Influence of Age-Specific Mortality on the Life History Traits of Two Estuarine Copepods*

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ABSTRACT: Life history traits – including day of first reproduction, lifetime reproductive output, and total lifespan – were determined in the laboratory for 2 estuarine copepods: *Scottolana canadensis* (Willey) and *Oithona colcarva* Bowman. The day of first reproduction was earlier for *O. colcarva* than for *S. canadensis*, but the latter had a much longer reproductive lifespan and a greater reproductive output in terms of nauplii produced per female. The copepods exhibited intrinsic rates of increase ranging from $0.01–0.19$ d^{-1} for *O. colcarva* (15°–25 °C) and $0.05–0.15$ d^{-1} for *S. canadensis* (20°–25 °C). A comparison of life history traits of *S. canadensis* and *O. colcarva* with the copepod *Acartia tonsa* Dana revealed differences which may reflect variation in age-specific patterns in mortality of the field populations. For *S. canadensis*, juvenile mortality (specifically of planktonic nauplii) may be higher and more variable than mortality of epibenthic adults. In contrast, mortality of planktonic *A. tonsa* adults may be high and more variable relative to their juvenile stages. The reproductive strategy of *S. canadensis* is characterized by a later day of first reproduction, more discrete egg production, and a longer lifespan compared to *A. tonsa*. Life history traits and variable age-specific mortality patterns of these species are consistent with current theory which predicts that variation in age-specific mortality acts as a selective force on the reproductive patterns of organisms.

INTRODUCTION

Current life history theory is based on the assumption that the evolution of a particular combination of reproductive traits or tactics proceeds towards increasing the fitness of the organism within the constraints of its environment (Stearns, 1976). Such tactics may reflect a compromise between predation, competition, coping with physical factors, and the ability to reproduce (Gadgil and Bossert, 1970; Pianka and Parker, 1975). Correlative studies of lifecycle characteristics with environmental conditions of both marine and freshwater zooplankton have resulted in some thought-provoking hypotheses regarding the adaptive value of such traits. For example, it has been proposed that when food resources are scarce, vertical migration to colder waters, resulting in delayed development of

some marine zooplankton, may ultimately result in an overall increase in fecundity and survival of offspring (McLaren, 1963, 1974). Life history traits also have been suggested to explain biogeographical trends between planktonic taxa (Allan, 1976). In general however, the lack of an adequate data base has meant that these theories are largely untested.

This paper addresses the contentions that age-specific variation in mortality may be an important selective force on the fitness-optimizing strategy of an organism (Murphy, 1968; Charnov and Schaffer, 1973) and that in particular where juvenile mortality is more variable than mortality of adults, smaller clutches and a longer lifespan will be favored (Schaffer, 1974).

Two estuarine copepods were chosen for laboratory determination of general life history traits: the epibenthic harpacticoid *Scottolana canadensis* (Willey) and the planktonic cyclopoid *Oithona colcarva* Bowman. They are seasonal species in Chesapeake Bay and usually occur in lower densities than the planktonic calanoid *Acartia tonsa* Dana. Specific predictions can be made concerning differences and similarities in the life history traits of the three species based on data

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concerning the natural sources of mortality to nauplii and adults. The nauplii of S. canadensis are more susceptible to variable sources of predation than adults whereas A. tonsa adults may have the greater risk (Lonsdale, 1981).

METHODS AND MATERIALS

Investigation of the survivorship and fecundity schedules of a species provides the relevant statistics which, according to life history theory, will reflect differences in age-specific mortality (Schaffer, 1974). It also allows determination of the intrinsic rate of population increase (r) which could reflect significant differences in reproductive strategies between species (MacArthur, 1972; Allan, 1976). To obtain these data, Scottolana canadensis and Oithona colcarva nauplii and adults were collected in plankton tows using a 63-µm mesh net at the pier of the Chesapeake Biological Laboratory, placed in 2-l Erlenmeyer flasks with filtered ambient (Whatman Glass Fiber 'C') Bay water and kept at 20 °C in an environmental box. To reduce the likelihood of inbreeding and to maintain genetic variability, copepod populations from different flasks were mixed every month, and new individuals from the field were added occasionally.

