

Inferring properties of mysid predation from injuries to *Daphnia*¹

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Abstract

Daphnia from Lake Washington occasionally have injured tail spines; laboratory observations suggest that such injuries are caused by handling by the crustacean predator *Neomysis mercedis*. A short-lived, brown "scar" that forms shortly after the tail spine is amputated provides the basis for a simple model for interpreting injury data. When combined with laboratory estimates of the duration of tail spine "scars," the model is used to infer some properties of mysid predation: the dependence of ingestion efficiency on prey size, vertical variation in predation intensity, and the absolute in situ feeding rate of *Neomysis* are estimated from injury frequencies in the plankton.

Since predators are not successful in every encounter with their prey, injured animals are often found in prey populations. The frequencies of injuries contain information about the process of predation; injury rates are related to the efficiency as well as the intensity of predation. Building on the attempts of terrestrial ecologists to interpret injury data (i.e. tail-breaks in lizards), Schoener (1979) modeled the accumulation of injuries in age-structured populations and gave methods for inferring properties of predation from injury frequencies.

Kerfoot (1975) observed a high incidence of mutilated or regenerated antennules among Lake Washington *Bosmina*, apparently reflecting heavy copepod predation and frequent escape by the prey. In subsequent work (Kerfoot 1977; Kerfoot and Peterson 1979), he used laboratory observations of predator-prey interactions to predict injury frequencies in the lake. Here I work in the other direction, attempting, like Schoener (1979), to infer properties of predation from injury data. A simple model exploiting the transience of one manifestation of injuries to *Daphnia* is used to interpret the frequencies of wounds inflicted by *Neomysis mercedis*. Three examples illustrate the

use of the model in making inferences about the quantity and quality of mysid predation in Lake Washington.

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Methods

I chose to analyze data from collections made on 13-14 September 1979 because of a high proportion of injured *Daphnia* in the plankton and because both mysids and zooplankton were extensively sampled on three trips—at dusk, midnight, and dawn. Collections were made at a 20-m deep station on the west side of the Madison Park trench in Lake Washington. Mysids were sampled, both on and off the lake bottom, with a small epibenthic dredge (520-cm² mouth area, 900- μ m mesh), and zooplankton were collected with a 12.5-cm-diameter Clarke-Bumpus sampler with a 73- μ m-mesh net. Both mysids and zooplankton were preserved immediately in 10% Formalin. About 92% of the *Daphnia* collected were *D. pulicaria*; the rest were *D. thorata*. All of the *Daphnia* were scored for tail-spine injuries, and most were measured (top of head to base of tail spine).

The lake was weakly stratified at the time, with the steepest part of the thermocline between 13 and 14 m. Average temperatures for the three strata consid-

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ered here were calculated from bathythermograph data supplied by W. T. Edmondson: 0–5 m, 19.4°C; 5–10 m, 19.2°C; and 10–20 m, 13.7°C.

The size composition of the diet was determined for a sample of *Neomysis* collected 3–5 m off the lake bottom at midnight. Mysid stomachs and intestines were dissected out and teased apart in drops of glycerine, and permanent mounts of the gut contents were examined under 100×. Widths of the molar surfaces of *Daphnia* mandibles and lengths of post-abdominal claws were measured at 430× with an ocular micrometer, and the sizes of prey consumed were calculated from least-squares regressions of body length against mandible and claw dimensions ($r > 0.96$). *Neomysis* size is expressed as total body length, from the apex of the rostrum to the apices of the telson.

I ran feeding trials, to determine the ability of predatory copepods to injure *Daphnia*, with adult *Cyclops bicuspidatus* ($n = 4$; mean length, head to end of caudal rami, 0.90 mm; range 0.84–0.94 mm), C5 and C6 *Epischura nevadensis* ($n = 7$, mean length 1.96 mm, range 1.59–2.25 mm), and the smallest *D. pulicaria* available in a several-month-old Lake Washington culture (9 trials) or in fresh plankton collections from the lake (2 trials). The *Daphnia* ranged between 0.74 and 1.23 mm (mean length 1.02 mm). In each trial a single copepod was placed in a 15-ml vial of filtered lake water with five *Daphnia*. Vials were kept at 20°C in dim light for 5–18 h; there was no mortality in control vials containing *Daphnia* without copepods. Each *Daphnia* was examined for injuries at the end of the trials, and both predator and prey were preserved and measured.

