Limnol. Oceanogr., 38(3), 1993, 613–622
© 1993, by the American Society of Limnology and Occanography, Inc.

The effect of peritrich ciliates on the production of *Acartia hudsonica* in Long Island Sound

Penny Weissman,[1] *Darcy J. Lonsdale,*[2] *and Jeannette Yen*
Marine Sciences Research Center, State University of New York at Stony Brook, Stony Brook 11794-5000

Abstract

We studied the effects of attached peritrich ciliates on the fitness of natural populations of *Acartia hudsonica* (Pinhey) in Stony Brook Harbor, Long Island Sound. Ciliate infection occurred during late spring, and ciliate load (No. ind.$^{-1}$) was not related to copepod age, stage, or body size. Simulated in situ experiments conducted throughout the period of abundance of *A. hudsonica* showed that egg production rate (No. d^{-1}) was positively correlated to ambient water temperature, but negatively correlated to ciliate load. Salinity and the concentration of total or >8–10 μm Chl *a* were not significant in explaining the variation in egg production rate. Egg hatching success (%) was not influenced by the infection status (presence or absence) of the female. Infected nauplii had lower survival rates (d^{-1}) compared to uninfected nauplii, but their developmental rates (molts d^{-1}) were not significantly different.

Significantly slower average sinking rates were found for infected adults compared to uninfected adults. Slower sinking rates for infected copepods may have been due to an increase in surface area which increased drag. Infected adults with slower sinking rates may be more susceptible to predation. Our findings show that peritrich ciliates can play a role in the seasonal decline and future recruitment of *A. hudsonica.*

Epibiotic interactions between stalked peritrich ciliates and copepod hosts have been observed in both marine and freshwater systems (Henebry and Ridgeway 1979; Nagasawa 1988; Sleigh 1989; Xu and Burns 1990). Copepod epibiosis has been reported for many sites on the eastern seaboard of the United States (Herman and Mihursky 1964; Herman et al. 1971; Turner et al. 1979; Woodhead and Jacobson 1985; South Carolina, Lonsdale pers. obs.), such as for *Acartia tonsa* in Long Island Sound (Conover 1956). *Acartia hudsonica,* a widely distributed congener in northern estuaries along the eastern coast of North America (Conover 1956; Jeffries 1962) and major constituent of the zooplankton population in Long Island Sound, was found to be infected with the solitary peritrich *Rhabdostyla* (identified by R. Willey; Fig. 1, above) in early summer 1989 and 1990. The attached ciliates on *A. hudsonica* adhered only to the surface, with no penetration of the exoskeleton (Fig. 1, below) as previously found by Herman et al. (1971). Ciliate infestation is often considered to be a phenomenon relevant only to senescent populations of adult copepods. Moreover, it has been suggested that ciliate load (No. copepod^{-1}) depends on both the size of the copepod and the size of the ciliate (Herman et al. 1971). Much of the past work on ecological interactions between copepods and attached ciliates has been to identify the ciliates, quantify the degree to which an individual is infected, and determine the percentage of the population infected.

Our research examined some demographic and movement effects of peritrich ciliates on *A. hudsonica* on Stony Brook Harbor, Long Island Sound. Our working hypothesis was that epibiont load was inversely related to copepod fitness. It was also our intention to study ciliate interactions with *A. tonsa,* but no infection of this species was found in the field study year (1989–1990). We examined egg production rate, egg-hatching success, and naupliar survival and development rate as measures of fitness. Sinking rates of adult copepods were also

[1] Present address: Bronx High School of Science, Biology Department, 75 West 205th Street, Bronx, New York 10468.

[2] To whom correspondence should be sent.

Acknowledgments

We thank A. Durbin for suggestions on our experimental design, A. Okubo for comments on an earlier draft of the manuscript, and R. Willey for the SEM micrographs.

This research was supported by the National Science Foundation (OCE 90-12540 to D. J. Lonsdale and F. C. Dobbs) and the Office of Naval Research (N00014-87-K-0181 to J. Yen).

Contribution 825 from the Marine Sciences Research Center, State University of New York at Stony Brook.

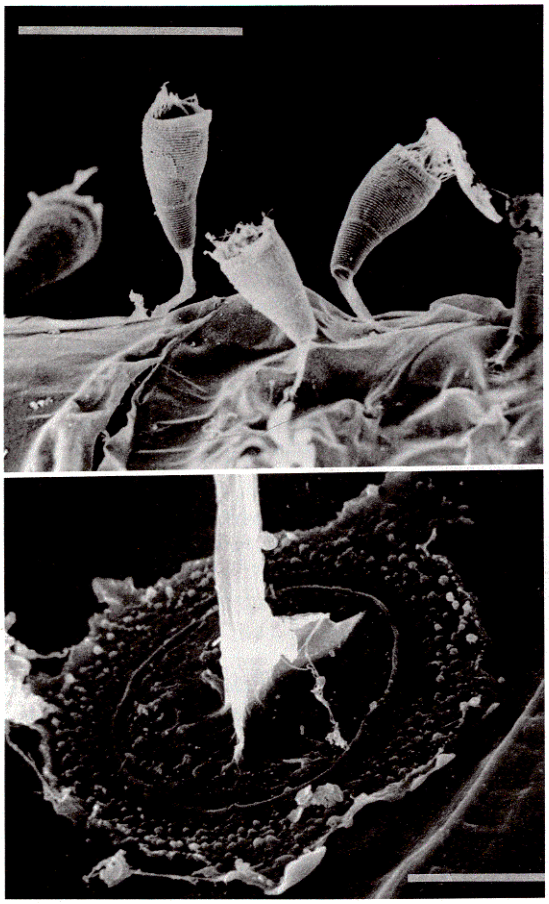

Fig. 1. Peritrich ciliates found attached to *Acartia hudsonica* collected in Stony Brook Harbor. Above: Scanning electron micrograph of *Rhabdostyla*, a stalked, solitary peritrich (bar = 1 μm; courtesy of R. Willey). Below: Scanning electron micrograph of the attachment disc and stalk of *Rhabdostyla* (bar = 1 μm; courtesy of R. Willey).

examined because they are related to susceptibility of predation and other behavioral attributes of copepods (e.g. diel vertical migration).