The copepods were fed a mixture of algae, Prorocentrum marieae-lebouriae variety and Pseudoisochrysis sp. (VA-12) approximately 2–3 times a week. Rotifers and ciliates which grew in the cultures usually were not removed.

Scottolana canadensis Life History Experiments

To allow for acclimation to test conditions, Scottolana canadensis copepods were placed in flasks containing 10, 15 or 20 ‰ S Millipore-filtered (MP-filtered; 0.45 µm) water and held at either 15°, 20° or 25 °C for 2 weeks prior to the beginning of life tables experiments. The experimental water was made from ambient Bay water combined with high-salinity seawater (31.5 ‰ S) obtained from the Delaware coast or with distilled water.

An algal mixture consisting of a 1:2 ratio of Prorocentrummarieae-lebouriae: Pseudoisochrysis sp. (VA-12) was used as the food source. The algae was grown in culture using Provasoli's ½ strength E.S. media (James, 1973) at 15 ‰ S and 15 °C on a 14:10 h light-dark cycle. Algal growth was maintained by adding fresh media to the cultures once a week. Experimental algal mixtures used to feed the copepods were prepared 2–3 times a week by combining 200 ml of the algal mixture with 100 ml of either distilled,

15 ‰ or 30 ‰ S (MP-filtered; 0.45 µm) water. Cell numbers usually were counted once a week on an electronic particle counter (Particle Data, Inc.).

Fifteen mating pairs of Scottolana canadensis were placed in covered 50-ml Stendor dishes with 20 ml of MP-filtered (0.45 µm) adjusted Bay water at the appropriate temperature (25 pairs were used for the experiments conducted at 15 ‰ S and 20 °C and at all salinities at 15 °C). Experiments were conducted in environmental boxes with a 12:12 h light-dark cycle. Each pair was fed 1 ml of the algal mixture daily for the duration of the experiments although females which lived beyond 2 months were sometimes fed 2 ml every other day. Experimental dishes were washed and the water changed once a week. The weekly initial quantity of algal food in both series of life table experiments, including Oithona colcarva, was always in excess of that normally encountered by zooplankton in the Chesapeake Bay; $1.0–1.3 \times 10^7 \, \mu m^3 \, ml^{-1}$ (Richman et al., 1977).

The mating pairs were observed daily; when a female produced her first egg sac, the males were removed. Females were placed in another dish when the nauplii hatched, and total numbers and day of hatching were recorded. Survival, development time to mature female and sex were determined for each brood. These statistics also were recorded for all subsequent broods and the survival of the original females was determined. Females were followed until all had discontinued egg production for 2 weeks or until Day 100. The survivorship data from all nauplii were combined and the time at which 50 % of the female copepodites became mature was determined (as evidenced by the formation of mating pairs or the appearance of ovaries). Data from the 2 schedules were combined by considering the day at which 50 % of the females matured equivalent to the first day of observations on the mating pairs.

Oithona colcarva Life History Experiments

Adult Oithona colcarva were removed from culture and placed in 120-ml watch glasses at 10, 15 or 20 ‰ S and 15°, 20° and 25 °C. The females were observed daily and removed to another dish as they became gravid. Approximately 10–15 newly hatched nauplii from these females were placed in a 50-ml covered Stendor dish and maintained under the different physical regimes. Ten to 15 dishes of nauplii were monitored. They were cultured and observed using the same schedule as for Scottolana canadensis, except that a third algal species Isochrysis galbana was added to the food mixture. Prior experimentation had revealed that less than 10 % of the newly hatched

nauplii survived beyond the second or third day unless this alga was present.

The nauplii were observed daily and monitored until they became gravid females. If both males and females appeared in one dish, the females were observed for survivorship and fecundity statistics. The appearance of ovaries and any unfertile eggs was noted.

