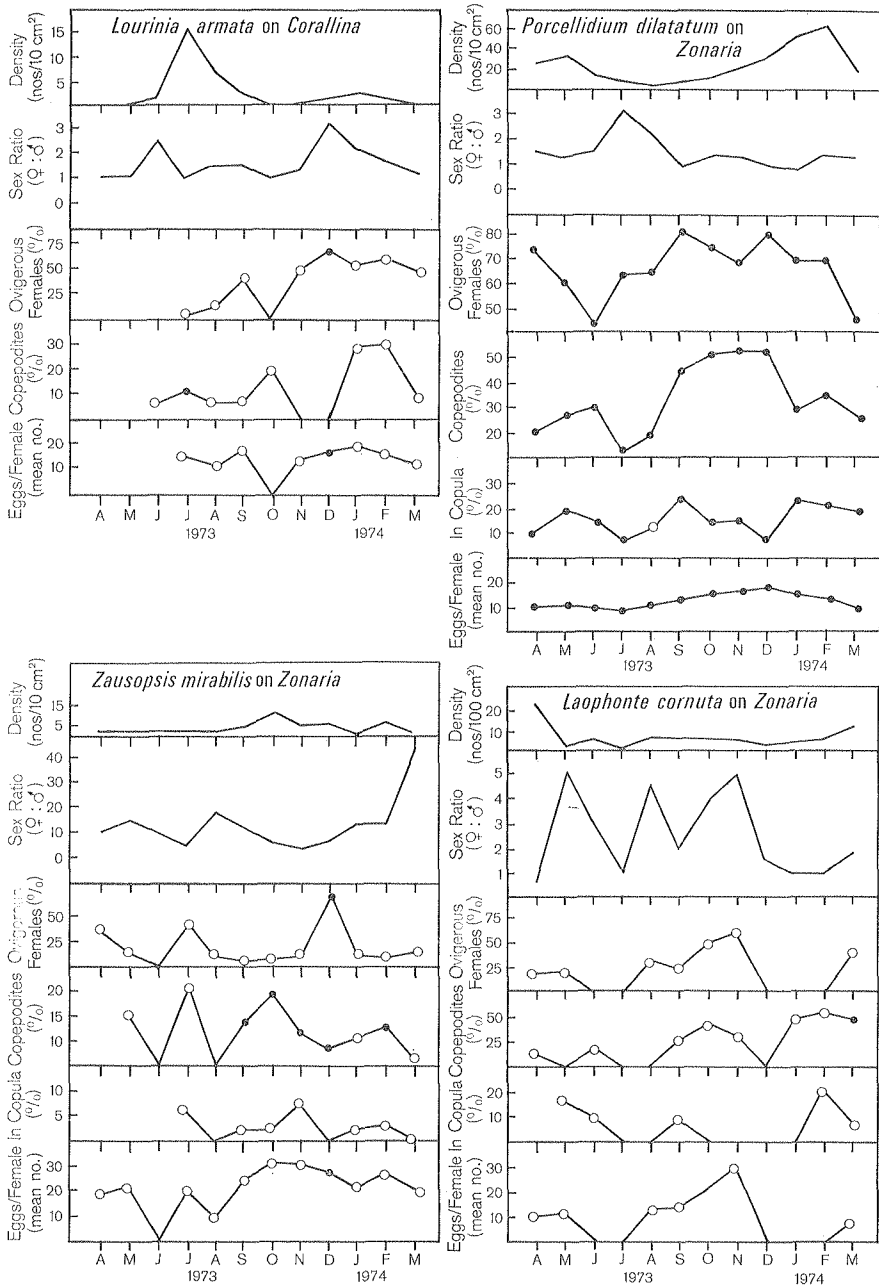


FIG. 4.—Seasonal breeding pattern of four species of alga-dwelling harpacticoid copepods at Island Bay, Wellington, New Zealand. Open circles represent data derived from 10 or fewer individuals in the population.

