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PRIMARY RESEARCH PAPER

Feeding behaviour, efficiency and food preference in yabbies *Cherax destructor*

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Abstract The influence of body size on the consumption of live zooplankton (*Daphnia* spp.) by freshwater crayfish was examined using yabbies (*Cherax destructor*) ranging from 5 to 45 g. Food preference between live zooplankton and inert pellets was also assessed under experimental conditions. In experimental tanks, yabbies of four size classes (<15, 15–24.9, 25–34.9 and 35–45 g) were presented with live *Daphnia.* All yabbies were held in separate tanks with five animals per size class. In yabbies less than 15 g, the feeding mode on zooplankton involved rapid searching and probing with the first two pairs of walking legs. Once a prey was located, the chelae on the end of these walking legs would grasp the zooplankton and then rapidly move it towards the mouthparts. Yabbies larger than 25 g tended to use their walking legs to push the *Daphnia* nearer to their third maxilliped which would then force or scoop the zooplankton towards the mouthparts. A short-term feeding trial showed that there was no significant difference between size classes in regards to zooplankton consumption ($P > 0.05$). Capture efficiency of live *Daphnia* by yabbies less than 15 g was significantly lower (76%, $P = 0.008$) than the three larger size classes (93.6%). Yabbies less than 15 g consumed a significantly ($P < 0.001$) higher percentage (5.2%) of their body weight than the other size classes (1.1%, 0.8%, and 0.6%, respectively). In the presence of both live zooplankton and a pellet diet, yabbies spent significantly ($P = 0.005$) more time feeding on zooplankton (85%) than on inert pellets (15%). This was the first study to quantify zooplankton consumption by yabbies and the results provide insights into understanding the trophic role of freshwater crayfish in structuring zooplankton communities and the husbandry management of crayfish farming.

Keywords Freshwater crayfish · Zooplankton · Food preference · Consumption · Capture efficiency

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Introduction

In Australia, the *Cherax* species of freshwater crayfish are of significant commercial importance to aquaculture. Cultured species include marron (*Cherax tenuimanus*) which is native to south-west Australia, red claw (*C. quadricarinatus*) which is native to northern Australia, and yabby (*C. destructor*) which is common to central and southeast Australia (Semple et al., 1990). Understanding the feeding behaviour and food requirements of crayfish has been the focus of numerous nutritional studies (Austin et al., 1997; Chavaz & Mitchell, 1995;

Figueiredo & Anderson, 2003). Stomach analysis of crayfish from natural environments often confirms the notion that following a non-selective or carnivorous juvenile stage crayfish become predominantly either detritivores or herbivores (Chavaz & Mitchell, 1995; Figueiredo & Anderson, 2003; Van den Berg et al., 1990). However, stomach contents are not easily determinable because crayfish exhibit a destructive feeding behaviour and there are differences in digestibility among different food items. Recent studies have shown that the proportion of detritus and plant matter in the diet is overestimated due to animal prey items being relatively easy to digest (Hollows et al., 2002; Momot, 1995). Stable isotope analysis in some crayfish species has also indicated that invertebrate prey such as snails, nymphs and chironomid larvae are more important than detritus in terms of assimilation and incorporation into crayfish biomass (Hollows et al., 2002).

Zooplankton have been shown to be the most stimulatory food item in a range of natural crayfish diets initiating a very strong feeding response (Kreider & Watts, 1998). Therefore, it is not surprising that numerous studies have indicated that a diet including zooplankton increases the growth and survival rates in juvenile crayfish and shrimp (*Penaeid* sp.) (Coman et al., 2003; Geddes et al., 1991; Mitchell & Collins, 1989; Smallridge et al., 1989; Verhoef et al., 1998). It is commonly believed that following the juvenile stage crayfish no longer posses the dexterity to capture zooplanktonic prey (Sierp & Qin, 2001). The increased capacity for extended periods of swimming by juvenile crayfish is likely to contribute to the capture success of planktonic prey (Goddard, 1988). However, whether crayfish prefer to feed on live zooplankton, or scavenge on dead particles is unclear (Geddes et al., 1991). Abrahamsson (1966) reported that crayfish (*Astacus astacus*) larger than 60 mm are not able to capture zooplankton, but no further study to date has examined the size at which freshwater crayfish lose this ability. The zooplankton capture efficiency of crayfish in general and *C. destructor* in particular is not known (Cronin et al., 2002). Therefore, the aim of this study was to test the hypothesis that as crayfish (*C. destructor*) grow larger, their ability to capture live zooplankton decreases. Along with investigating the size at which crayfish become inhibited in capturing zooplankton, we also aimed to quantify zooplankton consumption, investigate food preference between live zooplankton and an inert diet, and describe the feeding behaviour of crayfish consuming zooplankton.