Due to the skewed sex ratio observed in *Oithona* (5.3 ♀♀:1 ♂) and to indications that one mating may not be sufficient throughout the reproductive life of female *O. colcarva*, it was necessary to conduct a second series of experiments to obtain adequate adult survivorship and fecundity information. Nauplii were placed in 1-l beakers under the appropriate physical conditions and fed in excess daily. Approximately 25–30 copepodites (CIV) were placed in 120-ml covered watch glasses with 2 or 3 males and fed daily. As females became gravid they were placed in Stendor dishes. The day and number of nauplii which hatched were recorded. On that day, the female was returned to the large watch glass containing the males. Thus, it was not possible to follow the survivorship of successive broods as done with *Scottolana canadensis*. Data from the 2 schedules were combined by considering the hatching of the first fertile brood from the nauplius survivorship experiments equivalent to that of the first brood in the adult survivorship and fecundity experiments.

The instantaneous rate of population increase (*r*) for both *Scottolana canadensis* and *Oithona colcarva* was calculated from the following (Birch, 1948):

$$1 = \Sigma l_x m_x e^{-rx}$$

where l_x = probability of surviving to age x; m_x = number of female NI per female aged x, hatched during the interval of x to $x+1$; r = instantaneous rate of population increase (d^{-1}); x = age in days from NI.

RESULTS

Scottolana canadensis: Survivorship and Reproduction

The survivorship schedule (l_x) of *Scottolana canadensis* nauplii from day of hatching (Day 0) through adult was determined at 20° and 25 °C but was not obtained at 15 °C as no young were produced at that temperature (Fig. 1). Although the survivorship of all nauplii from the first through the last broods was combined in the survivorship schedule, survivorship of later broods (8–13) appeared to be less than that of earlier broods (1–7) (Fig. 2). The development time from NI to CI was approximately half the time from CI to CVI (Table 1).
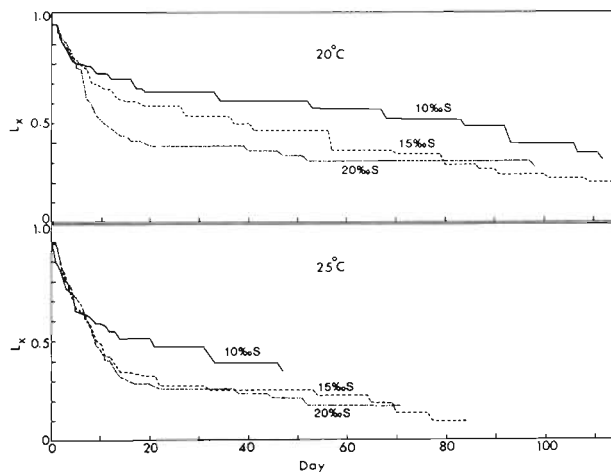

Fig. 1. *Scottolana canadensis.* Survival in the laboratory from day of hatching through reproductive-female stage, at 20° and 25 °C and in 3 different salinities. Lx = probability of surviving to age *x*
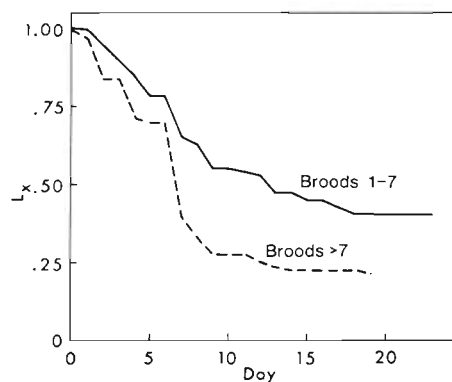

Fig. 2. *Scottolana canadensis.* Survival of nauplii hatching from early compared to later-produced broods. Lx = probability of surviving to age *x*

Salinity and temperature influenced the rate of instar survival in *Scottolana canadensis* (Fig. 1). Survivorship was greater at the lowest salinity (10 ‰ S) and temperature (20 °C). This influence of temperature may have been an experimental artifact. It appeared that a small proportion of laboratory mortality for nauplii and copepodites (CI-III) at 25 °C was caused by entrapment in the surface tension of the water. This problem did not appear to be important at 20 °C. These observations are supported by results obtained by D. R. Heinle (unpubl.) who found higher survival of *S. canadensis* nauplii at 25°–30 °C (0.83 on Day 6) in containers which had a much reduced surface area. However, the survival of nauplii at 20 °C was greater in my experiments despite the larger surface area.

