Predatory Feeding in Three Co-occurring Mysids (Crustacea, Mysidacea): Functional Responses to Different Prey Types

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Abstract

The functional responses of three co-existing nearshore mysid shrimps were analyzed using two branchiopodan and one copepodan prey types. ***Paramesopodopsis rufa*** *was the most efficient predator of the euryhaline daphniid prey,* ***Daphniopsis australis****. It showed a steeper linear functional response curve for this prey than the other two species,* ***Tenagomysis tasmaniae*** *and* ***Anisomysis mixta australis****, which showed similar flat linear curves. All three species exhibited similar predation success on* ***Artemia*** *sp. nauplii, and similar predation failure for the calanoid copepod* ***Gladioferens pectinatus****. The study provides evidence that differences in predatory feeding behaviour support feeding niche segregation which in turn explains the co-occurrence of the three mysid species.*

Introduction

Predatory feeding behaviour in many zooplanktonic species of both freshwater and marine habitats is a complex system which requires a more detailed study to elucidate its intricacies (Kerfoot, 1980; Price, 1988; Ohman, 1988; Gliwicz & Pijanowska, 1989). These reviews noted that success of predatory species, as those equivalent systems in the terrestrial environment, is influenced by several factors. There seems to be an optimum prey size in which a predator of a certain size may be efficient. However, other factors such as body pigmentation, shape, palatability, motion and escape manoeuvres have been also known to determine vulnerability of prey to various zooplanktonic predators (Ohman, 1988; Gliwicz & Pijanowska, 1989).

Predatory feeding of both freshwater and marine species of mysids include a variety of animal prey types (Mauchline, 1980; Morgan, 1982). The well studied freshwater species, *Mysis relicta* has been known to feed mainly on cladocerans, daphniids primarily (Lasenby *et al.* 1986); although it can

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also prey upon diaptomid calanoid copepods (Cooper & Goldman, 1980). Other freshwater species, e.g. *Neomysis mercedis* (Murtaugh a,b 1981), *N. intermedia* (Hanazato, 1990), N. integer (Bremer and Vijverberg, 1982), and *Mysis mixta* (Hansson et al, 1990) also prefer daphniid prey. Species that are found in the estuarine and/or marine habitats, on the other hand, have been reported to consume benthic harpacticoid copepods (*N. integer*, Mauchline, 1971), and calanoid copepods (*N. integer*, Siegfried and Kopache, 1980; *N. americana*, *Mysidopsis bigelowi*, Fulton, 1982; *M. gibbosa*, *M. didelphys*, *M. angusta*, Mauchline 1970). Artemia sp. nauplii have also been used as food to various mysid species, e.g. *Metamysidopsis elongata*, Clutter and Theilacker, 1971; *Mysidopsis almyra*, Reitsema and Neff, 1980; *Anisomysis* sp., Mullin and Roman 1986).

These zooplanktonic prey species vary in escape behaviour, size, pigmentation, swimming behaviour and other behavioural characteristics, and hence, their vulnerability to mysid predation. Different mysid species vary in size and overall predatory feeding behaviour which are also highly likely to influence rates of predation on the various prey types. The present study examines the effect of various prey types, sizes and behavioural repertoires (swimming behaviour and escape response) on the functional responses of the three coexisting mysids species, *Paramesopodopsis rufa* Fenton, *Tenagomysis tasmaniae* Fenton, and *Anisomysis mixta australis* Zimmer, in neritic waters off Tasmania.

Materials and Methods

Experimental Animals

Field collection and maintenance in the laboratory of mysids and the daphniid prey, *Daphniopsis australis*, are described in detail by Metillo and Ritz (1993).

Mature cysts of *Artemia* sp. (Artemia Revolution, New Technology, Kent, England) were hatched in the laboratory at 24°C water temperature and 40 °/oo salinity. Two day old metanauplii were used in the predation experiments.

Adult *Gladioferens pectinatus* were collected from six locations in the Derwent Estuary at a depth of either 1 m or 20 m using a 300 m mesh conical net. In the laboratory, these animals were kept in 50-litre plastic tubs containing seawater from the sampling area. At the time of collection, a large bloom of *Coscinodiscus wailesii* occurred. Buckets of these diatoms were collected and placed into the copepod tubs to serve as food. During the entire period of the experiment, the tubs with food and copepods were gently aerated, and kept at ambient temperature (15 °C), and at constant ambient salinity of 34 °/oo.