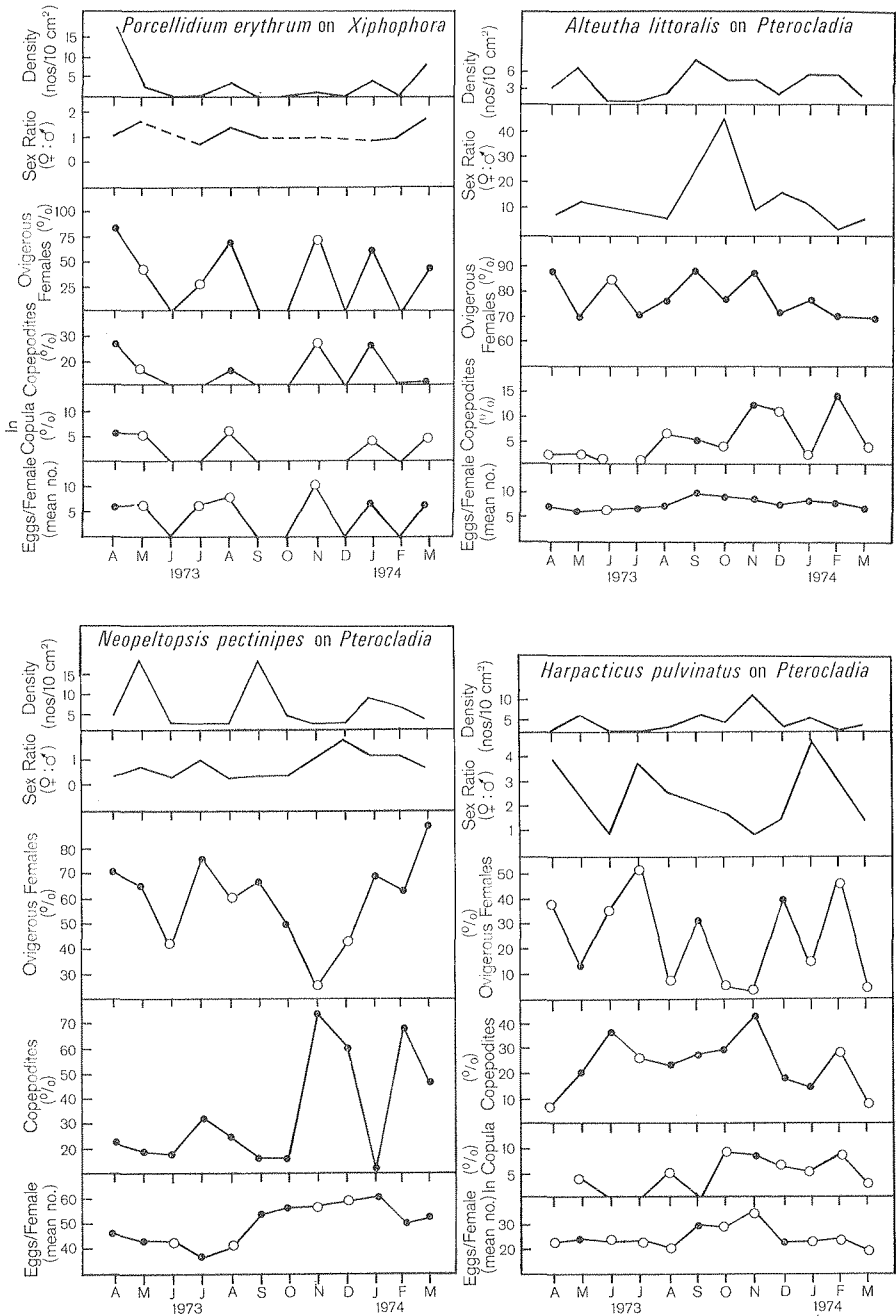


FIG. 5.—Seasonal breeding pattern of four species of alga-dwelling harpacticoid copepods at Island Bay, Wellington, New Zealand. Open circles represent data derived from 10 or fewer individuals in the population; broken

TABLE 1—Mean annual sex ratio of adult copepods, means and standard errors for annual percentage of females carrying ovisacs in the total female population, means and standard errors for annual number of eggs carried by ovigerous females, and reproductive capacities for all alga-dwelling copepods examined from Island Bay, Wellington, New Zealand, April 1973–March 1974 (figures in parentheses = size of sample of females)

SPECIES	SEX RATIO (♀ : ♂)	OVIGEROUS ♀♀ (%) (A)	NO. EGGS/♀ (B)	REPRODUCTIVE CAPACITY (AB)
<i>Ectinosoma australe</i> Brady	7.74 : 1	11.93 ± 0.67 (151)	15.12 ± 0.57 (98)	180.4
<i>Harpacticus pulvinatus</i> Brady	1.83 : 1	24.61 ± 0.70 (68)	24.69 ± 0.63 (48)	607.6
<i>Zausopsis mirabilis</i> Lang	5.94 : 1	19.47 ± 0.72 (140)	22.86 ± 0.64 (48)	445.1
<i>Tisbe ho'othuriae</i> Humes	0.66 : 1	14.27 ± 0.64 (124)	18.89 ± 0.54 (104)	269.6
<i>Scutellidium spinatum</i> Hicks	2.03 : 1	30.48 ± 0.54 (218)	37.56 ± 1.00 (67)	1144.8
<i>Porcellidium dilatatum</i> Hicks	1.19 : 1	66.45 ± 0.68 (1312)	13.25 ± 0.88 (276)	880.5
<i>Porcellidium erythrum</i> Hicks	1.26 : 1	57.03 ± 0.88 (201)	6.86 ± 0.84 (48)	391.2
<i>Alteutha littoralis</i> Pallares	11.46 : 1	78.01 ± 0.59 (625)	7.80 ± 1.00 (191)	608.5
<i>Eupelle regalis</i> Hicks	3.30 : 1	73.84 ± 0.58 (632)	8.02 ± 0.66 (275)	592.2
<i>Neopeltopsis pectinipes</i> Hicks	0.55 : 1	60.26 ± 0.70 (254)	50.09 ± 1.05 (109)	3018.4
<i>Paradactylopadia brevicornis</i> (Claus)	1.94 : 1	12.20 ± 0.67 (50)	25.32 ± 0.65 (33)	308.9
<i>Amphiascopsis cinctus</i> (Claus)	1.17 : 1	39.04 ± 0.95 (56)	18.91 ± 0.87 (45)	738.2
<i>Amonardia perturbata</i> Lang	0.84 : 1	31.83 ± 0.71 (739)	45.35 ± 1.03 (140)	1443.5
<i>Robertsonia propinqua</i> (T. Scott)	0.63 : 1	31.94 ± 1.02 (120)	16.62 ± 0.96 (63)	530.8
<i>Mesochra flava</i> Lang	3.17 : 1	32.63 ± 0.95 (195)	10.13 ± 0.84 (141)	330.5
<i>Orthopsyllus linearis</i> (Claus)	0.65 : 1	28.22 ± 0.83 (365)	22.15 ± 0.68 (187)	625.1
<i>Laophonte cornuta</i> Philippi	1.78 : 1	35.54 ± 0.68 (16)	15.45 ± 0.67 (14)	549.1
<i>Laophonte cornuta nigroctincta</i> Nicholls	1.73 : 1	36.31 ± 0.67 (140)	14.89 ± 0.62 (86)	540.7
<i>Parataxiohonte meinerti</i> (Brady)	1.42 : 1	29.70 ± 0.60 (475)	23.51 ± 0.58 (127)	698.2
<i>Lourinia armata</i> (Claus)	1.33 : 1	42.06 ± 0.62 (40)	15.58 ± 0.60 (35)	655.3