Methods

Field studies—Zooplankton were sampled from November 1989 through November 1990 from Stony Brook Pier on the north shore of Long Island, New York. Quantitative samples were pumped from ~2-m depth, filtered through a 64-μm mesh, and Formalin preserved (4%) for later analysis and quantification of percentage of population infected. A mercury thermometer and refractometer were used to measure temperature and salinity. In the laboratory, preserved zooplankton samples were enumerated by placing a subsample of the 20-liter filtrate obtained with a Stempel pipette into a Plexiglas counting chamber. Identification of zooplankton and copepod developmental stages, number of copepods infected by stage, and number of ciliates per copepod were determined. Water was also pumped for size-fractioned Chl *a* analysis, which began immediately upon return to the laboratory (Parsons et al. 1984).

Copepod egg production and viability—*A. hudsonica* females were collected routinely with a 64-μm net (0.5-m diam) towed on the surface at high tide and sorted as infected or uninfected individuals for laboratory experiments on egg production and egg-hatching success. Within 4 h of collection, single females were placed in a Plexiglas cylinder (i.d., 6.6 cm) inserted vertically into a 600-ml beaker that had a 210-μm Nitex screen siliconed to the bottom of the cylinder to separate the females from their eggs and nauplii which settle below the screen, thus minimizing cannibalism as observed by others (Landry 1975; Lonsdale et al. 1979; Durbin et al. 1983). The beaker was prefilled with 250-ml of 64-μm screened ambient seawater. The ambient seawater was filtered through a 64-μm screen to remove large predators and copepod eggs previously produced in the field.

During the period of ciliate infection on the copepods, an enriched food treatment was also prepared; it consisted of 64-μm screened seawater and laboratory-cultured algae [1 : 1 concentration by cell number of *Isochrysis galbana* (3H; flagellate; 4–6 μm) and *Thalassiosira weissflogii* (diatom; 10–14 μm) at 2.5×10^5 cells ml^{-1}]. The food enrichment treatment was used to examine the effects of epibionts when copepods were likely to be less food limited (sensu Durbin et al. 1983). During the period of ciliate infection, usually six females (three healthy, three infected) were placed in ambient seawater and six in enriched seawater, and all were placed in incubators kept close to ambient field temperatures. By July, we did not find enough *A. hudsonica* females in net tows for these experiments, but did evaluate three females (one infected, two uninfected) under enriched food conditions for egg-hatching success to determine the timing of diapause egg production (*see below*). At all other times,

6–12 females were incubated using only ambient seawater treatments. The term "infected" describes copepods with one or more attached ciliates.

The females were allowed to acclimate to experimental conditions for 24 h, after which additional food was added. Ambient seawater was collected daily from Stony Brook Harbor to prepare fresh food suspensions. The algae were cultured in f/2 enrichment medium (Guillard 1975) prepared with 25‰, 20-μm screened and autoclaved seawater, and grown at 20°C under a 14 : 10 h L/D cycle. Cell densities were determined with a hemacytometer.

After 48 h, the number of eggs produced per female was counted under a dissecting microscope at 50×. Starting with experiments conducted from 7 March onward, females were removed, anesthetized with M-amino-benzoic acid ethylester methanesulfonate (MS-222; CalBiochem), and the prosome length (Ambler 1985) and ciliate load (No. copepod^{-1}) were determined.

Egg viability experiments were carried out on the eggs obtained in the egg production experiments. Copepod eggs were placed in 50-ml Stender dishes containing 20-μm screened and autoclaved seawater (25‰) and algal cells (1 : 1 concn by cell number of *I. galbana* and *T. weissflogii* at 2.5 × 10^5 cells ml^{-1}). Egg-hatching experiments were conducted at ambient temperatures. Because *Acartia* produces both subitaneous eggs and later, diapause eggs when temperatures become unfavorable (Sullivan and McManus 1986), this study examined hatching success under two experimental regimes. When temperatures were >19°C, an additional step was needed to determine whether the eggs produced were diapause and not "nonviable." Following the methods of Sullivan and McManus (1986), the eggs of *A. hudsonica* that did not hatch after 14 d were incubated at a lower temperature (5°C) for 10 d to obtain total hatching percentages.

Observations for hatched nauplii and empty egg cases from infected and uninfected females were made under a dissecting microscope. Eggs and nauplii were removed and placed in 4% buffered Formalin with Rose Bengal added.

Naupliar survivorship and ciliate population growth—Infected and uninfected nauplii of *A. hudsonica* were collected from the field in the same manner as the adults. They were reared in 1-ml wells of a multidepression dish held in an airtight opaque plastic container. Distilled water in the bottom of the container served to decrease evaporation (after Lonsdale and Jonasdottir 1990). Ambient water was screened through a 64-μm mesh to remove the larger animals. For the enriched treatment, screened seawater plus an algal enrichment was prepared (as described in the egg production studies). Ambient seawater was collected daily to prepare the naupliar growth media. Nauplii (n = 18 for each food and infection treatment) were reared at ambient temperature (15°C) and under a 14 : 10 L/D cycle. The nauplii were transferred daily to clean dishes containing fresh naupliar growth medium. Mortality, number of molts, and ciliate load were recorded daily. It was also noted whether the nauplius lost the ciliates following molting.