All feeding experiments were performed simultaneously with each of the three mysid species held separately. The predation chamber was made of a 2- litre glass jar, wrapped entirely with black electrical tape to block any light, and filled to the brim with 5 um Millipore-filtered seawater. This chamber was covered with a tightly fitting black lid, placed onto a plankton "roller" and allowed to rotate at 0.83 + 0.02 SD rpm. The design of the chamber ensured the absence of refuges such as the surface film and prevented prey congregating due to uneven light distribution. The prey were individually pipetted into the chamber to give densities of 5, 10, 15, 20 litre^{-1} for *D. australis* and *G. pectinatus*. Treatment densities of *Artemia* metanauplii were 7.5, 15, 30, and 45 litre^{-1}. All of these prey densities were replicated four times. Feeding time which lasted for 2 hours started when four unstarved adult mysids was introduced into the chamber. At the end of the predation period, the contents of the chamber were emptied into plastic buckets. Predator and prey were removed and killed by placing them in vials containing 5% (v/v) buffered formalin in seawater. From these preserved samples, predator total lengths and the number of remaining prey were determined. Prey total lengths were measured from the control jar individuals. No prey mortality was observed in the control jars, thus any missing prey from the experimental predation chambers were recorded as captures. Since the three species of mysids consume their zooplanktonic prey in its entirety, ingestion/predation rates were expressed as number of prey mysid^{-1} hour^{-1}. Stomachs were dissected out to verify fullness and confirm that missing prey could be attributed only to ingestion.

Statistical Analysis

The non-parametric Kruskal-Wallis single factor analysis of variance (ANOVA) was computed to test the null hypothesis that predation (= ingestion) rates between prey densities (treatments) were equal, while treatment means were compared using the non-parametric Q test statistic for multiple comparison for unequal number of data with tied ranks (Zar, 1984). The functional response curves of the three mysid species were described from the relationship between ingestion rate and prey density. Curve fitting was performed using linear regression with replication, and slopes were compared using analysis of covariance followed by a Tukey test to determine significant differences between slopes (Zar, 1984).

All statistical analysis was conducted using the computer program SYSTAT for Macintosh computers (Wilkinson, 1992).

Results

Functional Response to Various Prey Types

Throughout the functional response experiments, similar sizes of *P. rufa*, *T. tasmaniae*, and *A. mixta australis*, and the different prey types were used (see Table 1) (CV within species < 5%).

Table 1. Predator and prey sizes in the funtional responses experiments.

Predator	Predator total length (mean ±SD mm)	Prey	Prey total length (mean ± SD mm)
Anisomysis mixta australis	6.08±0.15, n = 16	*Daphniopsis australis*	0.83±0.08, n = 92
	6.04±0.13, n = 20	*Gladioferense pectinatus*	0.81±0.01, n = 63
	6.43±0.41, n = 20	*Artemia sp.*	0.75±0.09, n = 40
Paramesopodopsis rufa	9.45±0.31, n = 16	*D. australis*	0.93±0.12, n = 92
	9.83±0.46, n = 20	*G. pectinatus*	0.81±0.01, n = 63
	9.00±0.60, n = 20	*Artemia sp.*	0.83±0.04, n = 40
Tenagomysis tasmaniae	7.88±0.37, n = 16	*D. australis*	0.95±0.10, n = 92
	7.85±0.68, n = 16	*G. pectinatus*	0.81±0.01, n = 63
	7.41±0.54, n = 20	*Artemia sp.*	0.80±0.01, n = 40

Functional Response to *Gladioferens pectinatus*

Very low predation rates were recorded for mature *P. rufa* feeding on adult calanoid copepod prey, *G. pectinatus* (see Table 2). Predation rates in this largest mysid species ranged from 0.17 ± 0.4 SD at a prey concentration of 5 litre^{-1} to 0.8 ± 1.3 SD at the highest prey concentration of 40 litre^{-1}. *P. rufa* predation rates on *G. pectinatus* were lower compared to the other prey types. No captures were recorded in the other two mysid species (Table 2).