Materials and methods

Experimental design and procedure

Yabbies used in this experiment were obtained from Aquaculture Management Services, South Australia. These yabbies were divided into four size categories: <15, 15–24.9, 25–35.9 and 35–45 g. Yabbies of each size were stocked into five 12 l tanks (30 cm wide × 20 cm high × 20 cm deep) filled with 3 l of water. In order to avoid antagonistic behaviour, each tank contained only one yabby with five replicate tanks for each size category. Aeration was gently supplied in each tank with an air-stone.

In order to test yabby feeding efficiency in the above tanks, *Daphnia* (1–4 mm) collected from the Flinders University Lake with a 100 μm zooplankton net were used as the live food. Captured zooplankton were filtered through a 1-mm screen to remove small daphnids and other zooplankters. In order to ensure that each tank would receive a similar amount of zooplankton, the large daphnids retained on the screen were then transferred into a container at a density of 50–60 ml^{-1}. Equal quantities of this zooplankton mixture were pipetted into twenty 250 ml containers and then each container was filled to 200 ml with distilled water. Zooplankton counts were then conducted by taking 10-ml samples from the 250-ml containers. The 10-ml sample was then released onto a zooplankton counting wheel and the *Daphnia* were counted and returned to the container they came from. This was replicated eight times before the average amount of zooplankton for each 250 ml container was calculated.

All crayfish were starved for 48 h before any feeding trial. An average of 501 ± 82 (SD) zooplankton was added to each tank (i.e. 167 ± 27 l^{-1}, or 140–194 l^{-1}). Feeding trials were conducted over a period of 1 h after which feeding activity had slowed considerably or had ceased. After the feeding trial had concluded, crayfish were removed from the tanks and the entire contents of the tank were filtered through a fine screen. Remaining zooplankton were then transferred back into the 250 ml containers and topped up with 200 ml of water. Zooplankton counts were conducted as previously described. However, zooplankton in the whole sample were individually counted if fewer than 50 zooplankton remained in the sample.

Determining weight of food consumed

In order to determine the weight of food actually consumed by the crayfish, a subsample of *Daphnia* were pipetted out onto absorbent paper and left for 2 min, so that all excess water would be absorbed. Using the end of a fine-pipette tip, 30 *Daphnia* chosen at random were lifted off the paper and placed onto a plastic zooplankton counting slide then weighed on an electric scale to the nearest 0.1 mg. The *Daphnia* were then removed and the slide weighed to the nearest 0.1 mg. The difference between the two-recorded weights was taken to be the weight of the 30 *Daphnia*. This was replicated thrice. Each replicate was taken from a different batch of collected *Daphnia*, so that the size of the zooplankton weighed was not dependent on the weight of any one particular batch. The weight of one *Daphnia* was calculated and used in determining the percentage body weight consumed by the yabbies.

Food preference

Five yabbies (*C. destructor*) (mean weight 24 ± 2.6 g) were held individually in 12 l tanks at 24°C. Each tank contained a PVC hide placed in one corner in a way that would enable full view of the rest of the tank. In order to avoid pre-conditioned effects to one particular food type, animals were fed a combination of pellets and zooplankton (*Daphnia* spp.) for 2 weeks prior to the trial and then fasted for 48 h prior to diet preference evaluations. At the commencement of each trial, four inert pellets (Wesfeed brand, 21% crude protein, 5% fibre, 0.4% salt, and 0.9% calcium) with an average combined weight of 0.376 g were simultaneously distributed directly in front of the hide containing the crayfish along with an excess amount of live zooplankton (*Daphnia* spp.). All crayfish were in their hide at the commencement of each trial. Preference trials were conducted for an hour. The total time spent feeding on each food type, or not feeding at all was recorded by observing the feeding yabby for the entire duration of the trial. Using a stopwatch, the observer recorded the time at which any change in behaviour occurred effectively logging the crayfish behaviour. From these logs, the amount of time spent feeding or not feeding on a particular food type could be calculated.