as the product of the mean number of eggs per female and the mean annual percentage of ovigerous females. For comparisons of reproductive capacity between species, females are assumed to produce one brood annually, although this may not always be so.

Enteromorpha intestinalis ASSEMBLAGE

Tisbe holothuriae Humes (Fig. 1), the dominant species associated with *Enteromorpha* (Hicks 1977b), reaches maximum breeding in autumn (March). The mean number of eggs in the single egg sac was 18.89 ($n = 104$), considerably lower than in laboratory cultured populations (Gaudy & Guérin 1977). Males dominated the population and amounted to 46.97% of the total in all samples.

The total breeding season of *Robertsonia propinqua* (T. Scott) (Fig. 1) lasted only 6 months, the species being absent from the supralittoral pools until October. Young which had developed from the December reproductive peak largely contributed to the February maximum in population density. As a percentage of the total mean annual population, copepodites represented 40.81% ($n = 906$), which was the highest of any species studied.

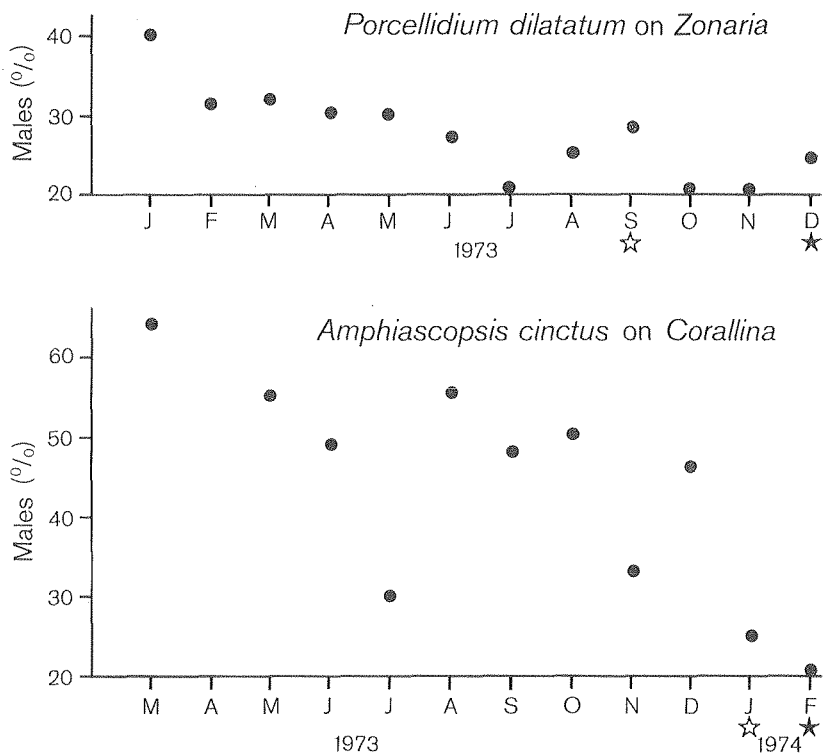


FIG. 6.—Percentage occurrence of males in the total populations of two species of alga-dwelling harpacticoid copepods at Island Bay, Wellington, New Zealand. Open stars = period of maximum occurrence of ovigerous females in the population; solid stars = period of maximum occurrence of copepodites.

Corallina officinalis ASSEMBLAGE

Egg production in *Eupelte regalis* Hicks (Fig. 2) was continuous, and the proportion of ovigerous females never fell below 50%. The autumnal peak of ovigerous females (90%) was one of the highest recorded for any species.

The reproductive season of *Amphiascopsis cinctus* (Claus) (Fig. 2) lasted 10 months, reaching a maximum of ovigerous females (83%) in mid-summer. Males in the population decline progressively following their maximum proportion (64%) in March (Fig. 6). The mean annual sex ratio alters seasonally, but favours the females (Table 1).

Amonardia perturbata Lang (Fig. 3) had a distinct winter breeding maximum; between July and August an average of 59.17% of the female population was ovigerous. The mean annual sex ratio favoured males (Table 1), but for 6 months of the year (April–August, January) females predominated, coinciding with low population densities. The copepodite

peak in September (36.36%, $n = 1006$) contributed to the population maximum, which was the highest recorded seasonal density of any species studied (Hicks 1977b).

