Vol. 5: 341–351, 1981 | MARINE ECOLOGY – PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published August 15

Regulatory Role of Physical Factors and Predation for Two Chesapeake Bay Copepod Species*

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ABSTRACT: Physical factors and invertebrate predators regulate the seasonal abundances of 2 Chesapeake Bay copepods, *Scottolana canadensis* and *Oithona colcarva*, which occur during spring and fall, respectively. The absence of population growth of either species during winter can be predicted on the basis of field temperatures, since laboratory experiments revealed that egg production and development were arrested at low temperatures. Temperature and salinity conditions in the field did not contribute to the absence of these species in summer, but were optimal for the growth of both species. A comparative analysis of field and laboratory data revealed that the per capita rate of population change in the field (d^{-1}) was consistently lower than that determined in the laboratory for comparable physical conditions. Predation by two invertebrate predators, the planktonic copepod *Acartia tonsa* and the lobate ctenophore *Mnemiopsis leidyi*, had profound detrimental effects on summer populations of *S. canadensis* and *O. colcarva*. Predation rates frequently exceeded the ability of copepod populations to increase.

INTRODUCTION

Studies of the population dynamics of dominant zooplankton species have implicated a variety of physical and biological factors as population controlling forces (Brooks and Dodson, 1965; Sprules, 1975; Lampert, 1978). Many of these studies have resulted in divergent opinions as to their relative importance. For example, comparing 2 studies of *Daphnia* assemblages, Allan (1977) has proposed that species succession may be explained by temperature alone through its influence on egg development, whereas Jacobs (1977) proposed that species abundances may be the result of variations in natality and mortality which exist independently of seasonal temperature.

Freshwater and marine zooplankton assemblages typically include several species which, due to their restricted abundance pattern, receive little investigation. A determination of the factors which regulate their growth compared to dominant species could be valuable in the assessment of the dynamics of zooplankton populations. The zooplankton fauna of the Chesapeake Bay includes 2 copepod species which, for the most part, are seasonally restricted. *Scottolana canadensis* (Willey) (Harpacticoida) is most abundant during spring while *Oithona colcarva* Bowman (Cyclopoida) is primarily a fall species. The principal aim of this study was to elucidate the factors regulating the numbers of *S. canadensis* and *O. colcarva* as examples of seasonally restricted species, and thereby to evaluate how the impact of regulating factors may differ between rare and more abundant species. As likely regulating forces, I investigated 2 physical factors, temperature and salinity, and 1 biological factor, invertebrate predation by the lobate ctenophore *Mnemiopsis leidyi* A. Agassiz and the calanoid copepod *Acartia tonsa* Dana.

METHODS AND MATERIALS

Estimates of Field Populations

The population densities of *Acartia tonsa* adults, *Scottolana canadensis*, and *Oithona colcarva* were estimated at 3 stations off Calvert Cliffs in the

* Contribution No. 1143 of the University of Maryland's Center for Environmental and Estuarine Studies

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0171-8630/81/0005/0341/$ 02.00

Chesapeake Bay, USA (Fig. 1). The samples analyzed are part of a collection obtained from September to December 1971 and January to December 1973 by Heinle et al. (1977). To obtain their samples, a deep-well submersible pump was towed at 3 different depths (1 m, mid-depth and near bottom) for a series of 3 separate samples. Maximum depths are approximately 7, 10 and 15 m at Stations 1A, 3A and 3B, respectively; 19 l of water were passed through a #20 (63–74 μm) net, concentrated to 100 ml and preserved with 10 % formalin. Salinity and temperature were measured in the field with either an Inter-Ocean CSTD probe (Model 500) or with a Beckman RS-5 salinometer.

In the laboratory, the zooplankters were again concentrated to approximately 30 ml and counts were based on subsamples totaling 4 or 10 ml. The larger volume was examined when either *Scottolana canadensis* or *Oithona colcarva* was present. Egg numbers were estimated for *O. colcarva* by the methods in Lonsdale (1981) and were counted directly from gravid *S. canadensis* females.

The per capita rate of population change ($r = dN/Ndt$) in units d^{-1} of the 2 populations in the field was calculated from Edmondson (1960).

In order to estimate more accurately the densities of adult *Scottolana canadensis*, which are epibenthic, meiofauna samples were obtained by SCUBA divers who took a core of sediment with a plastic pipe at each station in July (45 cm^2) and August (4.9 cm^2) 1978. The samples were preserved with 10 % formalin, returned to the laboratory, and the fauna was collected on a 63-

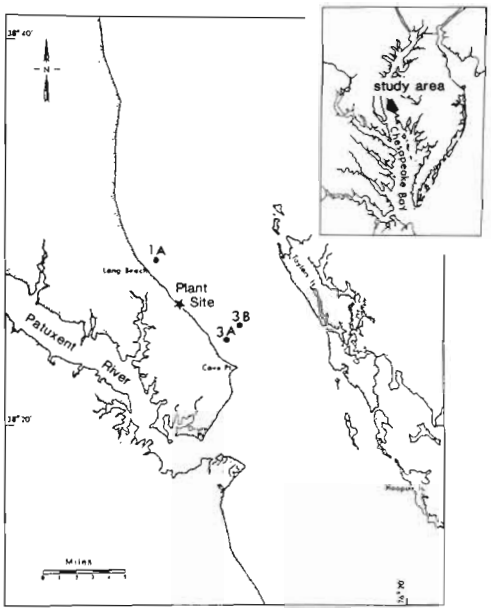

Fig. 1 Zooplankton sampling stations off Calvert Cliffs in Chesapeake Bay

μm sieve for identification. The number of copepods cm^{-2} was estimated.