Daphnia pulicaria individuals from the Lake Washington culture were anesthetized with a 0.1% chloroform-1.0% ethanol solution for several minutes while I injured or amputated tail spines using watchmaker's forceps under a dissecting scope. Removed to freshwater, the animals recovered completely after a few minutes; none of the anesthetized *Daphnia* failed to survive its operation.

Animals were kept in 15-ml vials of filtered lake water at 16°C and fed several drops from a suspension of yeast twice daily. I checked on the status of the injuries two or three times a day and noted the presence of exuviae. Some individuals were followed through as many as six instars; the time of a molt was estimated as the midpoint between the two observations spanning the event.

The injuries

The tail spines of *Daphnia* from Lake Washington are occasionally damaged or missing completely. Sometimes a dark brown "scar" marks the site of the wound (Fig. 1). The brown material, which may be clotted blood in which the tyrosine has been oxidized, is shed at the first or second molt following the injury (Anderson 1935), so the scar is actually short-lived. As Anderson (1935) pointed out, no part of the carapace need be removed to produce this phenomenon; animals with pinched but unbroken tail spines develop the brown coloration and cast off the part of the spine distal to the wound as well as the scar itself at a subsequent molt. At least some of the missing spine is eventually regenerated, but the tail spines of my laboratory-wounded animals were still abnormally short and blunt after four or five molts. The short duration of the scar, relative to the time required for the spine to regain a normal appearance, is the reason I confine my attention to scar-bearing injuries in the analyses that follow.

The tail-spine injuries of *Daphnia* from the lake are similar to those that sometimes result from encounters with *Neomysis*. In the laboratory I have observed mysids handling large (>3.0 mm) *Daphnia*, rotating the prey under the mouthparts before abandoning the apparently unmanageable items. *Daphnia* removed from the bottom of the feeding chamber were missing swimming antennae and tail spines.

Predatory copepods are another possible source of *Daphnia* injuries. Some information reported by Kerfoot (1977) makes it seem unlikely that the two im-



Fig. 1. Photomicrograph of injured *Daphnia pulicaria* (2.5–3.0 mm long) from Lake Washington. Included are scarred and unscarred animals lacking tail spines and one specimen (center) with a scarred but otherwise intact spine.

portant copepod predators in Lake Washington have much of an influence on *Daphnia*: *C. bicuspidatus* rarely attacks *Bosmina* larger than 0.5 mm, and *E. nevadensis* did not feed significantly on *Daphnia* in the laboratory. My attempts to feed small *Daphnia* to *Cyclops* and *Epischura* were completely unsuccessful; all 55 of the *Daphnia* that were confined in vials with the copepods were recovered alive and uninjured. Remains of *Daphnia* are sometimes found in *Epischura* fecal pellets from Lake Washington, however (A. H. Litt pers. comm.), so *Epischura* may occasionally injure very small *Daphnia*. Since only about 2% of the 13–14 September *D. pulicaria* were smaller than the smallest prey used in the copepod trials (0.74 mm), I conclude that *Neomysis* is responsible for virtually all of the injuries to *Daphnia* in the lake.

In interpreting frequencies of injuries in the lake, we must know the recovery period for that kind of injury. The brown scar that forms a few hours after an injury

is inflicted is shed at the next molt if the wound is made before three-fourths of the instar has passed, or at the second molt following the injury if the wound comes in the last quarter of the instar (Anderson 1933). If injuries are distributed randomly in time, the average or expected duration of a scar is $(3/4)(5/8) + (1/4)(9/8) = 3/4$ times the duration of the instar. Figure 2 shows instar and scar durations for *D. pulicaria* reared in the laboratory at 16°C. It is well known that instar duration increases with age for *Daphnia* (e.g. Ingle et al. 1937); my data show a significant positive correlation between instar duration and body size, and therefore presumably age (Spearman rank-correlation coefficient $r_s = 0.91$, one-tailed $P < 0.001$). The correlation between scar duration and body size is much weaker and is not quite significant ($r_s = 0.39$, one-tailed $P > 0.05$). The large uncertainty in individual measurements (vertical lines in Fig. 2b) and the broad range of scar durations possible for