Table 2. Predation by the three mysid species on the calanoid copepod *Gladioferens pectinatus*. Data in mean ±SD.

Mysid species	Initial prey density (litre $^{-1}$)	Ingestion rate (G. pectinatus eaten mysid $^{-1}$ hour $^{-1}$)
Anisomysis mixta australis	5	0
	10	0
	15	0
	20	0
Paramesopodopsis rufa	5	0.17±0.04
	10	0.50±0.8
	15	0.50±0.8
	20	0.83±1.3
Tenagomysis Tasmaniae	5	0
	10	0
	15	0
	20	0

Functional Response to *Artemia* sp. Metanauplii

A highly significant variation was shown in the linear functional response curves of the three mysid species preying upon *Artemia* sp. metanauplii ($F = 6.26$, $df = 50$, $p = 0.001$). The predation rate values in *P. rufa* were lower than those in *T. tasmaniae* ($p < 0.001$), but comparable to *A. mixta australis* ($p > 0.05$). The predation rates on *Artemia* sp. metanauplii by *T. tasmaniae* were double than those by *P. rufa* and *A. mixta australis*.. All three species showed an increasing linear curve as gainst increasing prey concentration (Figure 1A).

The lowest average predation rate for *A. mixta australis* was 0.36 ± 0.08 SE (standard error) metanauplii mysid^{-1} hour^{-1} at the lowest prey density (Figure 1A). *A. mixta australis* predation rates varied significantly over the increasing prey concentration ($H = 8.67$, $df = 3$, $p < 0.05$). The maximum predation rate of 1.77 ± 0.43 SE was recorded at the second highest prey concentration of 30 litre^{-1}. The mean predation rate at this prey concentration was only significantly different from those at the two lowest prey concentrations ($Q < 0.05$), while for the rest of the treatments, means were not significantly different ($Q > 0.05$ for all).

The average predation rates by *T. tasmaniae* also increased with increasing *Artemia* sp. metanauplii concentration with a minimum of 0.7 ± 0.08 SE