Adult copepod sinking rates—Fixed-frame, laser-illuminated video-imaging (Yen and Fields 1992) was used to compare the natural free-swimming behavior of infected and uninfected *A. hudsonica*. Comparisons of sinking rates were made between those adult copepods with no ciliates and those with a high degree of infection (>20 ciliates copepod^{-1}). Both types of copepods were placed in an 80-ml tank containing 25‰, 20-μm filtered, autoclaved seawater supplemented with algal cells (as in egg-hatching experiments). If no healthy field copepods could be found, lab-cultured *A. hudsonica* (originally from Stony Brook Harbor and kept at 15°C with the same algal suspension) were substituted. The live animals were acclimated to room temperature (26°C) which had no observed effect on their swimming behavior.

Copepod sinking was defined as passive, vertical, downward movement. Sinking rate can be computed by analyzing the downward distance traversed over time (mm s^{-1}) where sinking distance was determined from one view of the passively sinking copepod. Passive vertical movement of sinking copepods was verified by examining the orientation of the sinking copepods in two right-angle videotaped views. In each of the various orientations, the copepods showed passive sinking in a straight vertical plane with no sinking on an angle. Horizontal motion was observed only for those intervals during which a jump occurred. Analyses were made only on those copepods which

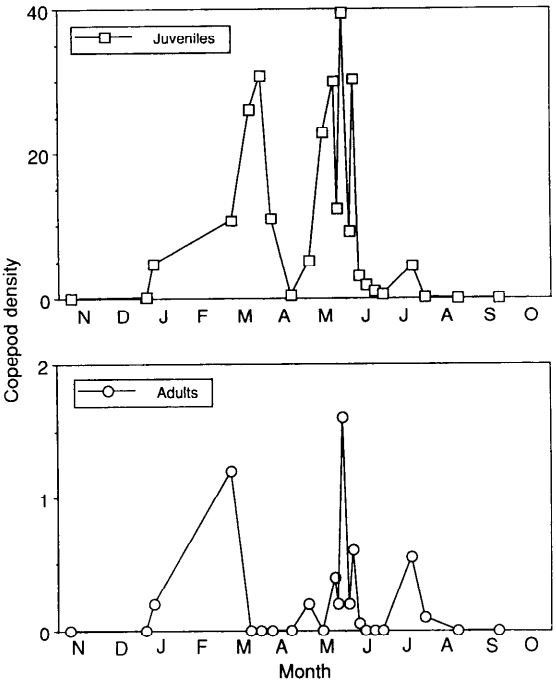

Fig. 2. Density (No. liter^{-1}) of *Acartia hudsonica* juveniles and adults from November 1989 to September 1990.

were away from the walls of the tank so that the walls did not interfere with their swimming. Sinking rates were obtained via frame-by-frame analysis of the videotapes, where a single copepod's movement was traced on acetate, measuring the head-to-head distance in each consecutive frame. Distance was calibrated by videotaping a millimeter ruler. For most individuals, at least three estimates of sinking rate were obtained to determine an average rate for each individual. The head-to-head distance and body lengths were measured with a digitizing pad (Summagraphics MacTablet) and calculations made with the NIH image-analysis software on the Macintosh II.

Results

Zooplankton abundance and incidence of infection—A. hudsonica dominated the copepod species composition in Stony Brook Harbor from January to June 1990 (Fig. 2). Juveniles tended to constitute the greatest proportion of the population during the months they were present. Infected adults and copepodites were

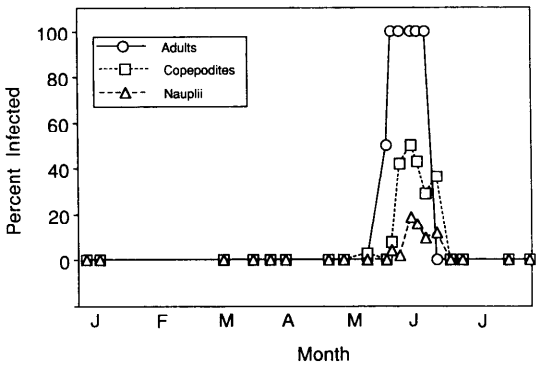

Fig. 3. Percentage of *Acartia hudsonica* adults, copepodites, and nauplii infected with peritrich ciliates from January to July 1990.

first observed on 14 May; infected nauplii were found 2 weeks later (25 May) (Fig. 3). The percentage of the population infected during this period ranged from a minimum of 50% to as high as 100% for the adults, 8–50% for copepodites, and 2–19% for nauplii. Ciliate load on adults range from 1 to 300 ciliates per individual, while copepodites and nauplii had as few as 1–100 ciliates per individual.

Total Chl *a* levels were maximal in January 1990 at 30.07 μg liter^{-1} and minimal in March at 1.84 μg liter^{-1} (Fig. 4). The period from November 1989 through the beginning of May 1990 showed a dominance of larger phytoplankton cells (>8–10 μm—average of 79.8% of the total Chl *a*). During the period of infection, mean total Chl *a* levels ranged from 6.20 to 6.86 μg liter^{-1}. A shift in the dominance to the smaller Chl *a* fraction (<10 μm) during this period accounted for 3.86–5.48 μg liter^{-1} or 56.3–92.0% of the total Chl *a* content. Screening the ambient seawater with a 64-μm mesh did not remove measurable amounts of Chl *a*.