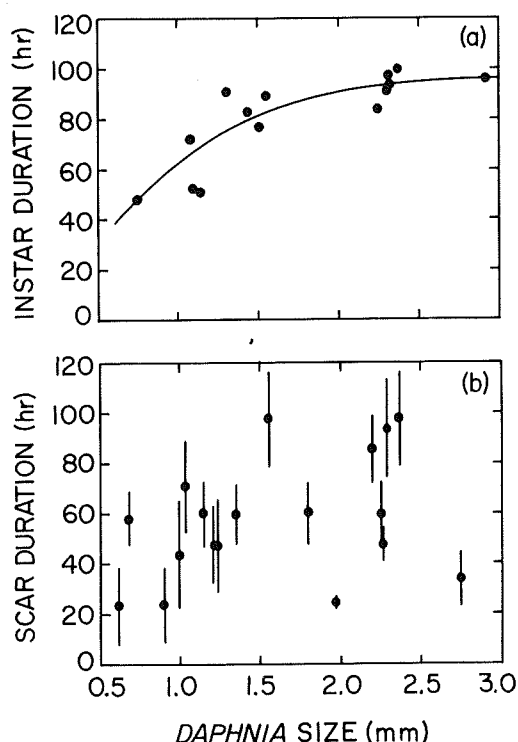


Fig. 2. Instar and scar duration as a function of body size for laboratory-reared *Daphnia pulicaria* at 16°C. a—Each point represents average instar duration for a single animal followed through one to several instars, plotted against average body size during that period. Curve is fitted visually. b—Estimated scar duration for individual *Daphnia* wounded in the laboratory. Vertical lines represent uncertainty in measurements due to time intervals between inspections of the animals.

large *Daphnia*, depending on the time of injury, are probably responsible for weakening the relationship. Nevertheless, the ratios of scar duration to instar duration calculated for individual *Daphnia* are consistent with Anderson's (1933) generalization: the average value of 0.84 is not too far from the predicted 0.75, and the observed range of ratios, 0.35 to 1.21, is within the predicted range of 0.25 to 1.25.

The model

The ephemeral nature of the brown scar that forms after a *Daphnia* tail spine is damaged proves useful in inferring properties of predation from injury fre-

quencies. The presence of a scar indicates a recent nonlethal encounter between predator and prey, and the accumulation of injuries with age, considered in the models of Schoener (1979), is not a complicating factor in interpreting injury data.

As did Schoener, I assume that all of the encounters between predator and prey result in either death of the prey (a fraction f of the time) or injury to the tail spine with survival of the prey (fraction $1 - f$). (Certainly, some encounters result in neither death nor injury. The consequences of violating this assumption are considered below.) Gerritsen and Strickler (1977) provided an expression for the rate of encounter between predator and prey in a three-dimensional environment: the number of encounters per volume per time is kPD , where P is the predator, D the prey density (organisms per volume), and k is a constant incorporating the encounter radius of the predator and the swimming speeds of predator and prey (volume per predator per time). A fraction $(1 - f)$ of these encounters results in injuries, and, if the encounters are randomly distributed in time, the density of injured animals at any one moment, N (injuries per volume), represents an accumulation over a period equivalent to the injury recovery period, T . The model, which depends on the assumptions that the duration of the injury is short relative to the lifetime of the organism and that individual prey are not attacked repeatedly during a recovery period, can then be written

$$\frac{N}{T} = kPD(1 - f). \quad (1)$$

Following are three examples of the use of this model to obtain information about mysid predation from injury frequencies in Lake Washington on 13–14 September 1979. For some purposes I pool data from all collections (three depth strata sampled at dusk, midnight, and dawn); the proportion of *Daphnia* bearing injuries is not significantly dependent on stratum ($\chi^2 = 3.37$, $df = 2$; $P > 0.10$) or sampling time ($\chi^2 = 2.09$,

df = 2; $P > 0.30$). In other cases (example 2) I partition the injury data by depth to ensure that vertical variation in the size composition of the *Daphnia* population does not confound the results. The size and abundance data reveal no evidence of vertical migration by *Daphnia* during the night.