The population of *Paralaophonte meinerti* (Brady) (Fig. 3) at Island Bay consists of two size forms (Hicks 1977a); figures for both forms were pooled, but counts of egg numbers per female were based on the larger form only. Breeding in this dominant species on *Corallina* was continuous, reaching a peak in November. Throughout the year the adult female population declined progressively as the population density increased.

Lourinia armata (Claus) (Fig. 4) increases breeding activity in late winter-early spring. Although this is a circumtropical (Wells 1967, Hicks 1977a) eurythermic species, it is at or near its southern distribution limit in New Zealand and this may explain the absence of breeding activity in early winter.

Zonaria turneriana ASSEMBLAGE

Porcellidium dilatatum Hicks (Fig. 4), the dominant copepod on *Zonaria*, bred continuously; the percentage of females carrying eggs never fell below 43%, and there appeared to be three peaks of production (September, December, and April). The mean number of eggs per female (13.25, $n = 276$) is similar to *Porcellidium rubrum* Pallares from Chile (Lepez 1974) which has an average of 13-17 eggs per ovisac. *Porcellidium dilatatum* had a mean annual percentage of mating couples of 16.17% ($n = 966$), which was the highest for any species studied, and probably relates to the rather tenacious coupling behaviour of this species. Males were in greatest abundance in January, after which they gradually declined at a nearly constant rate (Fig. 6); the greatest percentage of males was recorded during periods of high population density (April, May, January, and March).

Xiphophora chondrophylla ASSEMBLAGE

The rather confused pattern of reproductive activity in *Porcellidium erythrum* Hicks (Fig. 5) relates to the erratic occurrence of this species in the samples. This species had the lowest mean number of eggs per female of all species investigated (Table 1).

Pterocladia lucida ASSEMBLAGE

Alteutha littoralis Pallares (Fig. 5) had the highest mean percentage of ovigerous females in the population of any species in this study (Table 1); the level never fell below 69.35%. No clear peak of spawning was evident, but there was rather a high level of continuous egg production throughout the year. This species had the highest female complement (91.98%) in the total population of any investigated.

Breeding was continuous in *Neopeltopsis pectinipes* Hicks (Fig. 5), the dominant copepod on *Pterocladia* (Hicks 1977b); more eggs were

carried in the female's single egg sac than in any other species (Table 1). Males outnumbered females over the year, but females predominated during low population densities.

EGG NUMBER-LENGTH RELATIONSHIP

There is a relationship between mean length of ovigerous females and mean number of eggs carried. Measurements of three abundant species were made twice: when the minimum number of eggs per female was recorded, and when the maximum occurred. Total length measurements were made from the anterior edge of the rostrum to the posterior border of the caudal rami.

In *Porcellidium dilatatum* the mean length of females in July, when the average number of eggs per female was 9.71, was 0.921 mm ($n=46$) while in December when the average number of eggs per female was 18.43, the mean length was 0.982 mm ($n=66$), an increase of 0.061 mm. *Orthopsyllus linearis* (Claus) measured 1.302 mm ($n=38$) in February, when the average number of eggs per female was 17.00, and 1.352 mm ($n=42$), a difference of 0.050 mm, in October, when the mean number of eggs per female was 30.00. *Amonardia perturbata*, which showed the most noticeable seasonal fluctuation in numbers of eggs per female, increased in length from a November minimum of 0.992 mm ($n=58$), when the mean number of eggs per female was 35.28, to a maximum in September, when mean number of eggs per female was 72.65; the maximum length was 1.089 mm ($n=51$), an almost 10% increase. In other species with seasonal variability in egg numbers a similar relationship between number of eggs and size of female probably exists. Such relationships are well known in other crustaceans (e.g., Jones 1970), but the effect has been ignored here in the calculation of reproductive capacity (Table 1) so that a standardised comparison between species can be obtained.

DISCUSSION

PATTERNS OF BREEDING ACTIVITY

No two species are alike in their breeding pattern, and all indices of breeding activity (percentage of females ovigerous, percentage copepodites, percentage in copula, mean number of eggs per female, and the total population density) show almost as many variations as there are species (Fig. 7).

Nevertheless certain generalisations may be made. Most of the seaweed-dwelling forms included here show prolonged or continuous reproductive activity, which contrasts with the restricted breeding periods of many sediment-dwelling harpacticoids (see Barnett 1970, Lasker *et al.* 1970, Harris 1972, Coull & Vernberg 1975). On the other hand, continuous or protracted breeding seasons in temperate marine or brackish water harpacticoids has been reported by Barnett (1970), Bodin (1972a, b, c), Harris (1972), Heip (1973), McIntyre & Murison (1973), Coull & Vernberg (1975), Mielke (1976), and also in the tropics by

