THREAT-SENSITIVE PREDATOR-AVOIDANCE BEHAVIOUR IN THE THREESPINE STICKLEBACK (*Gasterosteus aculeatus*): ITS DEVELOPMENT AND SIGNIFICANCE IN THE LARVAL STAGE

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Abstract

Threat-sensitive predator-avoidance theory predicts that prey should assess the relative threat posed by a predator and then adjust their behaviour to reflect the magnitude of the threat. This is based on the premise that it is non-adaptive for prey to give up feeding or mating opportunities in the presence of non-threatening predators. In this study, larval threespine sticklebacks were tested for threat sensitivity by exposing them to conspecific predators of various sizes. Larvae were found to display behaviours which suggested threat-sensitivity, such as performing maximum predator-escape responses only to direct attacks and reduced responses to less threatening situations. The onset and disappearance of certain predator-escape behaviours during ontogeny may be related to the development of the dorsal and pelvic spines, along with independence from paternal care.

Other evidence for threat-sensitivity indicates that larvae exposed to larger predators displayed a reduction in feeding behaviour compared to larvae exposed to small predators or larvae not exposed to predators. This reduction in feeding behaviour may be influenced by the predator/larvae size ratio which indicates an increase in feeding behaviours associated with a decrease in the predator/larvae size ratio.

Responses of stickleback larvae to active conspecific and non-active, ambush type predators were compared to test the

hypothesis that the larvae would be more vigilant towards an active predator. Neither predator type were found to have significant influences on the behaviours performed by the larvae.

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So here it is. The end product of two and one half years of inquiry, analysis, and interpretation (with a bit of aggrevation and despair thrown in to liven things up). It wasn't easy, but a lot of good people made it a whole lot easier than it could have been.

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Introduction

An Introduction to Predation

Predation is a major driving force in the structuring of communities and population dynamics (Ricklefs, 1973) and ecological studies have usually examined the role of predation in terms of the direct effects that predators have on abundances and diversity of the prey species (Zaret, 1980; Taylor, 1984; Sih et al., 1985). For instance, Taylor (1984) describes a situation where an insect pest of trees and shrubs in California, the olive scale (Parlatoria oleae), was controlled with the introduction of a predatory wasp, Aphytis maculicornis, which subsequently caused a drastic decline in scale infestations. Zaret (1980) describes a change in zooplankton species dominance from larger zooplankton species to smaller species after the introduction of alewives (Alosa aestivalis), a zooplankton predator, into a pond previously free of these predators. The smaller species were less susceptible to predation, so their population increased with the decline in population of the larger species which were now prey to the alewives.

However, through evolution, predators also have another potential effect on their prey. Those prey that successfully avoid predation and survive to reproduce presumably possess advantageous traits in terms of physiology, morphology, or

behaviour for avoiding predators which, if these traits are heritable, will be passed on to the offspring. Therefore, through evolution, prey species have developed numerous physiological, morphological and behavioural adaptations to avoid or escape their predators (Edmunds, 1974; Stein, 1979; Keenleyside, 1979; Sih, 1987). For example, a black color morph of the Peppered moth (Biston bitularia) is predominant in areas where industrialization has blackened the trees, the usual resting area for the moth, while a grey morph is predominant where the trees are healthy and have lichens growing on them. Kettlewell (1956) was able to demonstrate that this distribution was due to selective predation on the more conspicuous morphs by birds. Therefore, the color of the moth is a morphological adaptation aiding the moth to stay hidden from predators. The whip scorpion (Mastigoproctus sp.), along with many other arthropods, has evolved a physiological defense secreting system which it uses to deter predators. In this case, when the scorpion is attacked it points its abdomen towards its attacker and squirts a fluid containing acetic acid (Eisner and Meinwald, 1966). Along with these various morphological and physiological forms of defense, behaviours known as anti-predator behaviours may also be employed.