The mean day of first reproduction of *Scottolana canadensis* was 25.3 at 20 °C and 16.3 at 25 °C. Reproduction continued after 100 d with females held at

Table 1. *Scottolana canadensis* and *Oithona colcarva*. Mean and standard deviation of development time (d) of naupliar and copepodite stages at 3 temperatures

Temperature (°C)	Scottolana canadensis					Oithona colcarva				
	NI–CI		CI–VI*	Days to 50% adults		NI–CI		CI–VI*	Days to 50% adults	
	$\overline{X}$	S.D.		$\overline{X}$	S.D.	X	S.D.		X	S.D.
15	–	–	–	–	–	13.8	1.2	12.2	26.0	0.0
20	4.9	1.1	10.1	15.0	1.6	8.1	1.1	9.0	17.1	1.1
25	3.9	0.9	8.1	12.0**	1.4	5.6	1.1	5.4	11.0	1.9

* Development time from CI-CVI was determined by subtraction of development time of NI-CI from total time to adult
** 12.0 d for development to reproductive adult may be an overestimate due to inadequate food resources for copepodites (McLaren, 1978) or to higher salinities. Harris (1977) found this time to be approximately 7 d, 25 °C and 10 ‰ S, while under the same physical conditions I found it took 10 d for 50 % of the females to reach t he adult stage. The data at 20 °C are consistent with Harris

20 °C, while it ceased after approximately 80 d at 25 °C. Female copepods held at 15 °C for 100 d never produced a viable brood. When they were moved to 20 °C for 2 d, several clutches of eggs were produced which resulted in viable nauplii. Moreover, this occurred without the reintroduction of a male. This suggests a mechanism by which overwintering copepods could begin reproduction almost immediately once an adequate temperature is reached.

Pseudoisochrysis sp. and *Prorocentrum marieaelebouriae* appear to be adequate foods for reproduction by *Scottolana canadensis* females. The average brood size at 25 °C of 18.9 ± 4.4 (S.D.) nauplii per brood (Table 2) was not significantly different from that reported by Harris (1977; refer to Table 2) of 21.82 ± 7.7 eggs per brood at 25 °C and 10 ‰ S when fed a diet of *Isochrysis galbana* and *Thalassiosira pseudonana* (0.20 < p < 0.30; t-test for differences between means). In addition, the brood sizes were not significantly different (0.10 < p < 0.20) from gravid females taken from the field in the summer months (≅ 25 °C) which were found to average 26.0 ± 6.8 eggs per brood (Lonsdale,

1981). However, food quality may have influenced lifetime fecundity. I calculated the average number of broods produced by *S. canadensis* to be 12.1 ± 5.6 from data reported by Harris (1977; refer to Table 1). While in this study an average of 6.8 ± 3.1 broods was calculated for females under a similar temperature and salinity regime (Table 2).

In the laboratory the sex ratio of *Scottolana canadensis* appeared to approximate 1:1 (1.3 ♀♀: 1 ♂ at 20 °C, 0.89 ♀:1 ♂ at 25 °C). The intrinsic rate of population increase, r, was calculated using the experimental survivorship curves and fecundity schedules based upon the observed sex ratio (Table 2). The greatest value (r = 0.13 d^{-1}) was observed at 25 °C and 10 ‰ S. All other values ranged between 0.08–0.05 d^{-1}. The r values also were calculated using a fecundity schedule which assumed a 1:1 sex ratio. Only the r estimate at 25 °C and 15 ‰ S (r = 0.10 d^{-1}) and at 20 °C and 10 ‰ S (r = 0.07 d^{-1}) were affected because actual sex ratios had shown the greatest deviation from 1:1.