Example 1: Size-related differences in prey vulnerability

Figure 3 shows size-frequency distributions of *Daphnia* from the 13–14 September collections. Injured animals tend to be larger than uninjured animals (Wilcoxon rank-sum test comparing scarred to unscarred *Daphnia*, two-tailed $P < 0.001$), suggesting that mysid predation is less efficient on larger prey. Animals with tail-spine damage but no scars are significantly larger than scarred animals (Wilcoxon rank-sum, two-tailed $P < 0.001$); this could be a result of the accumulation of persistent injuries in older animals. Finally, there is a difference between the distributions of scarred animals and those found in mysid stomachs (Kolmogorov-Smirnov two-sample test, $P < 0.005$). The mysid guts, from animals between 11.9 and 12.7 mm long, are not a random sample but do represent the modal size class of the September mysid population. The disparity between the distributions of injured and eaten *Daphnia* suggests that the probability of ingestion following encounter varies with prey size.

The comparisons above are a first indication that vulnerability depends on prey size, but a more careful quantitative analysis is needed. I assume below that prey size does not affect k , the constant based on predator and prey swimming speeds and encounter radius. I will consider the plausibility of this assumption in detail below.

Scar duration for a *Daphnia* size class can be estimated by multiplying average instar durations read from Fig. 2 by 0.75. Since instar duration is affected by temperature (MacArthur and Baillie 1929) and food availability (Ingle et al. 1937; Weglenska 1971), the accuracy of these

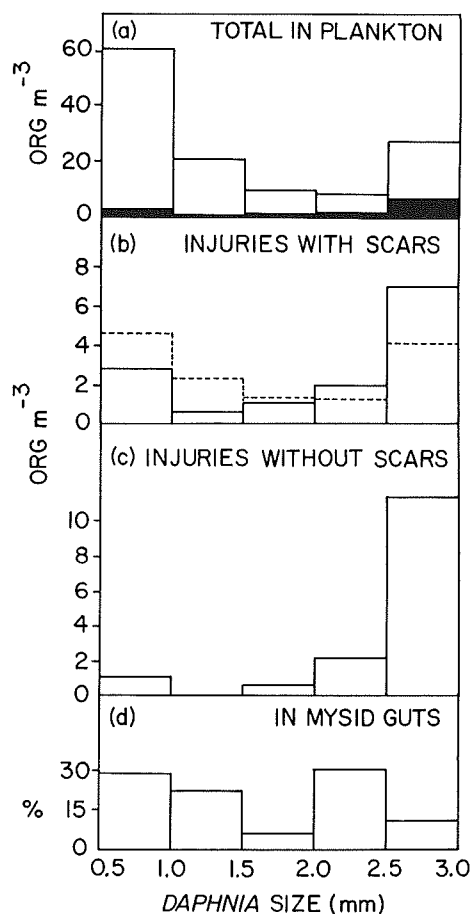


Fig. 3. Size-frequency distributions of *Daphnia pulicaria* from 13–14 September 1979. The histograms in a–c represent pooling of data from different depths and sampling times, expressed as whole-water-column average densities. a—Total *Daphnia* in the plankton ($n = 451$). Darkened area represents animals with tail-spine scars, shown on a larger scale below. b—*Daphnia* with injured tail spines and brown scars ($n = 62$). Dashed line represents distribution of scars expected if injuries were inflicted randomly with respect to size (see text). c—*Daphnia* with amputated or mutilated tail spines but no scars ($n = 70$). d—*Daphnia* ($n = 25$) in stomachs and intestines of 15 midnight-collected *Neomysis* between 11.9 and 12.7 mm long.

estimates depends on the similarity between laboratory and natural conditions. The average temperature for the 20-m water column, weighted according to the vertical profile of *Daphnia* abundance, was 18.5°C on 13–14 September (see methods and Table 2), so data from the

16°C trials would tend to overestimate the instar duration in the lake. On the other hand, the laboratory *Daphnia* had larger broods and presumably therefore had had more food available than the lake-caught animals; this difference in food would decrease the laboratory instar duration relative to that in the lake. Since the magnitudes of these opposing effects are unknown, the accuracy of the laboratory estimates of scar duration is also uncertain. If the relative values for different-size *Daphnia* are similar under varying temperature and food conditions, then the calculations of relative vulnerability below will be accurate.

Because instar duration increases with *Daphnia* size (Fig. 2), older instars would show more wounds even if injuries were inflicted indiscriminately. To verify that a difference in scar duration is not solely responsible for the bias toward large injured *Daphnia*, I calculated the distribution of scarred animals under random expectation, with injury density proportional to abundance and scar duration in a size class (dashed line in Fig. 3b). The observed distribution is significantly different from the expected ($\chi^2 = 19.83$, $df = 4$; $P < 0.001$), suggesting that differences in the efficiency of predation must be invoked to explain the injury data.