Behavioural Adaptations Against Predation

Anti-predator behaviour used by prey to avoid detection by

predators or to escape from the predator once it has been detected can be categorized into two types, avoidance or escape (Sih, 1987). Avoidance behaviour (termed 'fixed' in Stein, 1979) may be defined as a behaviour which is performed regardless of predation pressure and functions to decrease the encounter rate with predators. For example, diel vertical migration by zooplankton (Zaret, 1980) functions to restrict the activity of the zooplankton to places and/or times where the predators are inactive or not present, but migration is still performed regardless of the presence or absence of predators. Group-living is another form of avoidance behaviour which is often executed without the presence of a predator. It is hypothesised to aid in early detection of predators, to confuse predators, to deter predators through group defense and to decrease the chance of one particular individual being chosen from the group (see review in Bertram, 1978).

The second category of anti-predator behaviour is escape behaviour (termed 'reactive' in Stein, 1979). These are behaviours which generally occur only when a predator is present and function to decrease the chance that the prey will be attacked, captured or consumed (Sih, 1987). These behaviours may take many forms including reducing maintenance behaviours such as feeding (Dill and Fraser, 1984; Milinski, 1986; Fraser and Gilliam, 1987; Pierce, 1988;), seeking temporary refuge (Colley et al., 1989), the use of

morphological and/or chemical defenses (Edmunds, 1974; Harvey and Greenwood, 1978; Mclean and Godin, 1989) and fleeing or protean escape which is a form of escape where unpredictable changes in direction during the escape are made (Humphries and Driver, 1970).

Early research dealing with anti-predator behaviour focused on describing the behaviour of the prey or determining if what was thought to be an anti-predator behaviour did actually reduce predation upon the prey. Edmunds (1974), in his book "Defence in Animals", gives an excellent summary of the early descriptive work on anti-predator behaviour.

The Concept of "Trade-Offs" in Anti-Predator Behaviour

After the initial description of anti-predator behaviours, the next generation of questions asked what factors would influence the prey's response to a predator. Factors such as the hunger level of the prey, quantity and quality of food available to the prey, distance to refuge, etc. were used to determine how and when prey would react towards a predator (Ydenberg and Dill, 1986; Dill, 1987; Sih, 1987). Various studies found that instead of always escaping from predators when they were present, many prey were able to find a "happy medium" between escaping predators and performing other activities, or rather, the prey would "trade-off" mortality risk and energy gain in order to maximize their fitness (Krebs and Davies, 1981; Ydenberg and Dill, 1986; Dill, 1987; Sih,

1987). For instance, Ydenberg and Dill (1986) demonstrated that waterstriders (Gerris remigs) were less likely to avoid an approaching predator when feeding on a large food item compared to a small food item, and when they did avoid the predator, they allowed it to get closer when feeding on the large food item. The waterstrider gave up the small food quickly because it had less to gain from it, compared to the gain in energy from the larger food item. Edwards (1983) found that on Isle Royale, Michigan, cow moose (Alces alces) with calves chose to stay on small isolated islands that were free from wolves (Canis lupus), but had a poorer quality diet than the main island, which did have a population of predatory wolves. Therefore, the cow moose accepted a poorer quality diet to protect their reproductive investment from predation. Milinski and Heller (1978) demonstrated that when hungry sticklebacks (G. aculeatus) were given a choice of high or low density food patches after being exposed to a predator, the sticklebacks chose to feed on the low density food patch. Although hungry, the sticklebacks rejected the high density food patch because they could not be as vigilant for predators while trying to remove one individual from a moving swarm of food darting around their field of vision (Confusion effect, Milinski, 1979). The sticklebacks chose the food patch with the least energy gain, but the highest chance of noticing an approaching predator.

The Concept of "Threat-Sensitive" Anti-Predator Behaviour

The studies dealing with "trade-offs" have shown that prey are able to perceive the presence of a predator and then modify their behaviour to take into account the presence of the predator. However, most of these studies deal with changes in the prey's behaviour in the presence or absence of a predator and thus have not taken into account the possible variation in predator threat due to predator size, type or hunger level of the predator or the threat to the prey due to their size, stage of development, etc.. Studies which address these questions are called "threat-sensitive" studies because they focus on the ability of the prey to assess the relative threat of predators that vary in their predatory ability or how prey that vary in their vulnerability behave towards a predator (Dill, 1987; Sih, 1987; Helfman, 1989).