Data analysis

Capture efficiency (CE) was expressed as the amount of zooplankton before feeding divided by the amount of zooplankton after feeding. Specific consumption was calculated by the total mass of zooplankton consumed divided by the mass of yabby in each tank. A one-way ANOVA (SPSS statistics package) was used to test the effect of body size on zooplankton consumption per yabby, specific consumption and capture efficiency.

Percent of time spent feeding on each food type was used to assess food preference as not all animals fed for the entire test period. In order to determine preference, means of percent time spent feeding on zooplankton and percent time spent feeding on pellets were analysed with a paired *t*-test.

Results

Feeding behaviour observations

Yabbies (up to 45 g) were well adapted to capturing live zooplankton (*Daphnia* spp.) and showed an active response to this food type, indicating that zooplankton are a very attractive prey to crayfish. Upon adding zooplankton to the tank, it was quite often the case that crayfish would exhibit an immediate response that somewhat resembled a feeding frenzy, rearing up on their back walking legs and attempting to grab the zooplankton as they floated down through the water column.

The behaviours of crayfish to consume the zooplankton varied slightly depending on the size of the crayfish. In yabbies less than 15 g, the feeding behaviour involved rapid searching and probing with the first two pairs of walking legs. Once a prey item was located, the chelae on the end of these walking legs would grasp the zooplankton and then rapidly move it towards the mouthparts (i.e. first and second maxilliped, maxilla and mandibles). Once at the mouth region, the crayfish used its third maxilliped to ensure that the zooplankton was placed into the mouth where it was ground and ingested. On occasions when a zooplankton was close enough, the crayfish solely used the third maxilliped to guide the food into its mouth. Even when the crayfish was masticating its meal, the walking legs would continue probing and searching for the next zooplankton. Sometimes a yabby would place another item in its mouth before it had properly ingested the previous food item and a dead zooplankton could be seen floating out of the crayfish's mouth.

Yabbies larger than 25 g tend to use their walking legs less often than the smaller animals to grasp the *Daphnia*. Instead, they used their legs to push the *Daphnia* nearer to their third maxilliped which was then used to force or scoop the zooplankton towards the mouthparts. Larger yabbies were observed flattening themselves against the bottom of the tank in order to shovel low swimming zooplankton with their third maxilliped. However, it should be noted that the chelae on the end of the walking legs for a 35–45 g yabby were still effective at grasping onto the *Daphnia* and this behaviour was observed regularly. Larger crayfish also appeared to be able to produce a much stronger in-flowing current, which caused zooplankton to be drawn near the mouth area, and then could be held there with the third maxilliped. The response of the larger yabbies to the zooplankton was much the same as the smaller animals, except that large yabbies tended to take longer to react. In general, smaller yabbies responded immediately, while larger yabbies often took 5–10 s before beginning to forage. Once the animal began to feed, then the response was just as frantic as the smaller animals, chasing the zooplankton and making rapid feeding movements. Feeding activity usually ceased within a one-hour period.

Behaviours such as rapid movement to particular areas of the tank and probing with the first and second walking legs suggest that crayfish have visual, tactile, and chemical recognition to the presence of zooplankton in the tanks. While grabbing for zooplankton, the crayfish could obviously distinguish between non-food items (e.g. faeces and small plant material such as twigs) and zooplankton. Often the walking legs would grasp onto items that were not food and immediately drop them, whereas grasping of zooplankton was quickly followed by a rapid movement of the walking leg to the mouth region.

Zooplankton consumption

There was no significant difference ($P > 0.05$) among size classes in regard to the total number of zooplankton consumed per yabby within the 1-h feeding period. All size classes consumed between 417 and 470 *Daphnia* (Fig. 1). The data did however, indicate a significant difference between treatments for capture efficiency ($P = 0.008$) and the percentage of body weight consumed ($P = 0.001$). Capture efficiency was significantly lower in the smallest size class whereas no difference was detected between the remaining classes (Fig. 2). Conversely, yabbies less

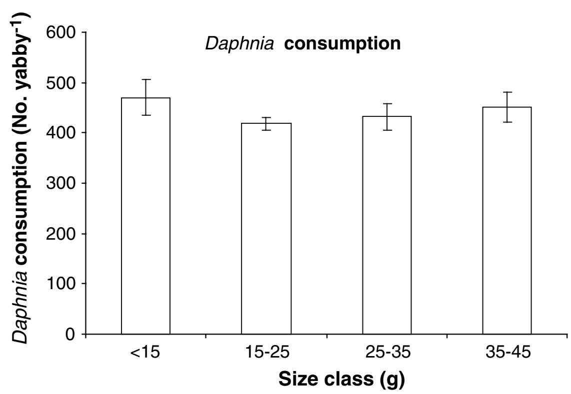

Fig. 1 Mean consumption of live *Daphnia* per yabby in one hour by four different size classes of yabbies