On the premise that nauplius mortality was unnaturally high in the laboratory at 25 °C, a third series of r

Table 2. *Scottolana canadensis*. Intrinsic rate of population increase, survival and reproductive statistics at different temperatures and salinities

Temperature (°C)	Salinity (‰ S)	Day of first reproduction	% survival of nauplii to adult	r (d^{-1})	Sex ratio ♀♀ ♂	Brood size		Number of broods		r(d^{-1}) sex ratio 1 ♀:1 ♂
						$\overline{X}$	S.D.	$\overline{X}$	S.D.	
25	10	13	59	0.13	0.99:1	13.4 ± 8.7		6.8 ± 3.1		0.13*
	15	17	42	0.07	0.53:1	24.2 ± 13.4		6.8 ± 5.0		0.10
	20	19	40	0.06	1.16:1	19.2 ± 11.8		6.0 ± 2.9		0.06
20	10	26	72	0.08	1.37:1	14.9 ± 9.5		4.0 ± 2.2		0.07
	15	23	67	0.05	1.34:1	14.1 ± 11.1		4.2 ± 3.2		0.05
	20	27	41	0.06	1.20:1	22.4 ± 10.3		6.1 ± 4.0		0.06

* Estimates of r at 25° and 10 °C ranged from 0.13–0.17 d^{-1} when survivorship data from Heinle (unpubl.; r = 0.14 d^{-1}) or fecundity data from Harris (1977; r = 0.15 and 0.17 d^{-1}) were taken into consideration

values was calculated by adjusting survivorship upward to 0.83 on Day 6 (Heinle, unpubl.). The r values at 25 °C and 10 and 15 ‰ S increased by 0.01 d^{-1} and 0.03 d^{-1} at 20 ‰ S. Salinity appears to effect the survivorship of nauplii and copepodites of *Scottolana canadensis* and thus this latter increase may be an overestimate.

An estimate of r also was obtained applying the fecundity statistics of Harris (1977) (mean brood size = 21.8 eggs per brood and mean number of broods = 12) and survivorship data from my studies. Assumptions were made that (1) the females produced broods at equal intervals throughout their lifespan (ranging from 57–84 d; data from Harris); (2) the days of first reproduction (nauplii hatched) were equivalent to those in my studies (Days 13–16 at 25 °C and 10 ‰ S); and (3) all eggs successfully hatched into nauplii. The r value obtained was 0.15 d^{-1}, an increase of 0.02 d^{-1} at 25 °C and 10 ‰ S. I also estimated r to be 0.17 d^{-1} using other fecundity statistics reported by Harris (1977; Table 1); mean brood sizes ranged from 24.9–35.5 eggs. These latter rates may be overestimates if all eggs did not successfully hatch, a phenomenon I have frequently observed.

Oithona colcarva: Survivorship and Reproduction

The survival of *Oithona colcarva* from Day 0 (day of hatching) through adult was lowest at 15 °C where only 13 % survived to reproductive maturity (Fig. 3). Maximum longevity observed was Day 81 at 15 °C, Day 53 at 20 °C and Day 39 at 25 °C. High mortality occurred in *O. colcarva* during the metamorphic change from NVI to CI. Mortality was low in the later copepodite stages and through the major portion of the adult reproductive stage. Possibly this poor survival indicates that further improvement in culturing technique is needed. However, high mortality at the NVI-CI molt has been reported in other laboratory experiments (Harris and Paffenhöfer, 1976), as well as in the field (Rigler and Cooley, 1974), and so these results may not be an unusual natural occurrence.