Estimates of ctenophore volume (ml ctenophore m^{-3}) in 1971 and 1973 were provided by Lubbers and Mihursky (1977). The volume of water passing through a 1 m plankton net (500 μm) was estimated by a General Oceanics digital flowmeter. Ctenophores were removed from the net while on ship and their population densities were estimated by sorting the ctenophores from the ichthyoplankton and combining all individuals to measure their total volume per sample (Lubbers, pers. comm.).

Egg Development Rates

In order to determine the effects of temperature and salinity on development time of eggs of *Scottolana canadensis* and *Oithona colcarva*, I conducted egg-hatching experiments at 10, 15 and 20 ‰ S and 15 °, 18 °, 20 °, 25 °, and 28 °C. I placed 25–50 nongravid adult females, which had been in culture at the appropriate conditions for at least 2 weeks, in covered 120-ml watch glasses. They were fed daily a mixture of *Prorocentrum mariae-lebouriae* variety and *Pseudoisochrysis* sp. (VA-12). Experiments were conducted under a 12:12-h light-dark cycle and observations were made at 8-h intervals. When females produced egg sacs they were isolated into 50-ml Stendor dishes and monitored until nauplii appeared. If the egg sacs were dropped or no nauplii survived, the observations were not included. Each adult female was returned to the original pool of females and observations continued until approximately 10 or more separate egg development times had been recorded at any one test condition. In several cases (*S. canadensis* at 15 ° and 18 °C, *O. colcarva* at 15 °C), 3 or more separate experiments were conducted as few females became gravid in any one.

Invertebrate Predation

Acartia tonsa

Acartia tonsa adults are predatory on the nauplii of copepods with which they co-occur: *Scottolana canadensis* and *Oithona colcarva*. Species and size of prey are significant variables which determine this predation rate. In order to describe the relationship of prey density to predation rates by *A. tonsa*, procedures similar to those described by Lonsdale et al. (1979) were followed. Adults (usually females) were collected from zooplankton tows made at the Chesapeake Biological Laboratory pier, sorted under a dissecting

microscope and kept for 1–2 h in Millipore-filtered (MP-filtered; 0.45 µm) ambient Bay water (10 ‰ S) prior to experiments. The nauplii, either wild or obtained from laboratory cultures, were sorted by approximate Stages I–III and IV–VI and also kept in MP-filtered Bay water. Single species experiments were conducted in 180-ml dilution bottles filled with MP-filtered Bay water to which were added 75, 50, 25, or 10 nauplii, and 5 adult *A. tonsa,* to approximate natural densities found in the Chesapeake Bay (Heinle et al., 1977). Controls contained only nauplii. These bottles were wrapped in black plastic and placed on a rotating plankton wheel (2 rpm) for 16–22 h. The copepods were recovered with a 44-µm sieve, preserved, and later counted and measured. Assuming that in any one experiment the density of prey decreased at a constant rate, the clearance rate (F = ml copepod^{-1} d^{-1}) of *Acartia tonsa* was calculated from Edmondson and Winberg (1971). The clearance rate estimates the number of mls of water which must be filtered with 100 % efficiency to cause the observed reduction in prey.

Mnemiopsis leidyi

The predation rates of cydippid larvae and newly metamorphosed adult *Mnemiopsis leidyi* were investigated using both adults and nauplii of *Scottolana canadensis* and *Oithona colcarva* as prey. The ctenophores were obtained from large holding tanks to which natural populations of zooplankton were added routinely. Prior to an experiment they were placed in filtered seawater for approximately 1 h before their addition to the experimental beaker. The experiments were conducted with several naturally occurring densities of prey (10, 25, 50, and 100 ind.$^{-1}$) and ctenophores (usually 2–3 individuals with a total volume 0.15–0.60 ml) placed in 1-l beakers, containing filtered seawater (Whatman GFC; 10 ‰ S). Experiments were conducted in the dark for approximately 15–24 h at 20 °C. Control containers contained only prey. An equal amount of algae with a ratio of 2:1 of *Pseudoisochrysis* sp. (VA-12) and *Prorocentrum mariae-lebouriae* was added to both the experimental and control containers resulting in a concentration ranging from 0.15 to 0.25 10^7 µm^3 ml^{-1}. The ctenophores were first recovered from the experiments and measured (maximum length and width) under a dissecting microscope and their approximate volume was estimated by the following:

$$V = \pi r^2(L) \cdot \text{ml}/1000\ \text{mm}^3$$

where V = ml ctenophore; r = radius of width of ctenophore (mm); L = length of ctenophore (mm; oral-aboral distance). The prey were recovered on a 44-µm sieve and also counted under a dissecting microscope. The number recovered in the control experiments was use to calculate the clearance rate (l [ml ctenophore]$^{-1}$ d^{-1}).

In an attempt to investigate ctenophore predation under more nearly natural conditions, I conducted experiments on natural zooplankton populations in 750-l polyethylene tanks. A 12:12 h light-dark cycle was maintained with 500-W Quartz-Iodide flood lights. A timer controlled a stirrer for each tank which ran four times daily for 15 min. The temperature of the tanks was manipulated by the use of a flow-through system of cold or ambient seawater which was pumped to a collar around the neck of each tank. The seawater added to the tanks was pumped from the waters around the Laboratory and continually collected in a single holding tank from which the experimental and control tanks were filled simultaneously.