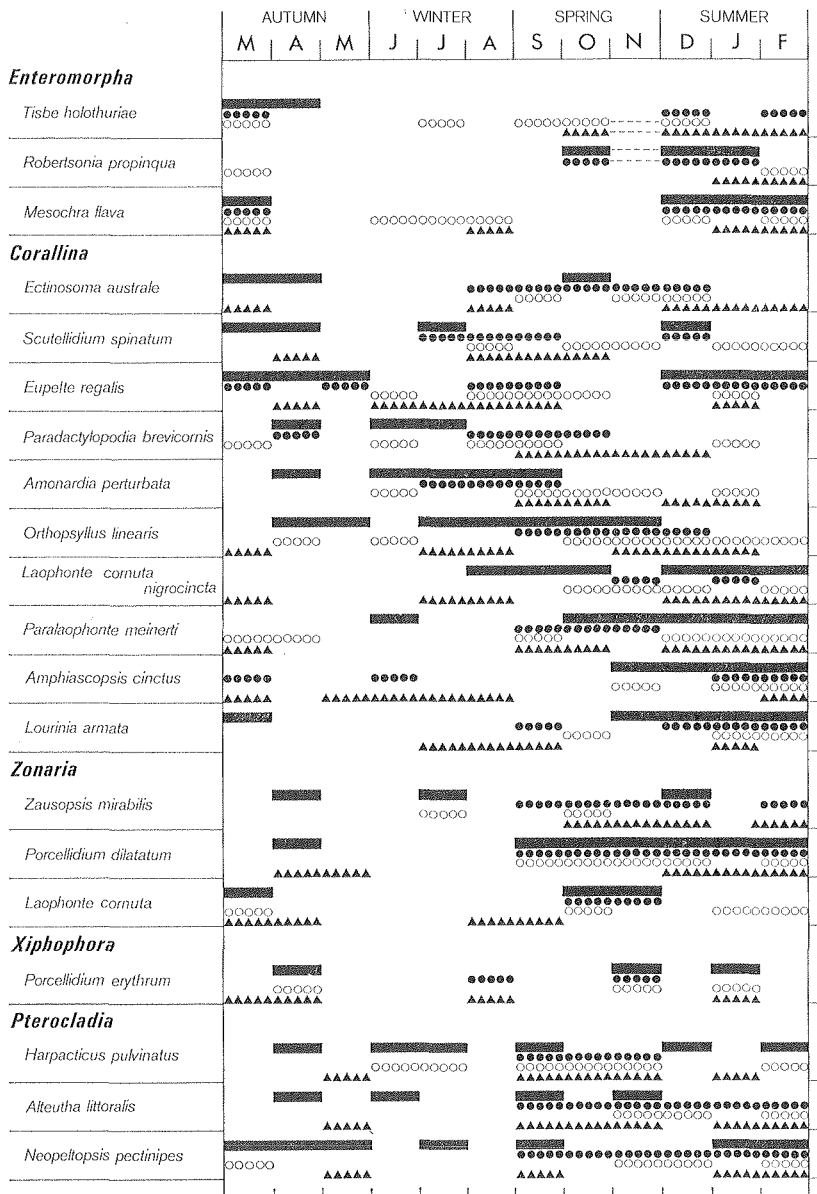


FIG. 7.—Calendar of maximum reproductive activity related to maximum population density for 20 species of alga-dwelling harpacticoid copepods at Island Bay, Wellington, 1973–74. Symbols are plotted when values exceed the mean annual percentage: solid bars = ovigerous females; closed circles = number of eggs per female; open circles = copepodites; solid triangles = population density. Dashed lines = sample missing.

Govindankutty & Nair (1972); most such species, however, show distinct peaks of breeding activity at some time during the year.

Percentage of ovigerous females, the index used by previous authors to signify maximum periods of reproductive activity, here shows that 40% of species reach maximum activity during autumn. Such an autumnal peak is similar to *Platychelipus littoralis* from Southampton Water, England (Barnett 1970), the French populations of *Pseudobradya minor* (Bodin 1972a) and of *Microarthridion fallax* (Bodin 1972b, c), and of *Halectinosoma* sp. (Coull & Vernberg 1975) from South Carolina; most other benthic copepods tend to exhibit spring and summer breeding maxima.

Because ovigerous females may predominate in autumn before overwintering, better criteria of breeding activity may be the levels of copepodites in the population and the peak in the number of eggs per female. These usually increase to a maximum in late winter, spring, or summer (Fig. 7), and generally lead to the observed maxima in total population density in the habitat (Hicks 1977b).

Among species studied, there tend to be inverse relationships between the number of eggs per female and the percentage of ovigerous females in the population. That is, species with a low mean number of eggs per female had a high mean percentage of ovigerous females, and *vice versa*. Considered thus, the species fall into five main groups (numbered in Fig. 8), which are unified by coincident times of peak copepodite and egg numbers:

Group 1: those with a high mean percentage of egg-bearing females in the population (57–78%), but with a low mean number of eggs per female (7–13). These are primarily spring and summer breeders (in terms of peaks in egg number and copepodites – Fig. 7) and all of these species belong to either the Porcellidiidae or Peltidiidae.

Group 2: those species with an intermediate level of ovigerous females (32–42%) and number of eggs per female (10–19). These are mainly summer and autumn breeders which produce an overwintering brood (Fig. 7), but *Laophonte cornuta nigrocincta* reaches its maximum in late spring.

Group 3: those with a low mean percentage of ovigerous females (12–30%), but with a moderate number of eggs per female (15–25). This group contains mainly late winter and spring breeders, with *Tisbe holothuriae* producing most eggs per female in autumn and *Ectinosoma australe* and *Paralaophonte meinerti* most copepodites in early summer.