The mean day of first reproduction of *Oithona colcarva* was 18.0 at 20 °C and 11.7 at 25 °C. The fecundity of *O. colcarva* may have been seriously affected by food quality. At 25 °C, in the laboratory the average number of nauplii which hatched per brood (10.5 ± 9.0) was significantly different (p < 0.005) from the brood size collected in the field[*] (16.8 ± 3.7 eggs per brood) at approximately 25 °C (Lonsdale, 1981). At 20 °C, the difference between brood size determined in the laboratory (6.1 ± 4.2 nauplii per brood) and that in the field (20.0 ± 4.2 eggs per brood) also was significant (p < 0.005). Although only 3 *O. colcarva* egg sacs
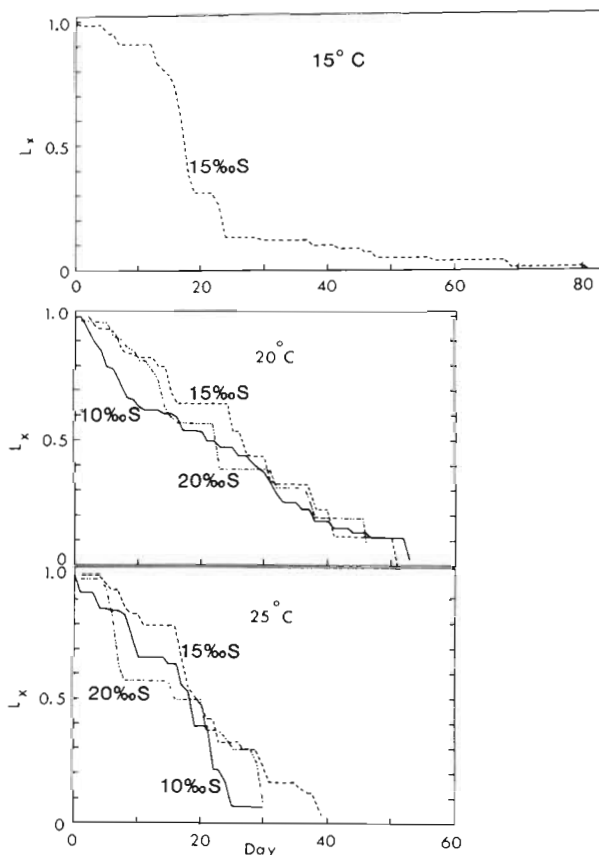

Fig. 3. *Oithona colcarva*. Survival in the laboratory from day of hatching through reproductive-female stage, at 15°, 20°, and 25 °C and in 3 different salinities

were found at 15 °C for all samples counted, the data suggest that there may be significant differences in brood size between the laboratory populations and those in the field (8.2 ± 9.9 versus 15.0 ± 2.4, respectively). It appears that r may have been underestimated due to these differences. Using the average field fecundity and assuming that each brood produced in the laboratory resulted in an equivalent number of viable NI, I calculated an increase in r ranging from 0.01–0.05 d^{-1} (Table 3). The lowered egg production of *O. colcarva* in the laboratory could have been due to the absence of animal prey (i.e. ciliates, rotifers or copepod nauplii) in the diet as it is probable that this cyclopoid copepod is omnivorous (Lampitt, 1978).

Estimates of brood sizes in the laboratory (nauplii per brood) and field (eggs per brood) may not be

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[*] The value of 16.8 eggs per brood is based on the number of eggs counted per individual sac, 8.4 ± 1.9, multiplied by 2. Many of the egg sacs had been separated from gravid females in preserved field samples as females will drop their eggs when treated with formalin. Healthy females in the laboratory usually carry two sacs and I presumed that this was true for females in the field

directly comparable for 2 reasons. First, not all eggs carried by females in the laboratory produced viable nauplii; this may also apply to eggs carried by females in the field. Second, values for brood size in the laboratory represent averages over the entire life span of the females. The average number of nauplii hatched was sometimes higher in the first few weeks of reproduction than later. For example, at 20 °C and 20 ‰ S, the number of *Oithona colcarva* nauplii hatched per brood averaged 12.4 ± 6.3 during the first week and only 3.5 ± 1.5 for the remainder of the experiment. Egg sacs carried by females in the field may represent first or second broods if adult mortality is high. Although this latter point may be important for comparing laboratory and field brood sizes and thus in assessing diet inadequacies, it was of lesser importance in influencing *r*. I calculated an increase of 0.01 d^{-1} at 20 ° and 20 ‰ S when the number of nauplii hatched per brood in the second week was assumed equivalent to that during the first week (12.4 nauplii per brood).

The average sex ratio of *Oithona colcarva* offspring was 5.4 ♀♀:1 ♂ for all experiments combined. This skewed sex ratio is similar to that observed in natural populations (6.8 ♀♀:1 ♂; personal observation). Therefore, *r* was determined using only the observed sex ratio for calculating the number of female births. The intrinsic rate of population increase of *O. colcarva* was greater at higher temperatures and salinities (Table 3).