Experimental zooplankton populations added to the tanks were obtained from pooled tows at the Laboratory pier and split into 3 separate containers by continually swirling and filling 1-l beakers to equal volumes. Laboratory-cultured *Scottolana canadensis* and *Oithona colcarva* were added in addition to the natural populations. The volume of individual ctenophores was measured by recording their displacement (ml) of estuarine water in a graduated cylinder. Each series of experiments included 2 replicate experiments in which ≃ 30-ml of mature ctenophores (usually 5–6 ml ind.$^{-1}$) was added to the tanks and one control. This density (40 ml m^{-3}) approximated densities found in the Patuxent River (Herman et al., 1968) and in the Chesapeake Bay (Lubbers and Mihursky, 1977).

Zooplankton samples (1-l each) were taken in both experimental and control tanks at 1600-h by dipping a 10-l bucket to mid-depth immediately following the stirring period. Samples were measured in a 1-l graduated cylinder and poured through a 44-µm mesh sieve. They were preserved in formalin for subsequent measuring and counting. The remainder of the zooplankton contained in the bucket was returned to the appropriate tank. At the termination of the experiment, ctenophores were recovered, counted and their volume determined. The salinity of the water was determined at the beginning of the experiment and temperature readings were taken once or twice daily.

RESULTS

Population Abundances

Highest densities of *Scottolana canadensis* (8000 ind. m^{-3}) occurred in April and May. *Oithona colcarva*

were present from mid-May to June (< 1000 ind. m^{-3}) but began to increase in measurably significant numbers (Heinle et al., 1980 unpubl.) from August to November (10 000–40 000 ind. m^{-3}; Fig. 2). An analysis of the age distributions of both species suggested that there were no significant differences in abundance between stages of nauplii; NI-III versus NIV-VI ($p < 0.05$ for a test of differences between means of $\log_{10}$ transformed densities). However, these results may reflect the fact that NI of both *S. canadensis* and *O. colcarva* were rarely encountered in preserved samples. They may have passed through the 63–74-μm opening of the net. Thus, in the field, this age distribution could actually have been more skewed toward the younger nauplius stages.

Benthic samples revealed that adult *Scottolana canadensis* were present only at Station 1A, a sandy bottom station, in July 1978 at densities less than 1 ind. cm^{-2}. All females in the July samples were gravid (26.8 ± 6.8 eggs $female^{-1}$). The average numbers of eggs carried by female *Oithona colcarva* varied. The number of eggs per female in August and September (16.8 ± 3.7) was significantly less than in late October (20.0 ± 4.2; $p < 0.05$ for a test of differences between means).

Acartia tonsa adults were present throughout much of 1973 but their densities were maximal from August to November (Fig. 2). The decline in early June of *Scottolana canadensis* (from 8000 ind. m^{-3} in late May to < 2000 ind. m^{-3}) coincided with the rise of *A. tonsa* adults (500 ind. m^{-3} in late May to < 2000 ind. m^{-3}).

Mnemiopsis leidyi was present from April to November, attaining its highest volume (> 30 ml ctenophore m^{-3}) in late August (Fig. 2). Overall, the appearance of *M. leidyi* in late spring coincided with the disappearance of both *Scottolana canadensis* and *Oithona colcarva* from the plankton while its decline in the fall was accompanied by an increase in numbers of *O. colcarva*.

A comparison of population abundances with annual temperature change (Fig. 3) suggests that temperature is potentially an important limiting factor. *Scottolana canadensis* began to increase in numbers when the average water temperature was over 10 °C and to decline when the temperature was 20 °C. However, 20 °C is not an upper limit for *S. canadensis* as it has a greater rate of daily population increase at 25 °C. *Oithona colcarva* began to appear in significant numbers when the average water temperature was 24 °C. However, *O. colcarva* can also grow and reproduce at temperatures below 24 °C (Lonsdale, 1981).

Salinity (Fig. 3) also may have had some influence

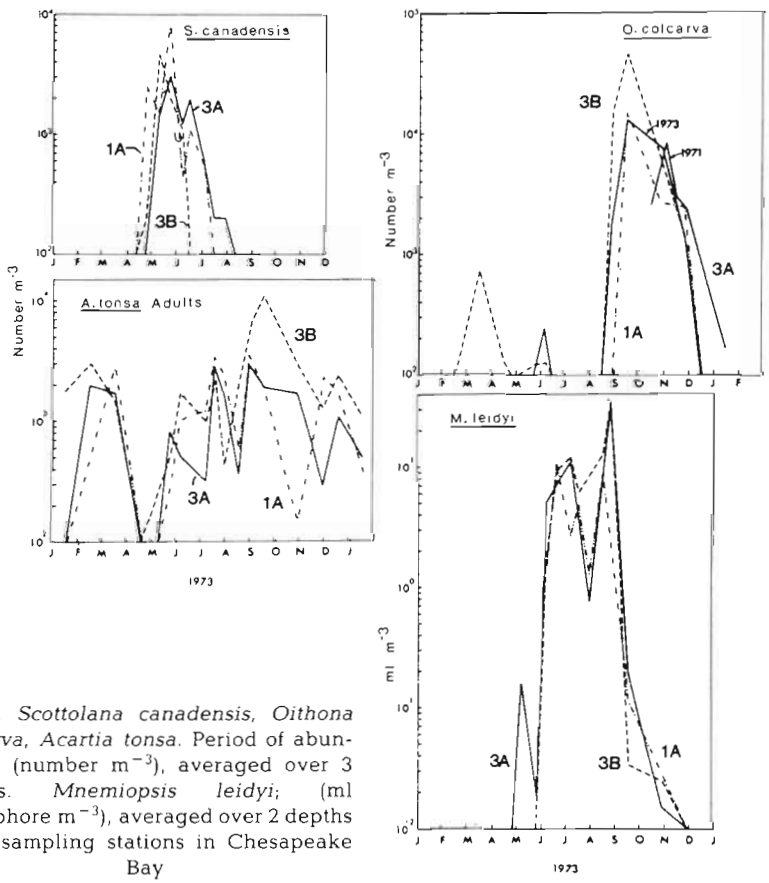

Fig. 2. *Scottolana canadensis*, *Oithona colcarva*, *Acartia tonsa*. Period of abundance (number m^{-3}), averaged over 3 depths. *Mnemiopsis leidyi*; (ml ctenophore m^{-3}), averaged over 2 depths for 3 sampling stations in Chesapeake Bay