The ability to assess and behave flexibly towards various degrees of predator threat should be selected for over evolutionary time because animals with this ability do not give up as many feeding or mating opportunities as an animal that responds with the most extreme form of predator avoidance to all types of predator threat (Stein, 1979; Coates, 1980; Sih, 1987; Helfman, 1989; Licht, 1989). The threespot damselfish, Stegastes planifrons, shows varying amounts of predator avoidance to varying degrees of predator risk from the atlantic trumpetfish, Aulostomus maculatus. The damselfish will perform a stronger predator avoidance response

to larger or attacking trumpetfish, and a weaker response to a smaller or non-attacking predator (Helfman, 1989). The same response was found for the aquatic insect Notonecta hoffmanni. In this case juveniles show a stronger escape response to cannibalistic adults than to slightly larger juveniles (Sih,1987). Guppies (Poecilia reticulata) were able to discriminate between a hungry and a satiated predator and spent less time adjacent to the hungry predator (Licht, 1989).

Such decisions are based on an assessment of the threat posed by the predator and have been demonstrated with adult animals. However, it is important also to study these decision-making processes in young animals where the threat of predation is usually very high.

Predation and Young Prey

In most groups of animals mortality is highest while animals are young, with starvation and predation being the greatest cause of this mortality (Lack, 1954; Taylor, 1984). Young animals are vulnerable to predation because of undeveloped sensory and motor systems (Fuiman, 1989; Hayes, 1989) and their small size, which makes them vulnerable to certain predators (Werner and Gilliam, 1984). As young animals grow they are excluded from the diets of certain predators because they become too large to be captured and consumed, thus their vulnerability to some predators decreases as body size increases (Stein and Magnuson, 1976; Zaret, 1980;

Bailey, 1984; Werner and Gilliam, 1984; Brown, 1985; Milinski, 1986; Foster et al., 1988). This has been demonstrated with gape-limited predators and through habitat change studies. Gape-limited predators ingest their prey whole, so once the size of the prey becomes greater than the size of the predator's mouth, the prey is free from predation by that predator (Zaret, 1980). For instance, Wong and Ward (1972) found that yellow perch (Perca flavescens) fry less than 18 mm. long were incapable of ingesting Daphnia pulicaria with a body depth greater than 0.7 mm. due to the size of the fry's gape. In terms of habitat change, it has been demonstrated that some small animals may seek refuge from predators in a densely vegetated habitat or one with many crevices and remain in this habitat until they have outgrown some of their predators (Mittlebach, 1981; Foster et al., 1988). Stamps (1983) demonstrated a habitat change in juvenile Anolis aeeneus lizards, however in this case the juvenile lizards moved from clearings to vegetated shady areas as they grew. The reason for this change was that adult Anolis richardi dwell in the shady habitat and are predators to juvenile aeneus. Therefore, only after aeneus had reached a certain size were they capable of moving to the shady habitat without being preyed upon by adults.

The Concept of "Threat-Sensitive" Anti-Predator Behaviour in Young Animals

Because predation pressure decreases as body size increases, young animals should grow as fast as possible in order to outgrow certain predators (Werner and Gilliam, 1984; Milinski, 1986). The fastest way to outgrow predators would be to feed continuously and ignore predators, however this is very risky. Alternatively, if young animals avoided all predators with the maximum form of response, they would give up feeding opportunities to harmless predators, resulting in a slower rate of growth and more time spent in the size range vulnerable to certain predators (Stein and Magnuson, 1976; Sih, 1987; Dixon and Baker, 1988). Threat sensitive predator escape behaviour would therefore enable young animals to react in the most advantageous way to both threatening and harmless predators.

Since threat sensitive escape behaviour has been demonstrated in various adult animals and could be advantageous to small, young animals, when does it occur in the ontogeny of the animal?

The Ontogeny of Predator Avoidance Behaviour

Ontogeny of predator avoidance has rarely been the focus of direct behavioural research. Those who have addressed this topic usually set out to determine how the prey's behaviour towards their predators change as the young prey develop and

when such changes in behaviour occur in the ontogeny of the animal (Brown, 1984, 1985; Giles, 1984; Dixon and Baker, 1988; Fuiman, 1989). Fuiman (1989) demonstrated that Atlantic herring (Clupea harengus) larvae increased response to approaching predators with the development of the auditory bullae that receive acoustical stimuli from an approaching predator. Brown (1984) found that largemouth bass (M. salmoides) fry increased predator avoidance behaviour at a time in their ontogeny when their protective adult male would be leaving them on their own.