DISCUSSION

The rates of population increase (*r*) obtained for both *Scottolana canadensis* and *Oithona colcarva* were lower at all temperatures than those reported for other estuarine copepods; e.g. *Gladioferens imparipes* (0.146 and 0.293 d^{-1} at 15° and 25 °C, respectively; Rippingale and Hodgkin, 1974) and *Acartia tonsa* (> 0.23–0.25 d^{-1} at 20 °C; Heinle, unpubl.) or of predicted ranges for copepods made by Allan and Goulden (1980; 0.28–0.40

d^{-1} at 25 °C). The discrepancies between these values can be due only in part to juvenile mortality or inadequate food quality in my study. Hence, they must reflect real differences between the species. Some factors which contribute to differences in *r* between *A. tonsa* and both *S. canadensis* and *O. colcarva* are differences in growth rate and development time of eggs (Table 4). At 20 °C, *A. tonsa* will develop at the rate of 1.6 stages d^{-1} (Heinle, 1969), while *S. canadensis* and *O. colcarva* develop at 0.8 and 0.7 stages d^{-1}, respectively. These results also are consistent with McLaren's (1978) observation that the two smallest copepods in Loch Striven, Scotland have the longest generation times. *A. tonsa* is the largest of the 3, with adult females averaging 1.25–1.5 mm in total length (Wilson, 1932). Adult females of *S. canadensis* average 0.96–1.21 mm, and *O. colcarva* average 0.65–0.77 mm (Wilson, 1932; Coull, 1972). *A. tonsa* eggs begin to hatch 20–22 h after being laid at 18 °C (Parrish and Wilson, 1978) while eggs of *S. canadensis* take 104 h and those of *O. colcarva* 46 h at 20 °C (Lonsdale, 1981).

Life history statistics of *Scottolana canadensis*, *Oithona colcarva* (this study), and *Acartia tonsa* (Parrish and Wilson, 1978) may reflect important changes in the selective forces operating during their respective life spans as the result of differences in adult habitat. Nauplius development of *S. canadensis* occurs in the upper layers of the water column of the Chesapeake Bay, and, upon metamorphosis to Copepodite I–II, individuals descend and maintain an epibenthic existence through the adult reproductive life. *Scottolana* populations may experience low mortality of adult stages relative to the planktonic nauplii owing to their epibenthic habitat which may serve as a refuge from visual predators (Allan, 1978). In contrast the totally planktonic *Acartia* spp., and *O. colcarva* in this study, may be subject to variable heavy predation on the larger, later stages (Miller et al., 1977).

Laboratory and field data provide evidence which suggests that the proposed pattern of differential survi-

Table 3. *Oithona colcarva*. Intrinsic rate of population increase, survival and reproductive statistics at different temperatures and salinities

Temperature (°C)	Salinity (‰ S)	Day of first reproduction	% survival of nauplii to adult	r (d^{-1})	Sex ratio ♀♀ : ♂	Brood size $\bar{X}$	Brood size S.D.	r (d^{-1}) using field brood sizes
25	10	13	66	0.08	5.3 : 1	15.8 ±	7.1	0.11
	15	12	80	0.16	6.0 : 1	13.6 ±	12.7	0.19
	20	10	58	0.13	4.7 : 1	7.6 ±	4.3	0.18
20	10	18	54	0.06	5.4 : 1	5.2 ±	7.8	0.11
	15	18	65	0.08	5.4 : 1	6.3 ±	2.9	0.13
	20	18	58	0.10	5.5 : 1	9.6 ±	6.9	0.13
15	15	29	13	0.001	5.4 : 1	8.2 ±	9.4	0.01

Table 4. Life-history traits of *Acartia tonsa* (at 18 °C) compared to *Scottolana canadensis* and *Oithona colcarva* (20 °C). Data for *A. tonsa* from Heinle (unpubl.) and Parrish and Wilson (1978)

Species	r(d^{-1})	Egg hatching time (h)	Stages d^{-1}	Lifetime production (per reproductive female)	Day of first reproduction	Reproductive lifespan (d)	Egg production
A. tonsa	> 0.23–0.25	20–22	1.6	516 eggs	7–9.0	24.7	continuous
S. canadensis	0.05–0.08	104	0.8	80–165 nauplii*	25.3	62.0	broods
O. colcarva	0.06–0.13	46	0.7		18.0	15.4	broods