With subscripts used to designate size classes, Eq. 1 can be rewritten

$$\frac{N_i}{T_i D_i} = kP(1 - f_i). \quad (2)$$

The proportion of *Daphnia* injured per day, $N_i/(T_i D_i)$, is directly related to the inefficiency of predation ($1 - f_i$). Table 1 shows the calculation of size-specific injury rates from the Fig. 3 data. Except for the smallest size class, injury rate is an increasing function of prey size: the larger the *Daphnia*, the more likely it is to be injured rather than killed in an encounter with *Neomysis*. This finding is consistent with the "avoidance" of very large *Daphnia* demonstrated in laboratory and field investigations of mysid size selection (Murtaugh 1981b).

The high rate of injury and low rate of consumption of the large *Daphnia* seem

Table 1. Calculation of injury rates for different size classes of *Daphnia*. Whole-water-column estimates of total (D_i) and injured (N_i) prey densities ($\text{org} \cdot \text{liter}^{-1}$) (Fig. 3) are used.

Size class (mm)	D_i	N_i	T_i Avg scar duration (days)*	$N_i/(T_i D_i)$
0.5-1.0	0.061	0.0029	1.57	0.030
1.0-1.5	0.021	0.0007	2.25	0.015
1.5-2.0	0.010	0.0011	2.70	0.041
2.0-2.5	0.009	0.0020	2.92	0.076
2.5-3.0	0.028	0.0070	2.99	0.084

* 0.75 times average instar duration from Fig. 2.

to imply that difficulty in prey handling reduces the mysids' success in ingesting these large animals, but this conclusion depends on the plausibility of the assumption that encounter rates are constant across prey size. Laboratory observations of *Neomysis* and the similarity of feeding rates in the light and dark (unpubl.) suggest that the mysids are tactile predators, perceiving prey by mechanoreception. The magnitude of the hydrodynamic disturbance generated by a swimming zooplankter depends on the animal's size and speed (Strickler and Twombly 1975), so encounter rate with a predator must also be influenced by prey size. If the effect of size is small enough, however, the conclusion above that size-related differences in vulnerability following encounter explain the preponderance of injuries among large *Daphnia* may still be valid.

In terms of the three-dimensional model developed by Gerritsen and Strickler (1977), my encounter-rate constant can be expressed as

$$k = \frac{\pi R^2}{3} \left(\frac{\bar{u}^2 + 3v^2}{v} \right), \quad (3)$$

where R is the encounter radius of the predator, \bar{u} is the mean swimming speed of the prey, and v is the speed of the predator. Note that my encounter-rate k is not the same as the clearance-rate k often used in studies of aquatic predators (e.g. Cooper and Goldman 1980); in fact, in the context of Eq. 1, $k(\text{clearance}) = k(\text{encounter}) \cdot f$.

One way that size enters into Eq. 3 is

through the prey swimming speed, \bar{u} . Pastorok (1978) reported that swimming speed increases linearly with *Daphnia* size. If speed is assumed to be directly proportional to size, then Pastorok's (1980) finding of an average speed of $1.93 \text{ mm} \cdot \text{s}^{-1}$ for 1.5-mm *D. pulicaria* (mean of seven determinations in his table 2) allows the calculation of swimming speeds for the two extreme size classes considered in my study: $0.97 \text{ mm} \cdot \text{s}^{-1}$ for 0.75-mm *Daphnia* and $3.54 \text{ mm} \cdot \text{s}^{-1}$ for 2.75-mm *Daphnia*. Incidentally, this simple model predicts swimming speeds that are close to those reported by Li and Li (1979) for two size classes of *Daphnia pulex*. If the predator's swimming speed v is taken to be $55 \text{ mm} \cdot \text{s}^{-1}$ (the "usual cruising speed" for 4–7-mm *Metamysidopsis* adults; Clutter 1969), and if the encounter radius R is independent of prey size, the ratio of the values of the encounter-rate constant k for the largest and smallest *Daphnia* size classes can be calculated from Eq. 3. There is a 0.13% difference between the two constants, so the effect of size-dependent prey swimming speed on the encounter rate is negligible.