Temperatures exceeded 19°C in late June when the seasonal decline of *A. hudsonica* was observed (Figs. 4, 2). Salinity levels (Fig. 4) had a maximum value of 31‰ in December 1989 and a minimum value of 25‰ in late June 1990.

Copepod egg production and viability—The egg production rate of *A. hudsonica* from November 1989 through June 1990 (Fig. 5) was positively correlated to ambient water temperature, but salinity and the concentration of total or >8–10 μm Chl *a* had no significant

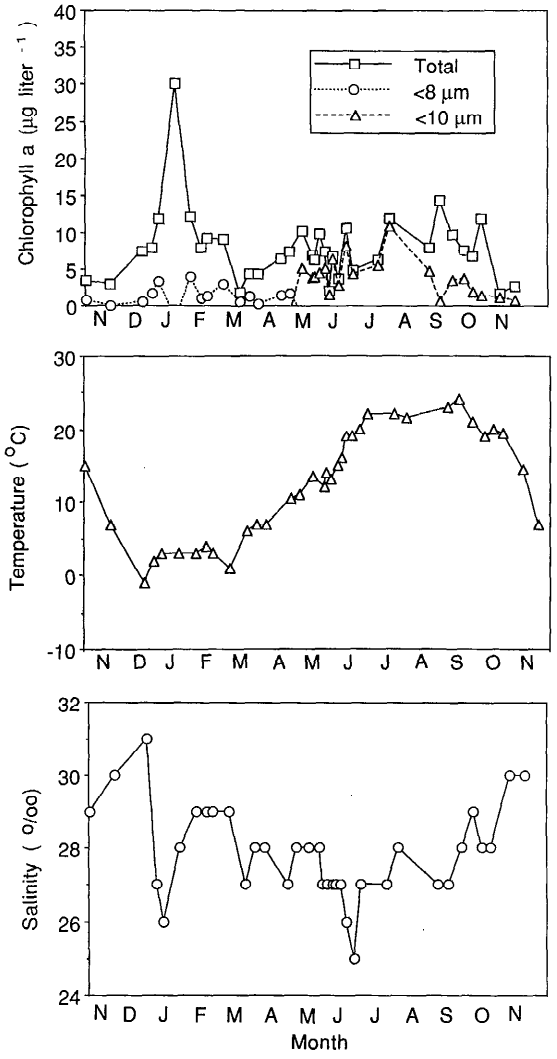

Fig. 4. Seasonal variations in total and size-fractionated Chl *a* concentration, temperature, and salinity from November 1989–November 1990.

effects (multiple regression; Sokal and Rohlf 1981; Table 1). In contrast, ciliate load (No. copepod^{-1}) was inversely correlated to rate of egg production (Table 1). A similar negative relationship between ciliate load and egg production rate was also obtained (df = 1,64; F = 4.410; $0.025 < P < 0.05$) with the data set from 7 March onward, when differences in copepod body lengths also could be included in the multiple regression analysis. Cephalothorax length was not a significant factor in explaining variation in rate of egg production (df = 1,64; F = 0.052; $P > 0.75$).

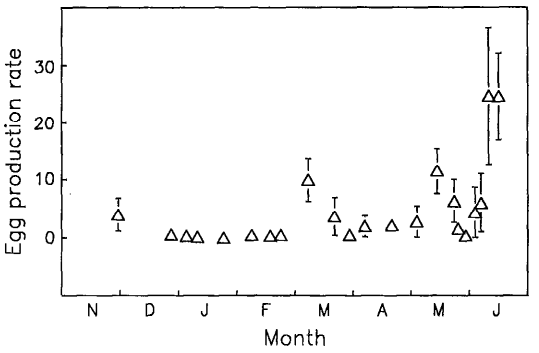

Fig. 5. Rate of egg production (No. female^{-1} d^{-1}) (mean ± 95% C.I.) of *Acartia hudsonica* under ambient food and water temperature conditions. Missing confidence intervals are smaller than the height of the symbol.

During the infection period, food enrichment resulted in a significant increase in the number of eggs produced, but infection status (presence or absence of peritrich ciliates) was not an important variable for experiments conducted during the infection period (two-way ANOVA, SAS; df = 1,67; F = 10.68 and 0.49; P = 0.002 and 0.485, respectively; Fig. 6). The mean rate of egg production under enriched food conditions was 22.3 d^{-1} (±6.8, 95% C.I.) compared to 9.7 d^{-1} (3.6) under ambient food conditions. For infected females, however, egg production rate was inversely related to ciliate load [n = 21; $Y = 17.527 - 0.082X$ (±0.074, 95% C.I.); $0.025 < P < 0.05$] under ambient food conditions, but not under enriched food conditions (n = 20; $P > 0.75$).

No eggs produced by either uninfected or

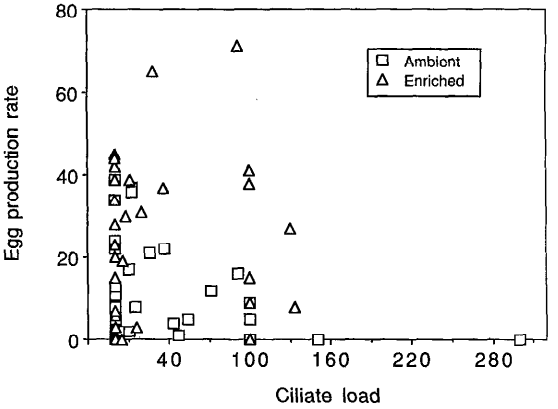

Fig. 6. Rate of egg production (No. female^{-1} d^{-1}) of *Acartia hudsonica* vs. ciliate load under ambient and enriched food conditions.