* The upper estimate assumes that total broods produced in a lifetime may be twice (9.6 broods female^{-1}) that actually observed for experiments conducted at 20 °C. Compare lifetime fecundity data at 25 °C with that of Harris (1977)

val of nauplii and adults may occur in the field. The nauplii of *Scottolana canadensis* are more susceptible to some sources of predation (from abundant planktonic invertebrates) than are their adults, and predation on the nauplii may be the primary regulating factor during the summer (Lonsdale, 1981). Moreover, in Chesapeake Bay, the diets of epibenthic feeding juvenile spot and bay anchovies are primarily composed of the large calanoid copepod *Pseudodiaptomous coronatus* while *S. canadensis* adults are rarely encountered (Homer and Boynton, 1978). Indirect evidence suggests that predation may be greater on the larger stages of *Acartia tonsa*; the instantaneous death rates for nauplii frequently are less than that for copepodites in both the Rhode River and Chesapeake Bay (Allan et al., 1976; Heinle et al., 1977; but see Heinle, 1966). Copepodite and adult mortality due to fish predation has been proposed to regulate the cycle of abundance of *A. clausii* in a small temperate lagoon (Landry, 1976). It is plausible that these patterns are the result of selection for *Acartia* adults by filter-feeding fish which demonstrate maximal filtering efficiency in the size range of the adults (1.2–10 mm; Durbin and Durbin, 1975) or by visual size-selective predators (Brooks and Dodson, 1965). Thus mortality of the adults would be greater than of either nauplii or copepodites. The susceptibility of *A. tonsa* adults to predation also is emphasized by the observation that they are more heavily preyed upon by ctenophores than are adults of either *S. canadensis* or *Oithona colcarva* (Lonsdale, 1981).

In a fluctuating environment where juvenile mortality is higher than that of adults, decreased reproductive effort, smaller clutches and a longer lifespan should be favored (Schaffer, 1974). A comparison of the life history characteristics of *Scottolana canadensis*, *Oithona colcarva* and *Acartia tonsa* lends support to these predictions (Table 4). At 18 °C in culture, *A. tonsa* had an adult reproductive lifespan of approximately 26.2 d (24.7 d from the beginning of reproduction; Parrish and

Wilson, 1978) while at 20 °C and 15 ‰ S the average adult mean reproductive lifespan of *S. canadensis* was 62 d and of *O. colcarva*, 15.4 d. However, the day of first reproduction was much earlier for *A. tonsa* than for the other 2 species. The egg production pattern also differs among these species. *A. tonsa* produce eggs almost continuously while the other 2 species produce broods at discrete intervals: e.g. *S. canadensis* averaged one sac of eggs every 5.8 ± 1.7 d at 20 °C and 15 ‰ S. Although this intermittent reproductive pattern is consistent with theoretical interpretations for variable juvenile survival, it also may be an adaptation for protection against egg predators. The delay between broods may reflect only the time necessary for many eggs to be produced, collected in a sac, and develop through hatching. There is evidence that *A. tonsa* eggs suffer constant heavy mortality by being released singly (Kimor, 1979).

These differences in the reproductive traits between *Acartia tonsa* and *Scottolana canadensis* are more striking than the differences between *A. tonsa* and *Oithona colcarva*. The former 2 are more similar in size and yet there are differences in day of first reproduction, pattern of brood production and total reproductive life span. This marked difference in reproductive strategy seems best explained by the differences in age-specific mortality patterns which may exist between *A. tonsa* and *S. canadensis*. Due to the fact that predation on the nauplii at times is the most important source of mortality to *S. canadensis*, their reproductive traits may be the result of a trade-off in energy resources in order to increase adult survival and thereby lengthen the time period over which nauplii could be produced. This would enhance fitness in an unpredictable environment by spreading the risk of nauplius mortality over time. In contrast, the reproductive traits of *A. tonsa* may be the result of less energy being devoted to adult maintenance and more to immediate reproduction, in an environment where the predation risk to adults is very high.

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