The other way that size might enter into Eq. 3 is through the encounter radius R , the distance at which prey are perceived. In his application of the Gerritsen and Strickler model to prey encounter by *Chaoborus* larvae, Pastorok (1978) set $R = r_p + r_h$, where r_p is the radius of the predator's perceptual field and r_h is the radius of the prey. If r_p is estimated for *Neomysis* as the average lateral extension of the antennae (measured along a line perpendicular to the main body axis for 13 preserved mysids close to the median size, 11.9 mm, of the 13–14 September population; mean radius 8.2 mm) and r_h is taken as half the length of the prey (u and v as in the preceding paragraph), then Eq. 3 predicts that k for 2.75-mm *Daphnia* will be 25% larger than k for 0.75-mm prey. This difference is not nearly enough to explain the 2.8-fold difference in injury rates observed for the two extreme size classes (last column of Table 1).

Other models of the effect of prey size on encounter radius might give quite different results. If R were directly proportional to prey length, for example ($R = c \cdot r_h$), there would be a roughly 13-fold difference between the encounter-rate constants for large and small *Daphnia*. For a predator whose sensory apparatus covers an area that is large compared to the size of its prey, however, it seems reasonable to assume that there is some moderate distance within which all prey are perceived with constant probability and that some form of Pastorok's (1978) model would therefore apply. The sensitivity of the encounter-rate calculations to the exact form of the relationship between prey size and encounter radius argues for the development of testable models of prey detection by invertebrates dependent on mechano-reception, analogous to those that have been constructed for visual predators (e.g. O'Brien et al. 1976).

Gerritsen and Strickler (1977) pointed out that pressure and shear disturbances created in the water around a moving predator may combine to reduce the sensitivity of the animal's receptors, and they speculated that, for a predator swimming fast enough, the encounter radius might shrink to some minimum corresponding to direct contact between predator and prey. This influence of predator swimming speed adds another layer of complexity to the analysis, and it provides another reason that the effect of prey size on encounter rate might be small compared to the effect of size on ingestion efficiency, which I originally proposed as the explanation for the preponderance of injuries among large *Daphnia* (Table 1).

Example 2: Vertical variation in predation intensity

It might be suspected that the results on size-dependent vulnerability, based on whole-water-column average densities, are artifacts of ignoring the spatial structure of the *Daphnia* population; depth-related variations in prey size distributions, and in the temperatures and

Table 2. Calculation of injury frequencies for three size classes of *Daphnia* in three depth strata. Total (D_i) and injured (N_i) prey densities in org·liter⁻¹.

Size class (mm)	0-5 m			5-10 m			10-20 m		
	D_i	N_i	N_i/D_i	D_i	N_i	N_i/D_i	D_i	N_i	N_i/D_i
0.5-1.0	0.114	0.0065	0.057	0.080	0.0028	0.035	0.023	0.0007	0.030
1.0-2.0	0.032	0.0014	0.044	0.041	0.0038	0.093	0.026	0.0013	0.050
2.0-3.0	0.084	0.0201	0.239	0.031	0.0094	0.303	0.017	0.0020	0.118
All sizes combined	0.230	0.0280	0.122	0.152	0.0160	0.105	0.066	0.0040	0.061

predator densities encountered by the prey, could conceivably interact to produce misleading results. I noted earlier that the overall frequency of injuries was not significantly dependent on depth, but it is still of interest to examine size-specific injury rates by depth and relate them to the vertical profile of predator abundance.

Table 2 shows injury frequencies calculated for different sizes of *Daphnia* in the three strata that were sampled. Within each layer, injuries per organism (N_i/D_i) are highest for the largest *Daphnia*, in agreement with the whole-water-column calculations above. The pattern of injury densities within a size class is somewhat variable, though the combined figures for all *Daphnia* show a decrease in predation intensity with increasing depth. Equation 1 states that the predator density P is proportional to the injury frequency N/D . The vertical distribution of mysids should then be in proportion to the vertical profile of injury frequencies in the last line of Table 2. (In fact, the higher temperature and shorter scar duration in the upper waters mean that a given injury frequency there indicates relatively more encounters with the predator than the same frequency in deeper water.) The density profile of *Neomysis* estimated from midnight sampling is quite different from this prediction: 6.11 mysids·m⁻³ in the 10-20-m layer, 0.21 in the 5-10-m layer, and none between 0 and 5 m. How can the high frequency of injuries in the upper waters be reconciled with the relative scarcity of predators there?