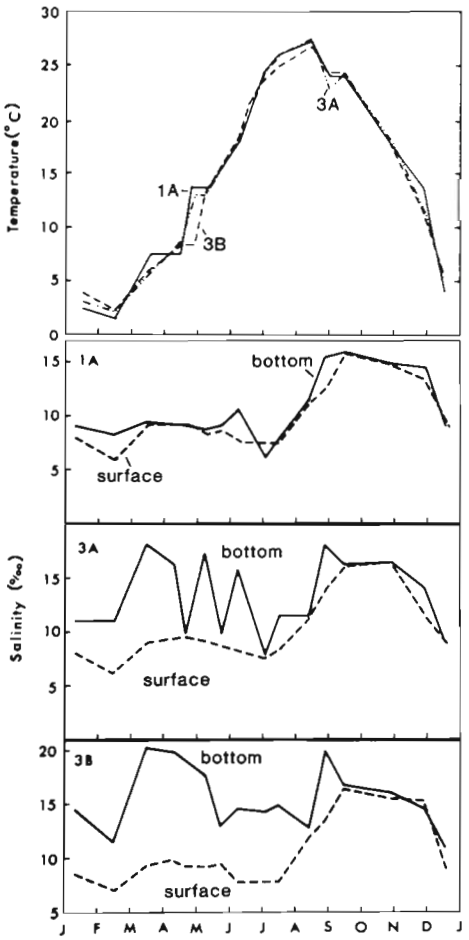

Fig. 3. Changes in temperature (°C) averaged over 3 depths (surface, bottom and mid-depth), and salinity (‰ S) at 2 depths (surface and bottom) for 3 stations (1A, 3B and 3A) in Chesapeake Bay

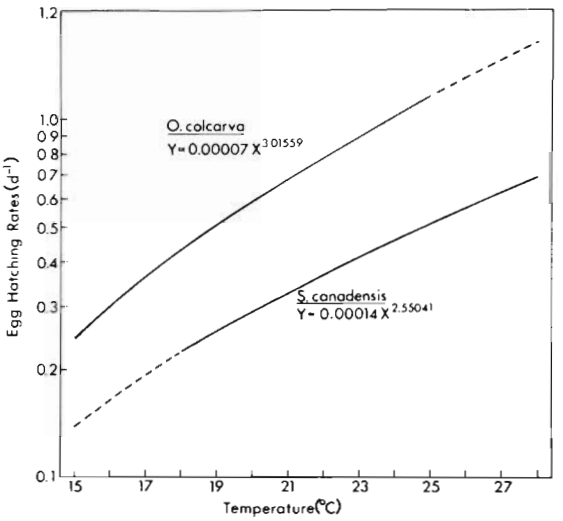

Fig. 4. *Scottolana canadensis* and *Oithona colcarva*. Egg development rates (d^{-1}) at different temperatures and salinities. Rates described by $Y = 0.00014\ X^{2.55041}$ ($r = 0.65$) for *S. canadensis* and by $Y = 0.00007\ X^{3.01559}$ ($r = 0.79$) for *O. colcarva*, where $Y = d^{-1}$ and $X = °C$

on the seasonality of these 2 copepods. Survival of *Scottolana canadensis* nauplii, which are most abundant in the upper surface waters, may have been greater in the spring due to low-salinity water (≅ 10 ‰ S). While these lower salinities may have been detrimental to *Oithona colcarva* (Lonsdale, 1981).

Egg Development Rates

Egg hatching time (h; dependent variable) was regressed on temperature (°C), salinity (‰) and a temperature-salinity interaction for both *Scottolana canadensis* and *Oithona colcarva*. Only temperature had a significant effect ($p < 0.0005$; Fig. 4). Increased temperatures resulted in decreased hatching time and explained 63 % (*S. canadensis*) and 51 % (*O. colcarva*) of the observed variability in hatching time. Because salinity did not significantly affect egg development time, developmental rates (d^{-1}) were pooled at each temperature and fitted to a variety of equations. Egg development rates (d^{-1}) were best described by $Y = 0.00014\ X^{2.55041}$ ($r^2 = 0.65$) for *S. canadensis*, and by $Y = 0.00007\ X^{3.01559}$ ($r = 0.72$) for *O. colcarva* where $X =$ °C.

Extrapolation of the results suggests that 4 mo to 1 y would be required for eggs of *Scottolana canadensis* to develop at field temperatures (3–5 °C) in January and February. Other evidence also suggests that nauplius development will not occur at these temperatures. D. R. Heinle (pers. comm.) observed *S. canadensis* nauplii over 38 d at 4 °C and found no development but 100 % survival. From late February to mid-April, field temperatures ranged from 5 °–10 °C, even at 10 °C completed egg development would still require a minimum of 3 wks. Laboratory observations made on the reproductive traits of *S. canadensis* revealed that many females would not produce egg sacs at 15 °C (Lonsdale, 1981). Hence, *S. canadensis* may have remained undetected in the plankton from late February to mid-April and in December due to a very low reproductive rate of the population. The arrested egg production of the majority of female *S. canadensis* at 15 °C in Chesapeake Bay may differ from that of a population of *Canuella canadensis (S. canadensis)* which occurs in the Columbia River estuary. The latter population showed peaks of abundance at ambient temperatures between 8 ° and 15 °C (Haertel et al., 1969) suggesting that significant variation in reproductive characteristics of this species may exist between locales. The lack of population growth of *O. colcarva* in mid-January to February and in December also can be

explained by low temperatures. Extrapolation of egg-development data suggests that at 5 °C, 4 mo would be required for nauplii to hatch; in mid-April, 2 wks would be sufficient.