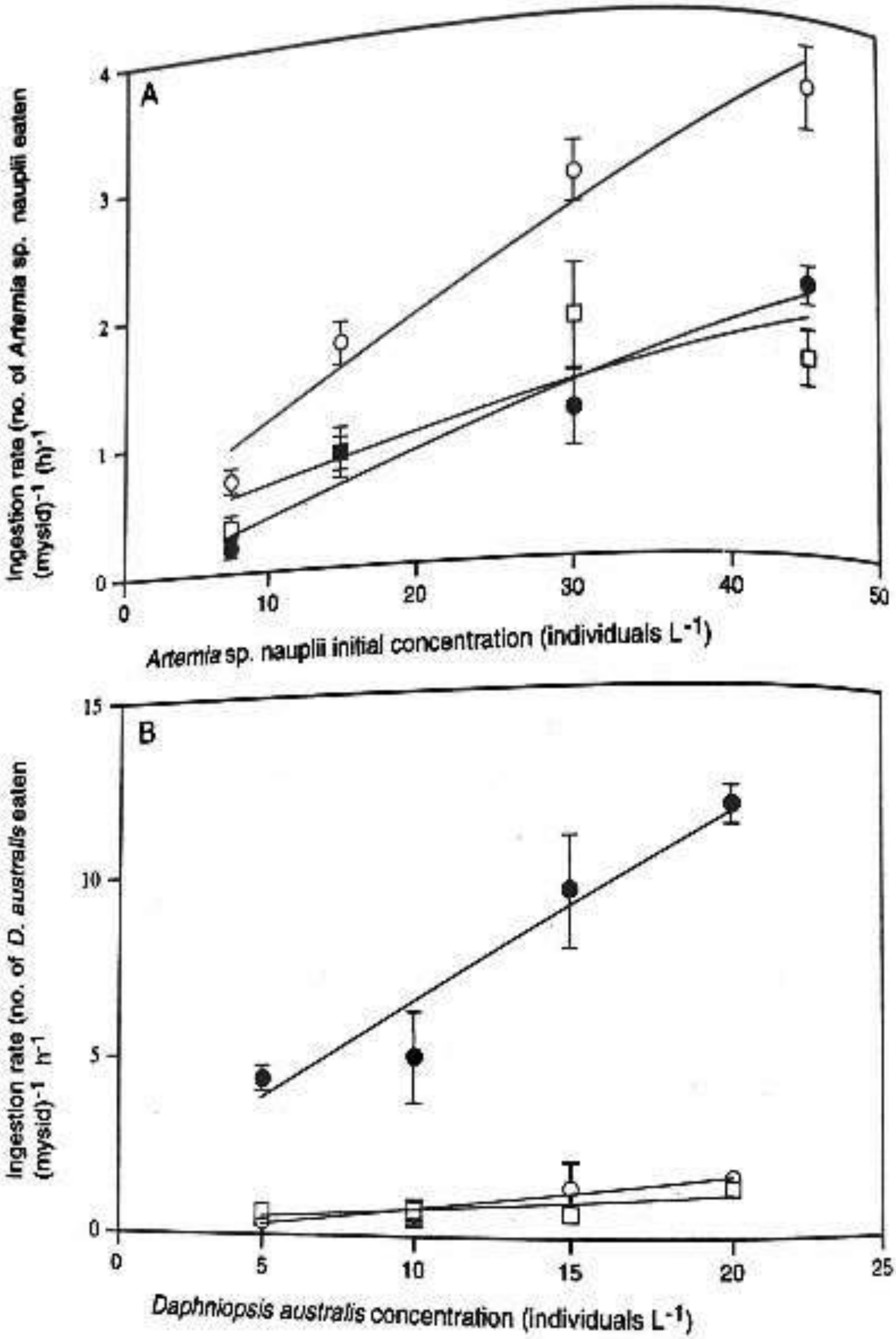

Figure 1. Functional response curves for the predation rate of the three mysid species feeding on two types of branchiopodan prey. *A. Artemia sp. metanauplii. B. Daphniopsis australis jubeniles.* Error bars: standard error. Squiares - *Anisomysis mixta australis*, closed circle - *Paramesopodopsis rufa*, open circle-*Tenagomusis tasmanice.*

and reaching a maximum of 3.5 ± 0.33 SE at 45 litre^{-1} ($H = 16.65$, $df = 3$, $p < 0.01$) (Figure 1A). The predation rate in the highest prey concentration differed significantly from that in the lowest prey concentration ($Q < 0.005$), but was similar to the second highest prey concentration ($Q > 0.05$). The latter was also significantly different from the predation rate at the lowest prey concentration ($Q < 0.05$), but not with that at the second lowest prey concentration ($Q > 0.05$). The predation rates at the two lowest prey concentration were similar ($Q < 0.05$).

The average predation rates by *P. rufa* on *Artemia* sp. metanauplii followed a linear relationship with increasing prey concentration, and these values varied significantly ($H = 14.25$, $df = 3$, $p < 0.05$) (Fig. 1A). Predation rates of P. rufa ranged from 0.2 ± 0.06 to 2.0 ± 0.13 *Artemia* sp. metanauplii mysid^{-1} hour^{-1}. The predation rate at the highest prey concentration differed significantly only with that at the lowest prey concentration ($Q < 0.05$). The rest of the rates at the other prey concentrations were similar ($Q < 0.05$ for all).

Functional Response to *Daphniopsis australis*

At the lowest prey density, average *P. rufa* ingestion rate was 4 ± 0.29 prey mysid^{-1} hour^{-1}, and it continued to increase with increasing prey density to a maximum ingestion rate of 11.75 ± 0.48 prey mysid^{-1} hour^{-1} at 20 litre^{-1} density (Figure 1B). Dissected mysid foreguts revealed 100 % fullness while those with very low ingestion rates showed 30% to 50% fullness. *P. rufa* ingestion rates varied significantly with increasing prey density ($H = 14.25$, $df = 3$, $p < 0.01$), although those at 5 and 10 litre^{-1} were the same ($Q > 0.05$). This is because two out of the four mysids fed at 10 litre^{-1} treatment density and 1 out of the four mysids at 15 litre^{-1} gave relatively very low (0.5 and 3 prey mysid^{-1} hour^{-1}, and 2.5 prey mysid^{-1} hour^{-1}, respectively) ingestion rates. These mysids were mature females without young in their brood pouches, and perhaps were about to moult. Mysid ingestion rates at the two higher prey densities differed significantly ($Q < 0.05$) from the two lower prey densities, but ingestion rates between the two higher prey densities were similar ($Q > 0.05$). The functional response curve of *P. rufa* to increasing density of juvenile *D. australis* is linear (Figure 1B).