Table 1. Multiple regression analysis of the relationship of ambient physical factors (°C and ‰), Chl *a* concentration (μg liter^{-1}), and ciliate load (No. female^{-1} d^{-1}) to egg production rate (No. female^{-1} d^{-1}) of *Acartia hudsonica* from November 1989 through June 1990. (df = 1, 129; *y*-intercept = −19.845.)

Variable	Partial regression coefficient	*F*	*P*
Temp.	0.773	30.801	<0.001
Salinity	0.628	1.465	0.10 < *P* < 0.25
Total Chl *a*	0.598	2.880	0.05 < *P* < 0.10
>8–10-μm Chl *a*	−0.638	3.389	0.05 < *P* < 0.10
Ciliate load	−0.045	7.053	0.005 < *P* < 0.01

infected females hatched at temperatures >19°C. These eggs began to hatch only after they had been transferred to 5°C. Some eggs left at 20°C as a control failed to hatch and some began to disintegrate as found by Sullivan and McManus (1986). There was no significant effect of infection status (presence or absence) or food treatment on egg-hatching success (two-way ANOVA on arcsine-transformed proportions, SAS; df = 1,86; $F = 0.41$ and 0.02; $P = 0.52$ and 0.89, respectively). The overall mean hatching success of *A. hudsonica* eggs was 46.1% (±3.8, 95% C.I.).

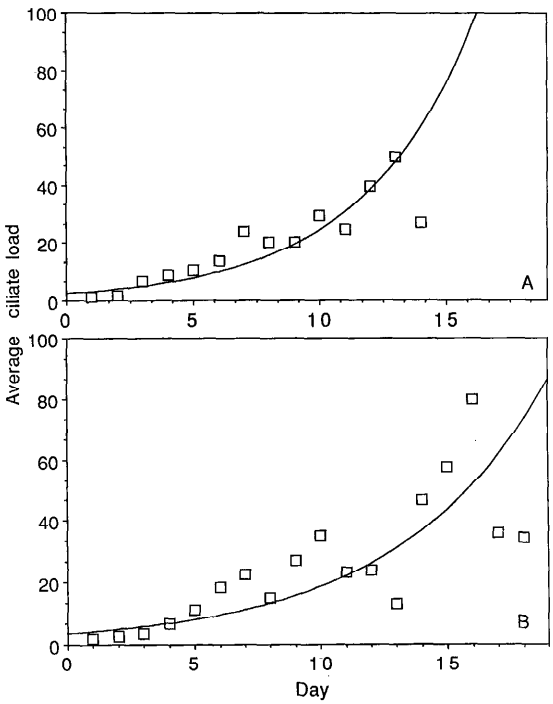

Fig. 7. Changes over time in average ciliate load (No. copepod^{-1}) on *Acartia hudsonica* nauplii reared at 15°C under ambient [A: $\log_{10} Y = 0.497 + 0.099X$ (±0.030, 95% C.I.)] and enriched [B: $\log_{10} Y = 0.600 + 0.074X$ (0.024)] food conditions.

Naupliar survivorship and ciliate population growth—Infected nauplii of *A. hudsonica* were found in field collections from late May to early June 1990. Initial ciliate loads on infected nauplii from 1 to 20 ciliates per nauplius. Many nauplii ranged from 1 to 20 ciliates per nauplius. Many nauplii with only one ciliate at the beginning of the experiment had as many as 40 ciliates at the end of the experiment, with some having as many as 60–100. Those nauplii with high degrees of infection were observed to have difficulty swimming against the motion of the attached ciliates. The population of peritrich ciliates increased exponentially during the course of the experiment ($P < 0.001$; Fig. 7), and the rates of increase did not differ significantly between food treatments as determined from 95% confidence intervals of the slope.

There was no significant effect of food treatment on the survivorship (d^{-1}) of infected nauplii (paired *t*-test with arcsine-transformed percentages of survivors for each day; df = 8;

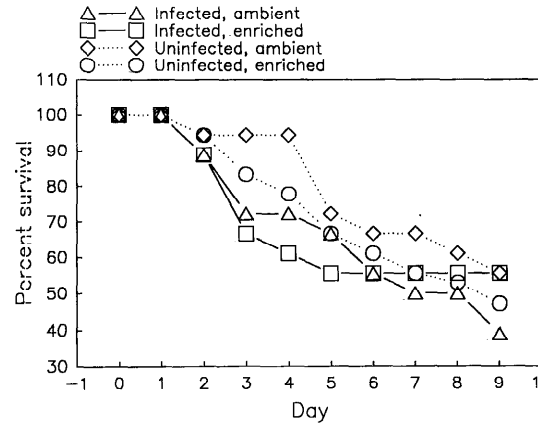

Fig. 8. Survivorship (d^{-1}) of *Acartia hudsonica* infected and uninfected nauplii reared at 15°C under ambient and enriched food conditions.