Rates of Population Increase

In order to separate the role of salinity and temperature from other possible sources of population control, such as predation or availability of food resources, I compared the calculated per capita rate of change, r (d^{-1}), in the field to appropriate values of r (d^{-1}) determined in the laboratory (Lonsdale, 1981). The results of this comparison suggest that both species were increasing at much less than their maximum capacity during summer (Fig. 5). Although temperature and salinity conditions were optimal for the growth of *Scottolana canadensis* from July to August, field data revealed that growth was suboptimal. Moreover, physical conditions should have been conducive to growth from September to November. *Oithona colcarva* also was able to grow and reproduce from May through November. Its absence from the plankton during the summer was not predicted by physical conditions. The late summer increase of *O. colcarva* did coincide with optimal physical conditions in terms of r, although r in the field was less than predicted.

This analysis of the role of physical factors indicates that low temperature was limiting for both *Scottolana canadensis* and *Oithona colcarva* in winter. However, neither temperature nor salinity was of primary importance in controlling numbers at any other time in 1973. Salinity had at most a limited impact on both species. Some form of biological regulation, such as predation, must have been responsible for the absence of both copepods from the plankton during the summer of 1973.

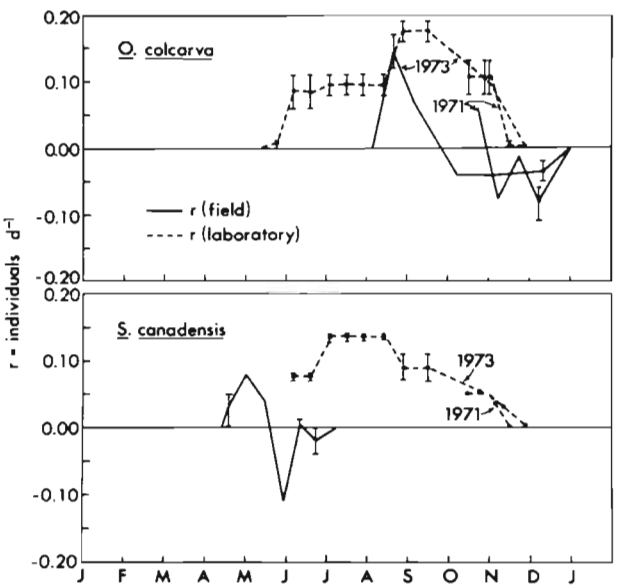

Fig. 5. *Oithona colcarva* and *Scottolana canadensis*. Comparison of per capita rate of change in the field (r field) with appropriate r values determined in the laboratory (r laboratory; data from Lonsdale, 1981)

Clearance Rates of *Acartia tonsa*

Clearance rates of *Acartia tonsa* (ml $adult^{-1}$ d^{-1}) were significantly affected by both prey item ($p < 0.001$) and prey density ($p < 0.03$; two-way analysis of variance; Design I). *Scottolana canadensis* I–III were preyed upon more heavily than were all 3 other prey items, and *A. tonsa* adults were less effective in removing older nauplii (IV–VI) particularily at the lower densities (55 and 139 prey l^{-1}; Table 1). The average clearance rate of *A. tonsa* at 55 nauplii l^{-1} of the former 2 prey items cannot be distinguished from 0.00 ml $adult^{-1}$ d^{-1} with 95 % confidence.

Table 1. Mean clearance rates (ml $adult^{-1}$ d^{-1}) of *Acartia tonsa* adults at different densities of *Scottolana canadensis* and *Oithona colcarva* nauplii

Species	Stage	Density No. l^{-1}	n	Mean	± 95% confidence
S. canadensis	NI–III	55	4	68.1	38.7
		139	4	50.3	48.2
		278	6	50.0	10.6
		416	4	58.3	39.1
	NIV–VI	55	4	1.3	4.0
		139	4	7.2	10.5
		278	7	26.6	9.3
O. colcarva	NI–III	55	4	28.0	17.7
		139	4	24.0	5.1
		278	8	26.8	10.5
	NIV–VI	55	4	25.1	25.1
		139	6	11.0	6.0
		278	4	42.4	11.6

Clearance Rates of *Mnemiopsis leidyi*

Ctenophore sampling both in the field and experimental tanks did not distinguish between cydippid larvae and lobate adults. Thus, experimentally determined clearance rates of the two predator types were pooled with regard to density of a specific prey item. Ctenophore clearance rates were significantly affected by prey type ($p < 0.001$) but not by prey density. An

Table 2. Mean clearance rates (liter ml ctenophore^{-1} d^{-1}) of *Mnemiopsis leidyi* with different copepod prey

Species	Stage	n	Mean	± 95% confidence
S. canadensis	NI–VI	34	3.6	1.0
	Adult	35	1.3	0.5
O. colcarva	NI–VI	31	1.7	0.8
	Adult	29	0.7	0.2

average rate of clearance (liter [ml ctenophore]$^{-1}$ d^{-1}) of the 2 ctenophore forms, on a particular prey item, was therefore calculated (Table 2). The mean predation rate of *Mnemiopsis leidyi* lobate adults on *Acartia tonsa* adults was calculated from Miller (1970).