Increasing density of *D. australis* did not increase predation rates in *T. tasmaniae* (Figure 1B) ($H = 16.66$, $df = 3$, $p > 0.24$). Very few individuals captured the prey. The lowest successful predation rate was 1 prey mysid^{-1} hour^{-1}, and the highest was 3. Averages from the four prey density treatments ranged from 0.75-3.25 prey mysid^{-1} hour^{-1}.

As in *T. tasmaniae*, very few *A. mixta australis* captured the prey. A predation rate of 0.5 prey mysid^{-1} hour^{-1} was the lowest, and the highest was 2. Increasing prey density did not increase predation rates ($H = 4.13$, $df = 3$, $p > 0.24$), and the average ranged from 1.25-2.75 prey mysid^{-1} hour^{-1}.

The functional response curves to the different *D. australis* concentrations by the three mysid species differed significantly ($F = 49.86$, $df = 45$, $p < 0.001$). The variability was attributed to the significantly higher predation rates by *P. rufa* compared to those in the other two species ($p < 0.001$). The predation rates of *A. mixta australis* and *T. tasmaniae* showed no significant difference ($p > 0.05$).

Discussion

The functional response of predators may be classified into types I, II, and III (Holling, 1959a,b). The type I or rectilinear response is characterized by a linear increase in consumption rate up to a certain prey concentration where the rate suddenly reaches a plateau and stays at zero with further increases in prey concentration. This is exemplified by filtration rate of filter feeders such as daphniids (Rigler, 1961), and calanoid copepods (Frost, 1972). The type II or exponential response is an initial proportional increase with increasing prey concentration which gradually decreases as saturation level of prey concentration is approached; beyond this predation rates remain stationary with further increase in prey concentration as in the type I functional response. These two types of responses have been considered destabilizing to predator-prey interactions because of the capacity of the prey to damp predation rates by simply increasing its density. In addition, at low prey density, predators could drive prey populations to extinction. This contrasts with the type III functional response in which predation rate remains low at low prey concentration and starts to increase at a certain higher prey density. The type III functional response is stabilising to the predator-prey interaction and is characterized by a sigmoid type of curve.

A Type 2 functional response curve is commonly observed among invertebrate predators (Holling, 1965). A Holling type II has been reported in *M. relicta* preying upon the copepod *Epischura*, but a Holling type III functional response was shown for another copepod prey *Diaptomus* (Folt *et al.*, 1982). Fulton (1982) reported a type II curve from laboratory experiments on *Mysidopsis bigelowi* preying upon *Acartia tonsa*. In contrast, a similar laboratory predation experiment involving *M. relicta* and *Epischura* collected from a different location showed a linear functional response (Cooper & Goldman, 1980). Estimation of *M. relicta* predation rates from field samples showed a similar linear type of curve which was attributed to food limitation (Bowers & Vanderploeg, 1982). These differences in mysid functional response have been attributed to prey vulnerability which varies according to prey types and their escape abilities (Folt *et al.*, 1982; Fulton, 1982; Ohman, 1988; Yen, 1983; McClatchie, 1988), predator hunger and feeding physiology (Yen, 1983), aggregative behaviour of both prey and predator (Folt, 1985), and temperature (Fulton, 1983).

The three mysid species were not efficient at capturing adult *Gladioferens pectinatus*. This is contrary to some reports on other mysid species which showed high capturing efficiency for adult calanoid copepods (e.g. Mauchline, 1980). However, other studies have also reported mysid species which are inefficient at capturing adult calanoid copepods (e.g. Siegfried & Kopache, 1980). The prey species used may explain differences in results. Low predation rates have been associated with the extremely agile and fast swimming attributes of adult calanoid copepods (Fulton, 1982; Yen, 1982; Ohman, 1988). The high frequency of this food type from gut content analysis may be attributed to the fact that estuarine mysids, being scavengers or necrophagous feeders, might be eating younger calanoid stages with weak escape motility (not tested in the present study) or moribond adult calanoid copepods.