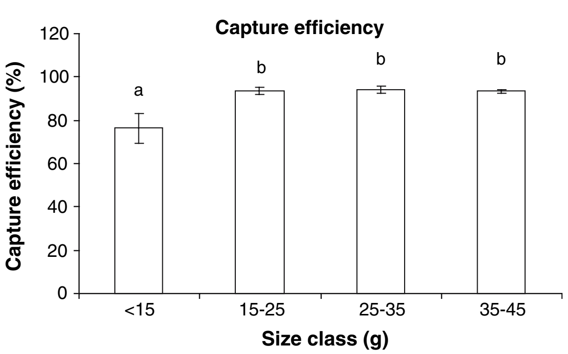

Fig. 2 Capture efficiency of live *Daphnia* by different size classes of yabbies. Bars represent standard error. Different letters indicate significant difference ($P < 0.05$)

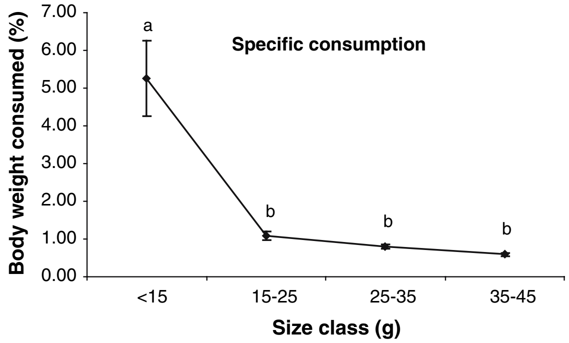

Fig. 3 Specific consumption of *Daphnia* by different size classes of yabbies. Bars represent standard error. Different letters indicate significant difference ($P < 0.05$)

than 15 g consumed a significantly higher percentage of their body weight than all other size classes (Fig. 3).

Food preference

Results from this experiment showed clear food preference ($P = 0.005$). Yabbies spent on average 85% of the time feeding on zooplankton (40.7 min), while feeding on pellets only occurred for 15% of the time (11.7 min, Fig. 4). On no occasion was more time spent feeding on pellets than on zooplankton. Less than 10% of total feeding time was allocated to consuming pellets in 60% of instances (5 min or less).

Discussion

Sierp and Qin (2001) conducted a field experiment to compare the population abundance of zooplankton in

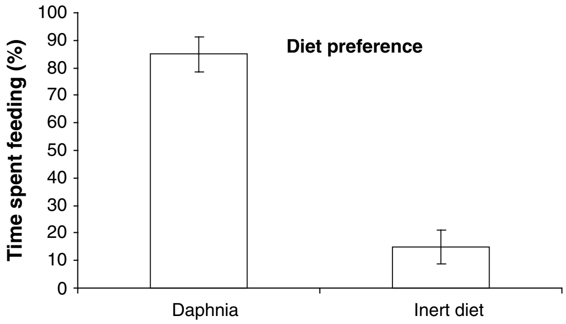

Fig. 4 Mean percentage of time spent feeding on *Daphnia* or inert diet by yabbies

the presence or absence of adult crayfish in ponds and found that zooplankton abundance did not differ between the two treatments, suggesting that adult freshwater crayfish are unable to effectively suppress zooplankton. In contrast, this study indicates that yabbies up to 45 g are just as efficient at capturing *Daphnia* as smaller ones (Fig. 2). In fact, yabbies over 15 g are 13% more efficient than the smaller yabbies at capturing *Daphnia*. All animals greater than 15 g captured more than 89% of the *Daphnia* presented to them while an average of 76% were consumed by the smaller animals. This difference is probably in part due to the fact that the smaller yabbies had reached satiation point quicker than large yabbies, and therefore ceased capturing *Daphnia*. In this study, yabbies less than 15 g consumed over 5% of their body weight. This was within the range indicated by Momot (1995) who stated that most species of crayfish consume 2–7% of their body weight per day. In contrast, yabbies at size classes 15–24.9, 25–34.9 and 35–45 g consumed only 1.08, 0.8 and 0.6% of their body weight, respectively, indicating the decline in specific consumption over size.