Invertebrate Predation in Zooplankton Assemblage Experiments

Neither the presence of (1) alternate prey (e.g. barnacle nauplii or rotifers) nor (2) a larger volume of water (which might provide a spatial refuge or increased likelihood of escape by swimming) appeared to be effective in eliminating the impact of predation on *Oithona colcarva* (Fig. 6). In order to test the hypothesis that copepod densities were higher during their period of growth in the control than in the experimental tanks, a paired t-test was conducted on $\log_{10}$ transformed data (number l^{-1}). *O. colcarva* maintained significantly higher densities ($p < 0.025$) in the control tank in September but not in October ($0.10 < p < 0.30$). However, even in the latter series the control population clearly had an extended period of abundance compared to that of the experimental populations. *Scottolana canadensis* was unable to establish a growing population in either the experimental or control containers and there were no significant differences between the populations.

The density of ctenophores (ml ctenophore l^{-1}) was estimated for the days between Day 0 and the termination of the experiment by assuming a logarithmic pattern of growth (ml of ctenophore). Throughout the experiments, the ctenophore populations remained viable and increased in total volume from 21–97 % except in Experiment C in September, in which it decreased by 16 %.

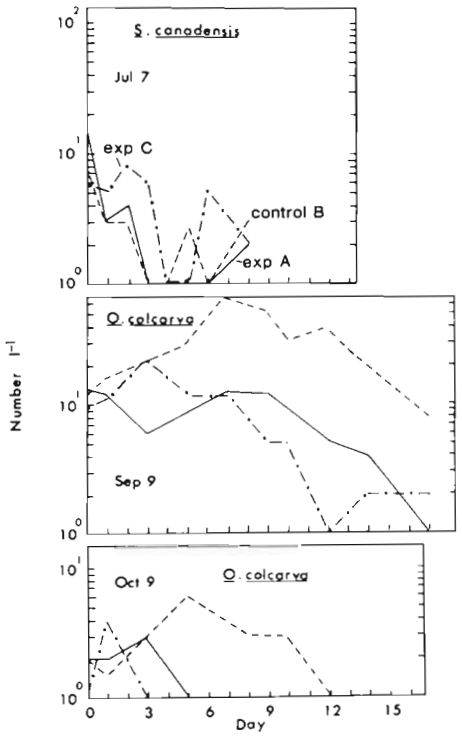

Fig. 6. *Scottolana canadensis* and *Oithona colcarva*. Density changes in populations over time in 2 experimental tanks containing *Mnemiopsis leidyi* compared to 1 control tank lacking ctenophore predators (July, September and October)

Table 3. Mean expected per capita death rate (d^{-1}) of *Oithona colcarva* and *Acartia tonsa* due to predation by *Mnemiopsis leidyi* in experimental tanks. Expected mortality was calculated from experimentally determined clearance rates and tank densities of predators

Species	Stage	Series	Expected per capita death rate (d^{-1})			
			Exp't 1		Exp't 2	
			Mean	Standard deviation	Mean	Standard deviation
O. colcarva	NI–VI	September	0.07	0.01	0.07	0.00
	Adult		0.03	0.00	0.03	0.00
	NI–VI	October	0.07	0.00	0.08	0.01
	Adult		0.03	0.00	0.03	0.00
A. tonsa	Adult	July	0.13	0.00	0.24	0.02
		September	0.19	0.02	0.15	0.00
		October	0.15	0.01	0.17	0.02

The expected per capita death rate (d^{-1}) of the various prey in these tanks was calculated as the product of predator density and the mean clearance rate of the predator (modified from Allan, 1973). The average expected mortality of *Oithona colcarva* due to *Mnemiopsis leidyi* predation was greater for the nauplii while mortality to the adults was less (Table 3). *Acartia tonsa* adults had a higher expected per capita death rate (d^{-1}) than those of *O. colcarva* in both the September and October series.

The daily per capita rate of change of the 2 populations was calculated during the period of increase of the control populations. The rate of change (d^{-1}) of *Oithona colcarva* and *Acartia tonsa* populations generally was higher in the control tanks where ctenophores were absent (Table 4). The difference in *r* between tanks probably was due to deaths from ctenophore predation. Yet nauplius predation by *A. tonsa* also may have altered copepod densities of *O. colcarva* in these tank experiments (Table 5). The expected per capita death rate of the nauplii (NI-III) from *A. tonsa* predation was always greater in the control tanks and thus the detrimental effects of ctenophore predation, in terms of the difference in *r*, may have been underestimated. The difference in *r* of *A. tonsa* between tanks ranged from 0.01–0.22 d^{-1} and the expected per capita death rate of adult *A. tonsa* from ctenophore predation alone could explain 68–100 % of this difference. Deaths to nauplii from ctenophore and adult *A. tonsa* predation could account for additional mortality (pers. obs.). In contrast, the expected mortality of *O. colcarva* adults accounted for less than 12–14 % of the difference in *r* (0.21–0.36 d^{-1}) while nauplius deaths could explain 19–33 %. Although ctenophore predation significantly reduced copepod densities, rapid growth and dominance by *A. tonsa* occurred in both experimental and control tanks (Table 4). Moreover, *A. tonsa* predominated despite the prediction based on single species ctenophore predation experiments (Miller, 1970) that it would suffer higher rates of adult predation relative to the other species. Compared to *O. colcarva* and *Scottolana canadensis*, *A. tonsa* has a much higher intrinsic rate of natural increase (Lonsdale, 1981); this may explain its predominance even when heavily preyed upon.