It seems unlikely that vertical redistribution of injured *Daphnia* could explain the anomaly; no vertical movement was

detected in the dusk-to-dawn sampling. The potential predator *Epischura* was fairly common in the top 10 m but could hardly be responsible for the injuries to large *Daphnia*. Apparently, the midnight assessment of mysid abundance does not reflect actual feeding intensity. Either I missed the full extent of the vertical migration, or, as suggested earlier (Murtaugh 1981a), the strong-swimming mysids may be taking short feeding excursions into the upper waters, returning to depth when satiated. The problems of interpreting the vertical distribution of such a migrator are mentioned by Pearre (1979).

Example 3: In situ feeding rate

If the constant k in Eq. 1 could be estimated, injury data could be used to calculate rates of encounter between predator and prey in the lake. Assume that for the largest *Daphnia*, 2.5-3.0 mm, the efficiency of predation is about zero, i.e. all *Daphnia* encountered are injured but not killed. (In fact, the gut-content data in Fig. 3d show that some of the large *Daphnia* are successfully consumed; the consequences of violating the assumption are considered later.) Then, setting $f_{2.5-3.0} = 0$, substituting a whole-water-column estimate of $P = 3.11$ mysids·m⁻³, and obtaining the values of the other parameters for the 2.5-3.0-mm size class from Table 1, I calculate $k = N/(TPD) = 0.027$ m³ per mysid per day.

This value of the encounter-rate constant, which is meaningful only for the size-distribution of *Neomysis* present on 13-14 September, can now be used to translate size-specific injury rates into in situ predation rates. Retaining the assumption that k is the same for all size

Table 3. Calculation of ingestion (*Daphnia* eaten per day) and clearance (liters \cdot d⁻¹) rates from injury data with $k = 0.027$ m³ per mysid per day and size-specific prey densities (D_i) obtained from Table 1.

Size class (mm)	f_i	$kD_i f_i$	kf_i
0.5–1.0	0.64	1.05	17.3
1.0–1.5	0.82	0.46	22.1
1.5–2.0	0.51	0.14	13.8
2.0–2.5	0.09	0.02	2.4
2.5–3.0	0	0	0
All sizes combined	0.48*	1.67	13.0*

* Weighted average.

classes, I calculate predation efficiencies (f_i), ingestion rates ($kD_i f_i$), and clearance rates (kf_i) (Table 3). Because *Daphnia* was very sparse in the plankton, the predicted total daily ration per mysid is only about 1.7 *Daphnia*. This is close to the average of 1.9 *Daphnia* per gut found in the midnight-collected *Neomysis*, but both the gut residence time and, therefore, the period of feeding represented by the gut contents, are unknown.

The model predicts an overall clearance rate of 13.0 liters per mysid per day (Table 3). While this is higher than rates usually observed in small experimental chambers (Murtaugh 1981a), it is within the range of values recorded for *Neomysis* in larger aquaria (unpubl.). The similar but slightly larger *Mysis relicta* may equal or exceed this feeding rate; clearance rates on *Daphnia* as high as 11.38 (Cooper and Goldman 1980) and 27.35 (Grossnickle 1978) liters per mysid per day have been reported from laboratory experiments.

The relative rates of ingestion of the different prey size classes calculated in Table 3 are fairly different from the observed rations (Fig. 3d). Obviously, part of the reason is the incorrectness of the assumption, used in the calculation of k , that predation on the largest *Daphnia* is 100% inefficient. Note also that the gut-content data may not be completely representative of the September mysid population; juvenile mysids, which prefer smaller prey than adults (Murtaugh 1981b), were fairly common in the lake

but not included in the diet analyses. Finally, the assumption of the constancy of k over all prey size classes may be inaccurate, as discussed earlier.