The predation rates by the three mysid species with increasing *Artemia* sp. metanauplii concentration ranged from 0.2 to 4 prey mysid $^{-1}$ hour $^{-1}$. The three species showed higher predation rates of 0.8 to 3 prey mysid^{-1} hour $^{-1}$ at 15 to 30 prey litre^{-1} compared to those reported by Stuart and Hugget (1992) of 0.54 to 0.83 prey *Euphausia lucens*$^{-1}$ hour $^{-1}$ at 20 *Artemia* sp. nauplii (of comparable body length with the present study) litre^{-1}. Differences in the prey capturing mechanisms between mysids and euphausiids may explain these results. Mullin and Roman (1986) fed *Anisomysis* sp. with 100 to 1000 *Artemia* nauplii litre^{-1} and obtained a range of 1 to 6 nauplii mysid^{-1} hour^{-1}. The mysid species they studied is comparable in terms of body length with *A. mixta australis* which at 45 prey litre^{-1} showed a predation rate range of 0.3 to 3 nauplii mysid^{-1} hour^{-1}. The functional response by the three mysid species to increasing *Artemia* sp. concentration generated were all linear. The linear responses shown by the three species do not match any of Holling's functional response models. This is attributed primarily to the considerable variability of predation rates. On the other hand, the linear responses probably indicate that the initial concentrations of prey are well below threshold levels. If this is valid then the functional responses obtained in the present study might form the linear portion of the rectilinear (type I) or perhaps the curvilinear (type II) models below the critical concentration of prey.

Linear functional responses best describe predation on juvenile *D. australis* by the three mysid species. Similar explanations as those responses for the *Artemia* sp. metanauplii are invoked.

P. rufa predation rates on *Artemia* sp. metanauplii were lower than on the juvenile stages of *D. australis*. The differences in the swimming patterns and body shape of these two branchiopodan prey species may strongly influence predation rates by *P. rufa*. The predation rates by the two other mysid species for both *D. australis* and *Artemia* sp. metanauplii were similar indicating that predation rates in this case are not affected by the two prey types. .The functional responses for *T. tasmaniae* and *A. mixta australis* were a simple line like that in *P. rufa*.

Aside from predator size, results here suggest that mysid species differ in the actual prey handling process as suggested from predation rates. *P. rufa* feeding coefficient for juvenile *D. australis* is 44 litre day^{-1} (calculated from a maximum ingestion rate of 12 prey mysid^{-1} hour^{-1} in a 2-litre predation chamber) which is more than twice the 20.2 litre day^{-1} feeding coefficient reported by Ramcharan *et al.* (1985) in *M. relicta*. In comparison to these two mysid species, *T. tasmaniae* and *A. mixta australis* predation rates are still relatively low. Apart from the small size of *A. mixta australis*, its habit of feeding upon small particulate materials (Fenton, 1986) may explain the low predation rates. *T. tasmaniae*, despite being larger than *A. mixta australis*, still showed comparable low predation rates. Most *T. tasmaniae* spent the two hour experimental period resting on the bottom of the jar reducing their chance of encountering the swimming *D. australis*. The fact that this species has been reported to be a substrate specialist and showed predominantly macroalgal detritus in its diet (Fenton, 1986) may explain the reduced predatory feeding performance.

Predation may not be limited by prey ingestion and handling time considering the very short duration associated with these processes. This conclusion, which is apparently true for *M. relicta* (Ramcharan *et al.* 1985), will be discussed in detail with particular reference to the apparently highly predatory *P. rufa* and the daphniid *D. australis* as prey. Using the average ingestion time of 0.37 min per juvenile *D. australis*, and the maximum ingestion rate (saturation point) of 12 prey mysid^{-1} hour^{-1}, *P. rufa* would only spend about 4.40 min ingestion time plus 0.04 minutes capture time in an hour. Hence, if an individual *P. rufa* is offered juvenile *D. australis*, saturation point ingestion rates contribute only 7.4% of its time, while 92.6% perhaps is spent cruising, searching, pursuing, and attacking prey or other essential behaviour. Again, prey morphology and escape tactics/behaviour may partly explain this pronounced non-feeding period in *P. rufa*. Gerritsen & Strickler (1977) noted that although their model predicts that increased swimming speeds of a cruising invertebrate predator would mean increased encounter rate with its prey, this does not necessarily cause increased prey ingestion rates. This is so because in real situations prey escape abilities may reduce their chance of being ingested after encounters with predators.