Invertebrate Predation in Field Populations

Predation by *Acartia tonsa* adults on *Scottolana canadensis* and *Oithona colcarva* nauplii (NIV-VI) was not an important factor in 1973 or the fall of 1971 as nauplii did not occur in densities above that at which a significant clearance rate occurred (55 000 ind. m^{-3}). This was not the case for NI-III. At the time when the field population of *S. canadensis* began to decline (late May through mid-June, 1973), the expected per capita death rate (d^{-1}) due to *A. tonsa* predation of the NI-III rose from a mean of 0.03 to 0.06 d^{-1} (Fig. 7). This predator induced mortality could account for 55–60 % of the difference between the actual rate of increase of the field population and the average rate predicted from laboratory experiments (Fig. 5). The rise of *A. tonsa* adults in the plankton appears to have caused

Table 4. Per capita rate of population change, *r* (d^{-1}), of *Oithona colcarva* and *Acartica tonsa* in experimental tank containing *Mnemiopsis leidyi*

Species	Series	°C	Per capita rate of population change (d^{-1})		
			Control	Exp't 1	Exp't 2
O. colcarva	September	23	0.26	−0.01	0.05
	October	19	0.22	−0.14	0.00
A. tonsa	July	24	0.77	0.59	0.61
	September	23	0.53	0.52	0.50
	October	19	0.27	0.09	0.05

Table 5. Expected per capita death rate (d^{-1}) of *Oithona colcarva* due to predation by *Acartia tonsa* adults in control and experimental tanks. Expected mortality was calculated from clearance rates determined in predation experiments, and tank densities of predators

Species	Stage	Series	Expected per capita death rate (d^{-1})					
			Control		Exp't 1		Exp't 2	
			Mean	S.D.	Mean	S.D.	Mean	S.D.
O. colcarva	NI–III	September	0.04	0.01	0.02	0.02	0.00	0.00
		October	0.06	0.04	0.01	0.01	0.01	0.01

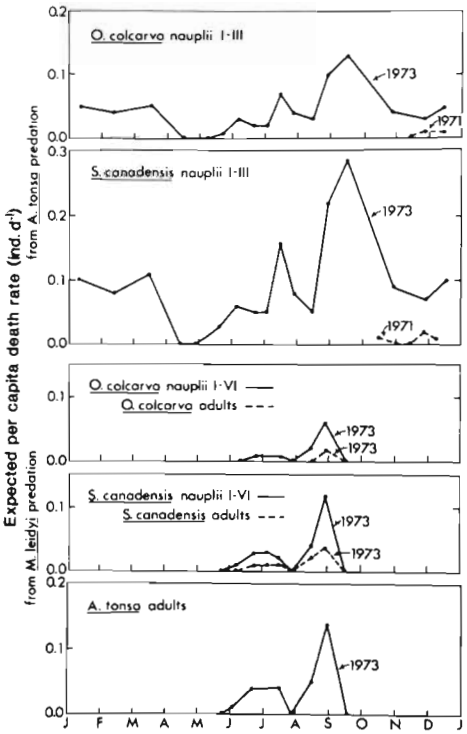

Fig. 7. Expected per capita death rates of field populations of *Oithona colcarva*, *Scottolana canadensis* and adult *Acartia tonsa* (d^{-1}) from invertebrate predators

the decline of *S. canadensis* due to nauplius (I–III) predation and may have prevented its population growth through November.

During the period of population growth in the late summer, the expected per capita death rate of *Oithona colcarva* NI-III due to *Acartia tonsa* predation may have accounted for 90–100 % of the difference in field and laboratory population growth (d^{-1}) and 27–75 % of its decline when growth was still possible in late October 1973 (Figs 5 and 7). Nauplius mortality induced by *A. tonsa* explained only 14–25 % of the population decline of *O. colcarva* in November and December 1971. The impact of this predator may prove to be more substantial than suggested by this study when the feeding behaviors of late stage copepodites (CIV-V) are investigated (see Petipa et al., 1970).

Alternatively, the expected per capita death rates of *Oithona colcarva* NI-III from adult *Acartia tonsa* predation could be overestimated as extrapolated predation rates (number of prey eaten adult^{-1} d^{-1} = $0.02x - 0.32$; where x = initial number of prey l^{-1}; r^2 = 0.74) suggest that at 16 000 nauplii m^{-3}, no significant predation should occur. Although the clearance rate of *A. tonsa* is clearly unaffected throughout the density of NI-III tested (55 000–278 000 ind. m^{-3}), it is plausible that it may reduce its predatory effort at low densities of these prey as with *Scottolana canadensis* and *O. colcarva* NIV-VI (but see Landry, 1978).

Ctenophore predation did not appear to be an important source of mortality for *Oithona colcarva* adults throughout 1973 and in the fall of 1971. The expected per capita death rate of their nauplii due to *Mnemiopsis leidyi* in mid-June (0.01 d^{-1}; Fig. 7) accounts for approximately 9–17 % of the difference between potential population increase and actual rate of increase in the field (0.06–0.11; Fig. 5). In late August 1973, a similar calculation (0.06 d^{-1}) accounts for 75–120 % of the discrepancy (0.05–0.08 d^{-1}; Fig. 5). There was very little overlap of *O. colcarva* and ctenophores. Hence, *M. leidyi* appears to be an important invertebrate predator in limiting *O. colcarva*.

The continued decline in numbers of *Scottolana canadensis* through June coincided with the appearance of ctenophores; the expected per capita death rate of *S. canadensis* nauplii from ctenophore predation ranged from 0.01–0.03 d^{-1} (Fig. 7). Ctenophore predation could account for an additional 7–37 % of the difference in r (0.08–0.14 d^{-1}; Fig. 5). Ctenophores could have had some impact on the adult population which appeared in the plankton.