Group 4: those with a moderate mean percentage of ovigerous females (30–32%) in the population, but with a large number of eggs per female (38–45). These species breed mainly in winter and spring. A good example is *Amonardia perturbata*, which produces its greatest number of young in September following the winter increase in ovigerous females and the dramatic rise in the number of eggs per female. *Scutellidium spinatum*, however, produces its maximum level of copepodites in mid-summer.

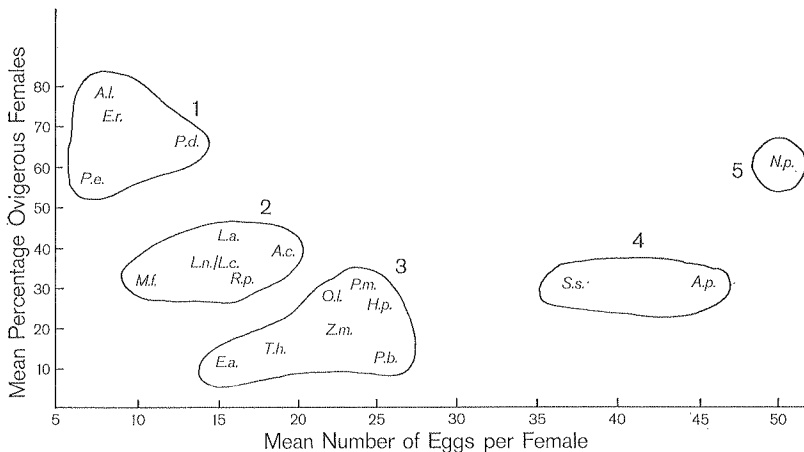


FIG. 8—Relationship of mean egg number per female to the mean percentage of ovigerous females of each of 20 species of alga-dwelling harpacticoid copepods, Island Bay, Wellington, New Zealand, 1973–74. Group boundaries are arbitrary and for visual assessment only; see Table 1 for actual data points.

A.l. = *Alteutha littoralis*
 Er. = *Eupelte regalis*
 P.e. = *Porcellidium erythrum*
 P.d. = *Porcellidium dilatatum*
 L.a. = *Lourinia armata*
 A.c. = *Amphiascopsis cinctus*
 M.f. = *Mesochra flava*
 L.n. = *Laophonte cornuta nigrocineta*
 L.c. = *Laophonte cornuta*
 R.p. = *Robertsonia propinqua*

P.m. = *Paralaophonte meinerti*
 O.l. = *Orthopsyllus linearis*
 H.p. = *Harpacticus pulvinatus*
 Z.m. = *Zausopsis mirabilis*
 E.a. = *Ectinosoma australe*
 T.h. = *Tisbe holothuriae*
 P.b. = *Paradactylopodia brevicornis*
 S.s. = *Scutellidium spinatum*
 A.p. = *Amonardia perturbata*
 N.p. = *Neopeltopsis pectinipes*

Group 5: *Neopeltopsis pectinipes* is a special case, with an extremely high reproductive capacity, indicated by a high mean percentage of ovigerous females (60%), and a high mean number of eggs (50) (Table 1). This capacity may have evolved to compensate for a very low overall percentage occurrence of females in the population (23.48%). *N. pectinipes* apparently does not produce pelagic young, as large numbers of early juveniles are invariably found on the algal substrate.

Whether a species has a larger number of eggs per female or a larger percentage of ovigerous females in the population to achieve a minimum reproductive capacity for survival may have some bearing on the time at which the main period of breeding activity takes place. For example, the level of ovigerous females in the populations of groups 2 and 4 (Fig. 8) are about the same, but since group 4 breeds mainly in winter, the production of a higher number of eggs would probably counteract greater juvenile mortality at this time. The production of a brood of eggs before the coldest part of the winter as in group 2 is advantageous to these species in that extra food energy may be converted into eggs during a time of food abundance and warmer temperatures between spring and autumn, thus permitting an earlier recruitment in the following spring. A broad concave abdomen characteristic of the females in group 1 serves to

protect the egg sacs, but in so doing may anatomically limit the females to small brood sizes. Compensation for a low number of eggs per female in all these species is evident in a continuously high percentage of ovigerous females in the population. In *Alteutha littoralis* and *Eupelte regalis*, for instance, the percentage of females with eggs does not fall below 50%.

The effect of extrinsic factors (temperature, food supply, and salinity) and of intrinsic factors (ratio of females to males, population density, and competition) in initiating and governing reproductive activity will be individually assessed below.