$t_s = 0.043$, $P > 0.9$; Fig. 8). Survivorship, however, was adversely affected by the attachment of peritrich ciliates ($t_s = 3.862$, $P < 0.01$; and $t_s = 2.986$, $P = 0.02$ in a comparison of pooled data on infected survivorship vs. uninfected survivorship at ambient and enriched food treatments, respectively). Although these experiments were conducted for up to 17 d (*see ciliate population growth*), <50% of the initial nauplii survived to day 9. Moreover, by this time, >25% of the nauplii had matured into copepodites, and copepodite survival in these experimental wells is less than optimal for *A. hudsonica* (D. Lonsdale pers. obs.). For these reasons, we made survivorship comparisons only through day 9 of the experiment. The poor survival of nauplii may be partially due to inadequate food resources, especially under the enriched food conditions. Unlike the positive effects of food enrichment found for female egg production, it was noted that the survival of uninfected nauplii was actually higher under ambient food conditions ($t_s = 3.581$, $P < 0.01$). Naupliar development rates (molts d^{-1}) were not affected by either infection status (presence or absence) or by food treatment (two-way ANOVA; df = 1,68; $F = 0.08$, $P > 0.778$ and $F = 0.00$, $P > 0.982$, respectively). The overall mean development rate was 0.62 molts d^{-1} (±0.05, 95% C.I.).

Adult sinking rates—A. hudsonica showed a typical rapid burst-and-sink pattern of movement (Tiselius and Jonsson 1990). Sinking was observed as passive downward movement while rapid bursts occurred in any direction. No continuous swimming behavior was observed. The mean sinking rate adjusted for cephalothorax length variation (Fig. 9) was significantly slower for infected adults (0.492 mm s^{-1} ± 0.065, 95% C.I.) compared to uninfected adults (0.804 mm s^{-1} ± 0.169) (ANCOVA, Sokal and Rohlf 1981; df = 1,40; $F = 7.891$; $0.005 < P < 0.01$). Moreover, there was a significant difference in the slopes relating sinking speed to body length (df = 1,39; $F = 7.312$; $P = 0.01$); a positive relationship was found for uninfected copepods, while no relationship was found for infected ones (Fig. 9).

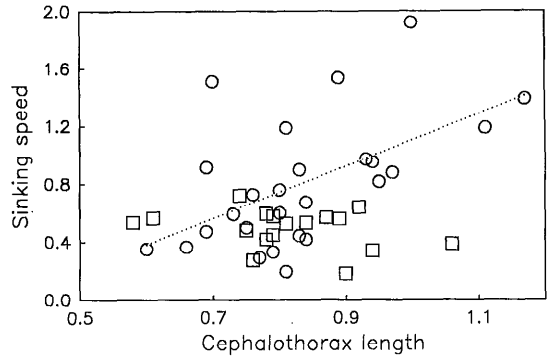

Fig. 9. Average sinking speeds (mm s^{-1}) of infected (□) and uninfected (○) *Acartia hudsonica* adults of various cephalothorax lengths (mm). Correlation was positive between sinking speed and length for uninfected copepods [$Y = -0.695 + 1.801X$ (±1.153, 95% C.I.); $0.001 < P < 0.005$]; no relationship was found for infected copepods ($P > 0.75$).

Discussion

The seasonal occurrence of *A. hudsonica* is primarily related to changes in water temperature and their interaction with salinity (Conover 1956; Jeffries 1962; Sullivan and McManus 1986). Ultimately, higher water temperatures controlled the decline of *A. hudsonica* during summer. Although maximal egg production of *A. hudsonica* occurred at 19°C, which is greater than *A. hudsonica*'s maximal reproductive rate at 15°C in Narrangansett Bay (Sullivan and McManus 1986), the eggs produced at 20°C were diapause eggs (as found by Sullivan and Ritacco 1985). Our study suggests, however, that ciliate infestation could also negatively impact the growth of *A. hudsonica* populations before water temperatures reached 20°C by reducing subitaneous egg production and naupliar and adult survival. Moreover, the recruitment of the next season's population from diapause eggs could be negatively impacted by ciliate epibiosis. We stress, however, that our study shows only a statistical negative correlation between copepod fitness and epibiont load in the field, and this fact makes it difficult to claim a true cause-and-effect. It may be that epibionts select physiologically stressed animals over healthy individuals, and thus epibionts per se may not be the ultimate reason for the poorer performance of infected copepods. But this latter possibility seems less likely based on our laboratory observations wihch showed infection on most cultured copepods when ciliate-carrying individuals were inadvertently introduced.

For *A. hudsonica* egg production, at least, attached peritrich ciliates may have an impact when the copepod is energetically stressed. Our

data suggest that food concentrations in Stony Brook Harbor are not adequate to allow heavily infected copepods to meet the additional energetic costs required to transport their burden. The impact of ciliate infection on rate of egg production, however, may be minimal in other environments where food resources are more adequate. Our findings are similar to those of Xu and Burns (1990) who found no significant effect of the colonial peritrich *Epistylis daphniae* on the reproductive efforts of the copepod *Boeckella triarticulatae* when food was more abundant. But when food levels were low, both the survivorship rates of juveniles and the reproductive rates of adults were lower for infected individuals compared to uninfected, suggesting that in a low food environment these colonial peritrichs may contribute to the population decline of the copepods.

Contrary to former hypotheses that ciliate infection pertains only to senescent copepods (Conover 1956), we found that the degree of infection was not proportional to age, stage, or body size (as suggested by Herman et al. 1971), as both *A. hudsonica* nauplii and copepodites had the same load as that of adults. Recently, extensive ciliate epibiosis on *A. tonsa* was found when it was beginning to replace *A. hudsonica* in Great South Bay, Long Island (June 1992; S. Jonasdottir pers. comm.) which also contradicts the senescence hypothesis. The attached ciliates on *A. hudsonica* (Fig. 1) adhered only to the surface of the exoskeleton as also found by Herman et al. (1971). We sometimes observed in the laboratory that ciliate bodies would break away from their attached stalks just before copepod molting. Apparently, these ciliates readily reattached to the newly molted nauplii. The sites of ciliate attachment for *A. hudsonica* occurred on all sides (ventral, lateral, and dorsal surfaces) of the cephalothorax and on the urosome, similar to that of adult *Limnocalanus macrurus* infected with *Tokophyra quadripartita* (Suctoria) in southeastern Lake Michigan (Evans et al. 1979). For heavily infected females, attachment sites of these ciliates may block the genital pore, interfering with spermatophore placement (P. Blades-Eckelbarger pers. comm.; Willey et al. 1990). This latter observation needs to be further investigated to better evaluate the demographic effects of ciliate infestation on population growth of copepods.