This study provides evidence to implicate invertebrate predation by adult *Acartia tonsa* and *Mnemiopsis leidyi* ctenophores as a major factor regulating the numbers of *Scottolana canadensis* in Chesapeake Bay from late spring through fall 1973. However, there were several occasions (early June and late July, 1973 and the entire fall of 1971) when invertebrate predation explained less than 80 % of the difference between laboratory predictions and actual field population growth rates (d^{-1}). Likewise, the regulation of *Oithona colcarva* populations by invertebrate predators may at times be dramatic, explaining more than 80–90 % of the difference in rates during August and September 1973. Yet on the average in 1973 invertebrate predation accounted for little over 60 % of this difference and a maximum of only 25 % in the fall of 1971. Further inquiries into the population dynamics both of *S. canadensis* and *O. colcarva* are warranted.

DISCUSSION

The spring decline and subsequent summer exclusion of *Scottolana canadensis* and *Oithona colcarva* populations in Chesapeake Bay are consequences of the fact that the field standing stocks of invertebrate predators can remove these copepods at a rate (expected per capita death rate) which may at times exceed their reproductive potential (laboratory r). Rippingale and Hodgkin (1974) proposed that high values of r allowed *Gladioferens imparipes* to co-exist to a

limited extent with its omnivorous predators. In this study, the potential mortality rate from summer standing stocks of the invertebrate predators exceeded 0.5–4.0 times the reproductive potential (laboratory *r*) of *S. canadensis* or *O. colcarva*.

One of the most striking contrasts between *Acartia tonsa*, and *Scottolana canadensis* or *Oithona colcarva*, is the ability of the former to persist in the summer plankton despite the fact that expected per capita death rates of *A. tonsa* adults from ctenophore predation are much higher than on either *O. colcarva* or *S. canadensis* adults. Their nauplii are also subject to predation by *A. tonsa* adults and ctenophores (Lonsdale et al., 1979; pers. obs.). Apparently, the higher intrinsic rate of population increase of *A. tonsa* (as much as 0.70–0.80 d^{-1} at 25 °C; Heinle, unpubl.) allows numbers to increase faster than these invertebrate predators can remove them from the plankton. The limitation of numbers of *A. tonsa* in the Chesapeake Bay during the summer may involve the combined effects of ctenophores and other predators. It has been proposed that in Rhode Island the late summer decline of natural zooplankton populations, primarily composed of *A. tonsa*, may be initiated by a shortage of food resources and only enhanced by ctenophore predation (Kremer, 1975).

This study suggests that the balance of population growth rates and invertebrate predation may be critical in determining the copepod species composition in Chesapeake Bay. This interpretation may explain why variations in physical and predatory regimes could result in changes in the zooplankton dynamics of a similar species assemblage in other geographical areas. For example, the numerical co-dominance of *Oithona colcarva* with *Acartia tonsa* in sub-tropical waters (Hopkins, 1977) is an intriguing phenomenon in the light of this study. The year-round abundance of *O. colcarva* in these waters which rarely go below 10 °–20 °C (Reeve, 1970) is possible as egg development may be arrested only rarely. In addition, higher year-round salinities (15–36 ‰ S) and temperatures are optimal for population growth (Lonsdale, 1981). Yet, higher temperature would also increase the growth rate of *A. tonsa* (Heinle, 1966, 1969). The presence of additional predators which demonstrate a selective preference for *A. tonsa* over *O. colcarva* could result in their co-dominance, simultaneously reducing the rate of population increase of *A. tonsa* relative to *O. colcarva* and the predatory impact on the nauplii of the latter. The ctenophore *Mnemiopsis mccradyi* is an important predator in these waters (Reeve and Baker, 1975) but as in Chesapeake Bay, its rate of removal of *A. tonsa* also may not be sufficient to restrict their numbers. Another important predator in many sub-tropical waters, which is not common in Chesapeake Bay, is the chaetognath *Sagitta hispida* (Reeve, 1966). In the laboratory, it exhibits a preference for active and larger prey items such as *Acartia* over smaller harpacticoids and copepodites. The active swimming behavior and larger size of *A. tonsa* relative to *O. colcarva* may contribute to a higher rate of mortality from chaetognath predation. Thus, in this sub-tropical system, rates of population increase of *O. colcarva* may be sufficiently high to allow their maintenance and growth despite the presence of various predators, while intense differential selection of *A. tonsa* as prey may result in the co-dominance of these two species. Unlike that in Chesapeake Bay, the balance between population growth and predation may be more equitable for both *O. colcarva* and *A. tonsa* populations.

Acknowledgements. J. D. Allan and D. R. Heinle were most influential in guiding the direction of this research. D. Bonar, B. Bradley, P. Donaghay, J. Fedyck, C. Miller, D. Morse, M. Reaka, and M. Reeve provided critical reviews of this manuscript. I also thank R. Fowler, R. Huff, H. Millsaps and N. Mountford for their technical assistance and G. Dittrich for preparing the manuscript. The field zooplankton samples used in this study were those from projects supported by the University of Maryland, the US Atomic Energy Commission, the US Department of the Interior, Office of Water Resources Research, and the US Energy Research and Development Agency. This research was supported by a fellowship from the Center for Environmental and Estuarine Studies, and funding from the Department of Zoology, and the Chesapeake Bay Fund at the University of Maryland.

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This paper was presented by Dr G.-A. Paffenhöfer; it was accepted for printing on April 29, 1981