Table 3. Maximum ingestion rates of daphniids by mysids in laboratory experiments.

Mysid Species (Location) (Reference) (Size in mm)	Prey	Intial Prey Density (litre^{-1})	Chamber Volume (litre)	Duration (h)	Predation Rate (prey mysid^{-1} day^{-1})
Mysis relicta (Lake Michigan) Grossnickle 1978 cited in Bowers and Vanderplog 1982) (14-17)	*Daphinia*	100.0 6.9		12	480.0 84.1
Mysis relicta (Lake Tahoe) (Cooper & Goldman 1980) (mean=15.8)	*Daphnia pulicaria*	14.8	3	12	34.1
M. relicta (Gull Lake, Ontario) (Ramcharan & Sprules 1986) (mean=18.6±2.0)	*D magna* *D. pulex*	40	10		120-125
Neomysis mercedis (Lake Washington) (Murtaugh 1981b) (9.6-10.2 for individuals preying upon *D. pulicaria* and *D. thorata*; 6.2-7.4 for individual preying upon *D. pulex*)	*D. pulex* *D. pulicaria* *D. thorata*	148 298	2.8 0.15-4	1.2-6.2	32 89
Neomysis mercedis Lake Washington (Chigbu and Sibley 1994) (mean ñ SE = 13.6±0.1)	small *D. magna*	25	2	12	60
	medium *D. magna*	15	2	12	37
	large *D. magna*	15	2	12	25.6
Paramesopodopsis rufa Present study (9.1-10.3)	*Daphniopsis australis*	20	2	2	96-288
Tenagomysis tasmaniae Present study (7.10-8.8)	*D. australis*	20	2	2	24-72
Anisomysis mixta australis Present study (5.7-6.4)	*D. australis*	20	2	2	12-24

Assuming adult *P. rufa* feeds on juvenile *D. australis* continuously within a day, our results if computed on a daily basis, would give daily ingestion rates ranging from 96 to 288 prey mysid^{-1} day^{-1} (Table 3). *A. mixta australis* showed the lowest daily predation rate compared to all mysids listed but this is mainly due to size difference. The daily predation rate of *T. tasmaniae* is comparable to those of *Mysis relicta* ingesting *Daphnia pulicaria*, and those of *Neomysis mercedis* ingesting *Daphnia pulex*. The minimum value is fairly close to the in situ ingestion rate of 89 prey mysid^{-1} day^{-1} reported by Murtaugh (1981b) in *M. relicta*. The maximum ingestion rate is nearly half the value (480 prey mysid^{-1} day^{-1}) reported by Grossnickle (1978 cited in Bowers and Vanderploeg, 1982) who used an initial prey density of 100 litre^{-1} in a laboratory feeding experiment with *M. relicta*. Higher ingestion rates in *P. rufa* may be attributed to the motion introduced by the plankton roller during the feeding experiment. It is speculated that these water movements increase rates of encounter and successful capture by the mysid. The increased encounter rate between predator and prey due to water movements has been very recently reported (Kils, 1992).

Although the majority were conducted in laboratory conditions, these studies have demonstrated that different mysid species show characteristic feeding behaviour in response to the various prey features. In the present study, the classical proportional increase of predation rate in response to prey availability is demonstrated. However, other prey characteristics, such as gross body shape, swimming movements, and perhaps palatability also influence the predatory feeding behaviour in the three co-occurring mysid species.

Various foraging strategies among competing predatory species may serve as means of achieving co-existence by resource partitioning. Food resource partitioning mechanisms have been linked with reducing or minimizing overlap of the food resource utilization curves between competing species and at the same time balancing or offsetting the effects of intraspecific competition (Schoener, 1974). In the case of the present study, the different predatory feeding behavioural response in the three mysid species to various prey types indicates a probable feeding niche dimension within which these three co-occurring mysid species partition.

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