The copepod hosts likely experience a decrease in swimming efficiency (Evans et al. 1979). Henebry and Ridgeway (1979) observed that those copepods heavily infected with epistylids had reduced swimming efficiency and spent more time on the bottom of the container. Unlike our study, where infected copepods had a lower sinking rate (0.492 mm s^{-1}) than uninfected ones (0.804 mm s^{-1}), Herman and Mihursky (1964) found that the sinking rates of preserved *A. tonsa* from the Patuxent River were higher for infected copepods (19.2 cm s^{-1}) than for uninfected ones (13.8 cm s^{-1}). However, the rates they measured were 200–300 times higher than ours and seem too high for a 1-mm animal. Tiselius and Jonsson (1990) also measured sinking rates of 0.30 mm s^{1} for *A. clausi,* which agrees more closely to our measurements.

Herman and Mihursky (1964) suggested that an increased energetic cost to the copepod may result from the weight of the ciliates. However, ciliates acting as projections on the surface of a copepod increase the surface area per unit of copepod body mass. This increase in surface area creates a parachutelike effect with a resultant increase in drag (A. Okubo pers. comm.). For small animals like copepods (~0.50 mm long) whose body shape is streamlined, any change in shape that increases drag can hinder locomotion (Vogel 1981). This increase in surface area, which results in a greater resistance to sinking, is analogous to warm-water species of copepods having branched, featherlike appendages to aid them in maintaining their position in a less viscous environment. Similar in theory is the formation of spines or helmets in rotifers and cladocerans, leading to a reduction in sinking rates of the larger spined or helmeted morphs (Stemberger and Gilbert 1985; *but see* Stemberger 1988).

Although spines, helmets, and featherlike appendages may decrease the energetic costs involved in maintaining the animal's position in the water column, they may also slow its escape responses. *A. hudsonica* exhibits a rapid burst-and-sink pattern of swimming behavior (Tiselius and Jonsson 1990). If a rapid burst is used as a means of escape, a more highly infected individual whose ciliate projections cause an increase in drag may be selected as prey over a faster, uninfected individual. Infected *A. hudsonica* may also be size selected over uninfected copepods by visual predators. Willey et al. (1990) showed increased preda-

tion for daphnids infected with *Colacium vesiculosum* which likely reflected increased visibility and a reduction in escape efficiency. They suggest that for slow zooplankton swimmers, such as *Daphnia,* a reduction in swimming efficiency would be less than for faster swimmers, such as copepod nauplii and *Ceriodaphnia.* This reduction in swimming efficiency, coupled with an increase in apparent size due to these epibionts, may increase the host copepod's vulnerability to predation by fish and invertebrate predators (Willey et al. 1990) and put the infected copepods at a disadvantage when competing with copepods that are uninfected (Herman et al. 1971). Reduced swimming efficiency can also affect vertical migratory ability (Evans et al. 1979).

Slower sinking rates found for infected adults may explain why 100% infection for the adult population was observed in pumped samples, but not in net tows on several sampling dates. Infected adults may have been selected over uninfected adults in the pumped samples because of reduced swimming efficiency. These observations also support the hypothesis that infected copepods may be subject to greater predation.

Those nauplii with a high degree of infection would also be disadvantaged in terms of swimming behavior. Too small to fight the motion created by the ciliates, their locomotion appears to be hindered, which could in turn make them more susceptible to predation. Although not directly tested, highly infected *A. hudsonica* nauplii were observed to have difficulty swimming against the currents created by the ciliates. Rather than follow their regular swimming pattern of sudden bursts and stops, these nauplii moved in a circular pattern. Occasionally they were able to overcome the ciliates' motion and attempted their own movement but would quickly succumb once again to this circular motion. Thus, if many nauplii are unable to swim efficiently resulting in a reduction in escape capability, and if they have become more visible to predators because of ciliate epibiosis, it is possible that naupliar recruitment will be negatively affected. Moreover, the additional energy required to swim against the epibionts may explain the lower survival of infected nauplii compared to uninfected nauplii found in our laboratory experiments.

Changes in water temperature may, at times, only partially explain the timing of the decline of *A. hudsonica* in Stony Brook Harbor. Ciliate epibiosis, in part, may play a role and also influence future copepod recruitment. Infected *A. hudsonica* may be at a fitness disadvantage compared with uninfected copepods, especially when food resources are inadequate. Many unanswered questions remain regarding the ecological impact of ciliate epibionts on copepod dynamics in Long Island Sound. For example, why were *A. tonsa* copepods not infected in 1990 as had been documented in previous years (Conover 1956; Woodhead and Jacobsen 1985)? Are there species-specific interactions between ciliates and copepods? What are the mechanisms by which ciliate attachment results in lowered copepod growth and survival? More specifically, do they interfere with food gathering or result in increased metabolic costs or both? Does ciliate attachment increase a copepod's susceptibility to predators, and if so, what is the mechanism (Willey et al. 1990)? To better understand the population dynamics of the epibionts, it would be interesting to determine whether there is selection against heavy loads due to increased predation risk of the host. Our results suggest that future ecological studies of the impact of epibionts would contribute to a better understanding of the mechanisms regulating the population dynamics of estuarine zooplankton.