EXTRINSIC DETERMINANTS

TEMPERATURE: Temperature is thought to be the crucial environmental factor affecting reproduction in sediment-dwelling copepods (e.g., Muus 1967, Harris 1972) with distinct periods of increasing reproductive activity (i.e., % females with eggs) correlated with rising seawater temperatures. There is little apparent correlation with temperature in the present study, except perhaps in the timing and initiation of breeding in *Robertsonia propinqua*, *Amphiascopsis cinctus*, *Mesochra flava* and *Lourinia armata* where reproductive activity increases with a rise in water temperature. Conversely, *Amonardia perturbata* and *Paradactylopodia brevicornis* show the opposite relationship with increasing temperature, having their peaks of reproductive activity in autumn and winter. The fact that most species show little correlation of breeding activity with temperature could be due to the small difference between mean summer and mean winter temperatures at Island Bay. In Harris' (1972) study at Whitsand Bay, Cornwall, this differential was 11–12° C, but the annual range at Island Bay is only 6–7° C. The narrow continental shelf in the study area and strong winds experienced in Cook Strait (Brodie 1960, p. 250) give these waters a more oceanic character. Summer warming of coastal waters in this area is therefore limited. Continuous breeding, similar to that found in the present harpacticoids, has been observed previously in Cook Strait in some other groups, e.g., mussels (Flaws unpublished 1975), sphaeromatid isopods (Jansen 1971, Fincham 1974), with peaks of breeding activity occurring at different times. Harpacticoids from other localities around New Zealand where greater summer-winter temperature ranges prevail, may very well exhibit more distinct periods of reproductive activity. Furthermore, Bodin (1972b) recorded continuous breeding of *Asellopsis intermedia* from the semi-estuarine biotope of Fouras-Nord (La Rochelle, France) which was unlike the distinct seasonality of the species in Scotland (Lasker *et al.* 1970), although the breeding maximum occurred at the same time. Bodin's samples, however, were bimonthly and of only 9 months' duration. The difference in physical factors including temperature is likely to be responsible for such variability.

FOOD SUPPLY: Food supply can influence reproduction of copepods. Feeding greatly affects the rate of maturation and also the rate of egg production (Marshall & Orr 1955, Smyly 1970); moreover, the onset of

egg-laying and naupliar development may be delayed in some species by inadequate food supply (Smyly 1973, Coull & Dudley 1976).

Phytoplankton-dwelling copepods exhibit peak breeding activity at different times of the year (Fig. 7). With no noticeable seasonality observed in the macrophytic substrates (Hicks 1977a), alga-dwelling food organisms, by occurring in well-lit shallow waters and also perhaps gaining considerable mineral and energy requirements from the seaweed itself, may not show such large seasonal fluctuations in abundance as the local phytoplankton (see Bradford 1972). Although a spring and summer maximum in food material may occur, perhaps food (diatoms, bacteria, fungi, algal mucilage, etc) for shallow water phytoplankton-dwelling copepods may not be seasonally limiting, and therefore different physiological responses to available food by separate species may be operating. Very little comparative evidence of physiological differences between species is available, although Harris (1973) shows that differing proportions of food assimilated are used in growth, metabolism, moulting, and egg production respectively in three copepod species.

SALINITY: In the supralittoral rockpool environment, where physico-chemical extremes are experienced, no other species appear to be influenced by salinity to the extent of *Robertsonia propinqua*. In this species, salinity appears to interact with temperature to initiate reproduction. *R. propinqua* is circumtropical and euryhaline and occurs on thick growths of filamentous algae in saline tide pools and Australian saline lakes (Bayly & Williams 1966, Bayly 1970, Hamond 1973a, b). This type of habitat is similar to the supralittoral pools from which the species is collected in Wellington. Bayly & Williams and Bayly record *R. propinqua* during March, September, and December only, and established a salinity range for the species of 23.4–61.9‰. Hamond (1973b, p. 426) notes, “. . . ovigerous females were found only at 10B (Bayly's station in December 1969), but for such a scarce species the negative data probably reflect paucity of observation rather than seasonality of reproduction”. Their observations, however, conform to the seasonal pattern of reproduction found for *R. propinqua* in N.Z. (Fig. 1), with the maximum percentage of females with eggs occurring in December.

The appearance of *R. propinqua* in the October samples is at a time of rising temperature and salinity (Hicks 1977a). Unfortunately, no data are available for November, when the monthly mean salinity drops to 16.2‰, but breeding intensity increases to its apparent peak in December, with rising salinity. The peak of copepodites and total population density occurs during the annual maximum of supralittoral temperature and salinity in February. Thus the combined temperature/salinity regime of 13–14°C at about 30–35‰ determines the reappearance of *R. propinqua* into the population and the consequent onset of reproduction. The possibility of overwintering resistant eggs in this species should not be dismissed (see Bayly 1970), as recent evidence for the neritic Calanoida (Zillioux & Gonzalez 1972, Grice & Gibson 1975) suggests that such quiescent eggs may be rather more prevalent in copepods than previously recognised.

INTRINSIC DETERMINANTS

SEX RATIO AND POPULATION DENSITY: Sex ratios vary markedly amongst copepods, and experiments have shown that sex may be influenced by a range of environmental and genetic factors such as temperature and inbreeding (Volkman-Rocco 1972). Furthermore, biotic determinants such as predation intensity, population density, and food availability have been suggested as influencing sex ratio (Heinle 1970, Moraitou-Apostolopoulou 1972). In the study area, sex ratios fluctuate widely from season to season (Figs 1-5). As population levels of most species are not directly related to temperature, which could influence sexual differentiation, sex ratio is more likely to be related to the intrinsic effects of population density. In some species (*Ectinosoma australe*, *Porcellidium dilatatum*, *Tisbe holothuriae*, *Mesochra flava*, *Paradactylopodia brevicornis*, *Neopeltopsis pectinipes*, *Lourinia armata*, *Scutellidium spinatum*, *Paralaophonte meinerti*, *Harpacticus pulvinatus*, *Zausopsis mirabilis*, and *Amonardia perturbata*) the sex ratio varies relative to the density of the total population, with females occurring in larger numbers when the population is near its lowest levels. Paradoxically, in others (*Amphiascopsis cinctus*, *Laophonte cornuta nigrocincta*, and *Alteutha littoralis*) females are more numerous when the population level is at its highest. No obvious relationship exists for *Porcellidium erythrum*, *Eupelte regalis*, *Laophonte cornuta*, *Orthopsyllus linearis*, and *Robertsonia propinqua*.