The growth of yabbies up to 45 g does not change the morphology of the feeding apparatus enough to inhibit the capture of zooplankton with their walking legs and they are in fact, equally capable, and possibly more efficient at capturing large numbers of zooplankton than animals less than 15 g in the same period. Abrahamsson (1966) suggested that as crayfish grow, the precise movements required for feeding on zooplankton are reduced. In this study, we did not observe the impaired ability of yabbies up to 45 g in feeding on *Daphnia* spp. As the structure of feeding morphology in crayfish is similar between *Cherax* and *Procambarus* species (Moloney, 1993), the capacity to feed on zooplankton may be applicable to a wider range of freshwater crayfish species. Momot (1995) believes that when crayfish reach high densities, a reduction in available benthic animal protein may lead crayfish to increase their consumption of plant material or planktonic prey. The presence of zooplankton as a source of animal protein may therefore still be important in ecosystems where benthic invertebrates have been diminished at a high crayfish density.

In most fish ponds in South Australia, *Daphnia* density is in the range of 50–200 l^{-1} (Culver &

Geddes, 1993; Sierp & Qin, 2001). However, the absence of the cold and dark hypolimnetic layer of water in shallow lakes or ponds restricts the ability of *Daphnia* to avoid predation through performing vertical migration (Burks et al., 2002). Instead, zooplankton performs a horizontal migration into the shallow vegetated littoral zones (Burks et al., 2002). This accumulation of zooplankton in the littoral zone would allow *Daphnia* to become susceptible to crayfish predation, while crayfish are foraging on plant materials in shallow areas. Burns (2000) states that in shallow lakes and ponds, diel horizontal migration of *Daphnia* can result in very high densities of 1000–4000 l^{-1} of zooplankton in the littoral zones. The density of *Daphnia* used in our experiments averaged 167 l^{-1}, so consumption rates from this present study are not likely to be overestimated and crayfish could possibly consume more under conditions of greater zooplankton abundance.

One of the greatest difficulties in the study of freshwater crayfish feeding is quantifying the actual amount of food ingested (Ruscoe et al., 2005). Our study is the first to endeavour quantifying zooplankton consumption by the freshwater crayfish *Cherax destructor*, and could provide new insights into the role of zooplankton in crayfish diets. The data demonstrated that post juvenile crayfish are not only capable of capturing live zooplankton (*Daphnia* spp.), but also when given the opportunity, can effectively consume large quantities in a relatively short period. This ability of crayfish to consume zooplankton indicates that zooplankton may still play an important role in the diet of crayfish up to a size of 45 g and possibly beyond. In this study we did not, however, test the maximum consumption of zooplankton by yabbies at different size. It is possible that yabbies could have consumed even more zooplankton if zooplankton had been continuously brought in to maintain the prey density in the ambient environment.

Along with the availability of zooplankton as a food source, preference may play a role in determining if crayfish are actually feeding on zooplankton. In our study, live zooplankton was preferred over inert food by yabbies, suggesting a moving prey item may stimulate or influence feeding preference in crayfish. Austin et al. (1997) also noted the impact of live zooplankton on crayfish behaviour with a reduction in antagonistic behaviours among conspecifics. The evidence from this study demonstrates a clear preference for feeding on live zooplankton by crayfish and that crayfish could feed on live zooplankton much longer in their feeding ontogeny than what is conventionally thought.

The size at which crayfish become inefficient at capturing zooplankton was not reached in this study. However, the observation on the feeding behaviour indicates that feeding on zooplankton by crayfish may not depend on the animal size because zooplankton capture and ingestion relies on the manipulative ability of mouth parts. As these animals become larger, the chelae on the first two walking legs might become too large to be useful in capturing small zooplanktonic prey, but the morphology of mouth parts does not seem to change much over animal size. We observed that large yabbies could effectively use their mouth parts to catch zooplankton, suggesting that the feeding apparatus is still adaptive to collecting zooplankton despite the overall size increase of the animal. The present study indicates that 15–45 g crayfish can effectively consume zooplankton at an initial prey density of 140–194 l^{-1}. Therefore, crayfish may have played a more important role in structuring plankton communities than current research has revealed. Our study has shed a light for further study into the feeding ecology of crayfish on zooplankton. Future research to investigate variation in live and dead daphnia consumption by yabbies may provide evidence useful for determining the mechanism involved for identification and attraction to this food source. In addition, the differences in yabby consumption of different zooplankton species may also prove useful in further elucidating the feeding biology of crayfish in freshwater ecosystems.

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