This calculation of feeding rate is the most tenuous of the three applications of the injury model, not only because it relies on estimates of scar duration of unknown accuracy, but also because it is sensitive to some of the simplifying assumptions of the model. In particular, the model assumes that all encountered prey are attacked and that all attacks result in either death or injury of the prey. Surely not all perceived prey are attacked, especially if the predator is satiated or finds itself in an area of high food density. More important, many attacks must result in the escape of the prey unharmed; my laboratory observations of foraging mysids suggest that lunges at prey are often unsuccessful. Kerfoot (1977) reported that the frequency of attacks by *Cyclops* on *Bosmina* depends on prey size and that the success of these attacks is very low. Compared to *Cyclops*, *Neomysis* is relatively much larger than its prey, so attack success is likely to be higher. Yet the assumption that all encounters result in death or injury is unrealistic, implying that my estimates of encounter rate from injury frequencies are conservative.

Another way of estimating the encounter-rate constant is to substitute independently derived estimates of swimming speeds and encounter radius into the formula provided by Gerritsen and Strickler (1977); this is the approach taken by Kerfoot and Petersen (1979) in predicting rates of encounter between *Bosmina* and its copepod predators in Lake Washington. Preliminary estimates of encounter radius and predator and prey swimming speeds (Table 4) allow the prediction of the encounter-rate constant for *Neomysis* and *Daphnia* from Eq. 3. If the figures are adjusted to an 8-h foraging period, corresponding roughly to the mysids' nighttime excursion into the upper waters, Eq. 3 predicts $k = 0.335$ m³ per mysid per day, with a range of possible values between 0.046 and 1.780. Even the lower limit of this range is almost

Table 4. Values of encounter radius and swimming speeds used in calculation of encounter-rate constant from Eq. 3.

Quantity	Value (range)	Source
Encounter radius, R	8.2 mm (4.1–12.3)	Mean lateral extension of antennae of 11.9-mm <i>Neomysis</i> , $\pm 50\%$
Mean prey swimming speed, \bar{u}	1.93 mm·s ⁻¹ (1.29–3.40)	Mean and range of seven determinations for 1.5-mm <i>Daphnia pulicaria</i> (Pastorok 1980)
Predator swimming speed, v	55 mm·s ⁻¹ (30–130)	Cruising speeds for 4–7-mm <i>Metamysidopsis</i> (Clutter 1969)

twice as large as the value derived from the injury data (0.027), suggesting that the model seriously underestimates the encounter rate.

The observed injuries, then, probably represent more encounters than originally predicted by the model, but what is the accuracy of the feeding-rate estimates? The model can be modified to incorporate attack frequency and success explicitly in an effort to answer this question. Let g be the fraction of encounters resulting in attack, f' the fraction of attacks resulting in death (note that $f' = fg$), and h the fraction of attacks resulting in no harm to the prey; the rest of the symbols are as in Eq. 1, which can now be rewritten

$$\frac{N}{T} = kPDg(1 - f' - h). \quad (4)$$

Before, I assumed that $g = 1$ and $h = 0$; it is more likely that $g < 1$ and $h > 0$. Algebra shows that the encounter-rate constant k was therefore underestimated. Furthermore, the ingestion rate and clearance rate, which are now given by $kDgf'$ and kgf' , were underestimated by the same factor. The questionable assumptions of the earlier version of the model led to conservative estimates of feeding rates as well as encounter rates.

Conclusions

Each application of the injury model is beset with uncertainties—about the effect of body size on encounter rate, the extent of copepod-induced injuries, the accuracy of the estimates of scar duration—yet each example provides new information that is consistent with existing

knowledge. The low efficiency of predation on the largest *Daphnia* provides an explanation for their underrepresentation in the *Neomysis* diet (Murtaugh 1981b); the lack of concordance between the vertical distributions of injuries and of mysids suggests that feeding intensity is not necessarily reflected by mysid abundance in a stratum; and the overall frequency of injuries implies a feeding rate that is not wildly different from rates measured in the laboratory. That such a simple model extracts apparently useful information from injury data is encouraging.

The approach taken here, of inferring properties of predation from injury frequencies, is exactly the opposite of that taken by Kerfoot and Peterson (1979), who used carefully gathered information on swimming speeds and encounter radii to predict encounter and injury rates in the lake. Both approaches are of course necessary; the utility of the injury model, in fact, could be improved with better information on the mechanics of mysid predation. It is important to know, furthermore, whether the details of predator-prey interactions that are observed in the laboratory are the same as those in the dilute concentrations and patchy distributions found in lakes. *Daphnia* tail-spine injuries provide a rare, if indirect, glimpse at predation working in nature.

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