References

AMBLER, J. W. 1985. Seasonal factors affecting egg production and viability of eggs of *Acartia tonsa* Dana from East Lagoon, Galveston, Texas. Estuarine Coastal Shelf Sci. **20:** 743–760.

CONOVER, R. J. 1956. Oceanography of Long Island Sound, 1952–1954. 6. Biology of *Acartia clausi* and *A. tonsa.* Bull. Bingham Oceanogr. Collect. **15:** 156–233.

DURBIN, E. G., A. G. DURBIN, T. J. SMAYDA, AND P. G. VERITY. 1983. Food limitation of production by adult *Acartia tonsa* in Narragansett Bay, Rhode Island. Limnol. Oceanogr. **28:** 1199–1213.

EVANS, M. S., L. M. SICKO-GOAD, AND M. OMAIR. 1979. Seasonal occurrence of *Tokophyra quadripartita* (Suctoria) as epibionts on adult *Limnocalanus macrurus* (Copepoda: Calanoida) in southeastern Lake Michigan. Trans. Am. Microsc. Soc. **98:** 102–109.

GUILLARD, R. 1975. Culture of phytoplankton for feeding marine invertebrates, p. 29–60. *In* W. L. Smith and M. H. Chanley [eds.], Culture of marine invertebrate animals. Plenum.

HENEBRY, M. S., AND B. T. RIDGEWAY. 1979. Epizoic ciliated protozoa of planktonic copepods and cladocerans and their possible use as indicators of organic

water pollution. Trans. Am. Microsc. Soc. **98:** 495–508.

HERMAN, S. S., B. C. COULL, AND L. M. BRICKMAN. 1971. Infestation of harpacticoid copepods (Crustacea) with ciliate protozoans. J. Invert. Pathol. **17:** 141–142.

———, AND J. A. MIHURSKY. 1964. Infestation of the copepod *Acartia tonsa* with the stalked ciliate *Zoothamnium.* Science **146:** 543–544.

JEFFRIES, H. P. 1962. Succession of two *Acartia* species in an estuary. Limnol. Oceanogr. **7:** 354–364.

LANDRY, M. R. 1975. Seasonal temperature effects and predicting development rates of marine copepod eggs. Limnol. Oceanogr. **20:** 434–439.

LONSDALE, D. J., D. R. HEINLE, AND C. SIEGFRIED. 1979. Carnivorous feeding behavior of the adult calanoid copepod *Acartia tonsa* Dana. J. Exp. Mar. Biol. Ecol. **36:** 235–248.

———, AND S. H. JONASDOTTIR. 1990. Geographic variation in naupliar growth and survival in a harpacticoid copepod. Biol. Bull. **179:** 113–120.

NAGASAWA, S. 1988. The copepod *Centropages abdominalis* as a carrier of the stalked ciliate *Zoothamnium.* Hydrobiologia **167/168:** 255–258.

PARSONS, T. R., Y. MAITA, AND C. M. LALLI. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon.

SLEIGH, M. A. 1989. Protozoa and other protists. Edward Arnold.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd ed. Freeman.

STEMBERGER, R. S. 1988. Reproductive costs and hydrodynamic benefits of chemically induced defenses in *Keratella testudo.* Limnol. Oceanogr. **33:** 593–606.

———, AND J. J. GILBERT. 1985. Body size, food concentration, and population growth in planktonic rotifers. Ecology **66:** 1151–1159.

SULLIVAN, B. K., AND L. T. MCMANUS. 1986. Factors controlling seasonal succession of the copepods *A. hudsonica* and *A. tonsa* in Narragansett Bay, Rhode Island: Temperature and resting egg production. Mar. Ecol. Prog. Ser. **28:** 121–128.

———, AND P. J. RITACCO. 1985. The response of dominant copepod species to food limitation in a coastal marine ecosystem. Ergeb. Limnol. **21:** 407–418.

TISELIUS, P., AND P. R. JONSSON. 1990. Foraging behavior of six calanoid copepods: Observations and hydrodynamic analysis. Mar. Ecol. Prog. Ser. **66:** 23–33.

TURNER, J. T., M. T. POSTEK, AND S. B. COLLARD. 1979. Infestation of the estuarine copepod *Acartia tonsa* and the ciliate *Epistylis.* Trans. Am. Microsc. Soc. **98:** 136–138.

VOGEL, S. 1981. Life in moving fluids: The physical biology of flow. Princeton.

WILLEY, R. L., P. A. CANTRELL, AND S. T. THRELKELD. 1990. Epibiotic euglenoid flagellates increase the susceptibility of some zooplankton to fish predation. Limnol. Oceanogr. **35:** 954–959.

WOODHEAD, P. M. J., AND M. E. JACOBSON. 1985. Epifaunal settlement, the process of community development and succession over 2 years on an artificial reef in the New York Bight. Bull. Mar. Sci. **37:** 364–376.

XU, Z., AND C. W. BURNS. 1990. Effects of the epizoic ciliate, *Epistylis daphniae,* on growth, reproduction and mortality of *Boeckella triarticulata* (Thomson) (Copepoda: Calanoida). Hydrobiologia **209:** 183–189.

YEN, J., AND D. FIELDS. 1992. Escape responses of *Acartia hudsonica* (Copepoda) nauplii from the flow field of *Temora longicornis* (Copepoda). Ergeb. Limnol. **36:** 123–134.

Submitted: 26 June 1992
Accepted: 12 January 1993
Revised: 18 February 1993