In most species the observed variations in sex ratio appear to be a homeostatic mechanism for maintaining the population at a viable level throughout the year (Heinle 1970). Females predominate during periods of low population density which would ensure a sufficiently large number of females in reproductive condition, and would be an adaptation for survival at low densities. An alternation to a predominance of males takes place during periods of high total population density (which is usually related to the periods of copepodite maxima). The mechanism involved in such alternation of sex ratio is unknown, but may be by way of a hormonal pathway in response to the level of physical contact.

The scarcity of females in *Orthopsyllus linearis*, *Neopeltopsis pectinipes* and *Tisbe holothuriae* during this study could result from a greater mortality during the subadult and maternal moults. Alternatively, the high incidence of "maleness" in the latter species may be due to an increased homozygosity within the population. This species is very sensitive to inbreeding and since they are commonly found in supralittoral tidepools may represent isolated populations which have little gene exchange with each other (Dr B. Volkman, Istituto di Biologia del Mare, Venice, pers comm.). This may also be the case for *Robertsonia propinqua*, which is a strictly seasonal inhabitant of the same tidepools.

INTERSPECIFIC COMPETITION: Interspecific competition may provide an additional control to breeding patterns. Within the densely populated *Corallina* assemblage, a succession in reproductive activity is evident (Fig. 7). The upsurge in winter breeding of *Amonardia perturbata* is

followed by increases in *Orthopsyllus linearis*, *Laophonte cornuta nigro-cincta*, *Paralaophonte meinerti*, and the summer breeding of *Amphiascopsis cinctus* and *Lourinia armata*, all of which inhabit the surface of the holdfast sediments of *Corallina*. This reproductive separation might ensure a reduction in competition between coexisting species. Greater niche availability following the decline of other species in winter is exploited by *Amonardia perturbata*, which has a high reproductive rate in this season (Fig. 3, Table 1). Similar cases of reproductive partitioning have been noted by Heip (1973) and Coull & Vernberg (1975) in brackish-water and estuarine copepods.

LIFE CYCLE OF *Porcellidium dilatatum*

The number of generations produced each year by the seaweed-dwelling species and the length of life of each species are unknown, and only detailed studies on growth from field data will resolve this question. Harpacticoid longevity and brood number varies greatly in laboratory populations (see review in Rosenfield & Coull 1974), but in natural populations the evidence points to only one to two generations per year (Barnett 1970, Lasker *et al.* 1970, Dinet 1972). However, based on an analysis of the time between peak numbers of mating couples and ovigerous females in *Porcellidium dilatatum*, three generations appear to be produced annually (Fig. 4). From the time of sperm deposition by the males to the liberation of the young, the period of egg maturation within the female of this species is about 3–4 months. The development period from hatching of the juvenile to copulation as an adult would be 4–5 months. A total life cycle of female *P. dilatatum* is thus about 8 months, but estimates of life span are complicated by egg-laying and development occurring throughout the year. These estimated times compare favourably with the findings of Barnett (1970) who recorded an egg maturation period of 4 months for *Platyhelipus littoralis*, and 8–10 months for *Platyhelipus laophontoides*. Lasker *et al.* (1970) indicated an egg maturation period of 9 months and a 12 month life span in *Asellopsis intermedia*. Total longevity of the former species was 6 (possibly 12) months for *P. littoralis* and 13 months for *P. laophontoides*. Chilean *Porcellidium rubrum* females produce two generations per year; both have a duration of 11 months (Lepez 1974). In all these species the males have a much shorter lifespan than the females. In *Porcellidium dilatatum*, as with *Platyhelipus littoralis* which breeds throughout the year, there is a tendency for a reduced life cycle and more than one generation annually.

CONCLUSIONS

Pronounced seasonal changes in population density occur in the alga-dwelling harpacticoid copepods at Island Bay, Wellington (Hicks 1977b). Such temporal variability is now shown to be largely the result of periodic fluctuations in the reproductive activity of the harpacticoid species. The initiation and regulation of breeding patterns involves many factors: temperature, food, salinity, competition, and possibly population density

appear to variably affect different species. In contrast, temperature seems to have an overriding effect on sediment-dwelling species. Total reproductive capacity is higher in alga-dwelling harpacticoids than in interstitial species (cf. Harris 1972). Egg number is in general similar to other epibenthic forms (see Lasker *et al.* 1970), but total reproductive capacity is probably higher in alga-dwellers owing to the longer overall duration of reproductive periods. High numbers of eggs per female and a higher mean percentage of ovigerous females in alga-dwelling species could be a response to a less stable environment and/or to higher levels of predation and competition.

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