The next logical extension of study dealing with the ontogeny of predator avoidance would be a study of the ontogeny of threat sensitive behaviour. One of the predictions arising from threat sensitive behaviour is that as young animals grow in size, certain smaller predators may become relatively harmless and the prey's behaviour in the presence of these predators would change (Brown, 1984 and Stein and Magnuson, 1976). Brown (1984) demonstrated that once largemouth bass (Micropterus salmoides) fry reached a certain size they no longer avoided a small conspecific predator, but started to display aggression towards it. Similarly, Stein and Magnuson (1976) found that small crayfish (Orconectes propinguus) reduced movement and feeding activity and chose substrates affording the most protection when presented with a smallmouth bass (Micropterus dolomieui) predator, whereas crayfish which were too large to be prey for

the bass did not reduce their feeding or movement activity and did not seek refuge in the presence of the bass. These studies have focused on how the young animals react to a reduction in threat due to their increasing size. Questions dealing with the ontogeny of threat sensitive behaviour in relation to the threat posed by a size range of predators or type of predatory behaviour have not been dealt with.

I therefore set out to answer the following questions: Do larval fish show an increase in anti-predator behaviours towards larger or more active predator types and does this change as the size of the larvae increases? If it does change, when does this change occur in the development of the larvae and can it be attributed to changes in the morphology and/or life history of the larvae?

The Threespine Stickleback as the Study Species

The threespine stickleback (*Gasterosteus aculeatus*) is an appropriate species to work with due to the large amount of information available on predator avoidance behaviour in the adults and the lack thereof in the larval stage (Wootton, 1984; Fitzgerald and Wootton, 1986).

Stickleback larvae are prey to various predators including conspecifics (Foster et al., 1988), heterospecific piscivorous fish (Wootton, 1984) and aquatic insects such as odonate nymphs (Reimchen, 1980). When sticklebacks are attacked by such predators they may seek refuge, flee or freeze (Wootton,

1984). However, sticklebacks also have dorsal and pelvic spines which may be erected to increase their cross-sectional diameter, thus enabling them to escape from some gape-limited predators (Endler, 1986). In a classic experiment, Hoogland et al. (1957) found that sticklebacks with their spines removed were preyed upon quicker by perch (Perca flavescens) than those with their spines intact.

Research on juveniles and adults has found that in the presence of a predator, reduction in foraging leads to a compromise between feeding and avoiding predators (Milinski and Heller, 1978; Fraser and Huntingford, 1986; Ibrahim and Huntingford, 1988). Milinski and Heller (1978) found that in the presence of a predator, sticklebacks chose smaller patches of food thus decreasing their feeding rate but increasing their vigilance towards predators. Experience with predators (avian and piscivorous fish models) is not necessary for the development of predator avoidance behaviour in adults and fry (Giles, 1984; Tulley and Huntingford, 1987a,b). Giles (1984) demonstrated that young fry raised in the laboratory and naive to avian predators showed an appropriate fright response when attacked by a model bird. Stickleback fry raised in the laboratory, and thus naive to predators, showed escape responses to a model predatory fish appropriate to the predation risk of the population from which they were obtained (Tulley and Huntingford, 1987a). Fry from a lake with predatory fish showed stronger escape responses than fry from

a lake lacking these predators. Tulley and Huntingford therefore suggest that the differences in response may be due to a heritable control of predator escape response.

Therefore, I suggest that threat sensitive predator escape behaviour could be an advantage to larval threespine sticklebacks. Once the larvae reach a size where they are no longer vulnerable to a certain predator, they should recognise the lack of risk associated with the predator and choose not to escape from it. This would then allow for more feeding opportunities.

Materials and Methods

This study was carried out at the Ocean Sciences Centre in Logy Bay in the spring and summer of 1988 and 1989. The protocol for the methods to be used in 1989 were determined during 1988.

Preliminary Studies

In April 1988 a population of adult threespine sticklebacks (*Gasterosteus aculeatus*) were found in the O.S.C. freshwater reservoir. Adults were captured with minnow traps and brought into the laboratory at various times from April to July. The adults were placed in 37 litre holding tanks supplied with air, water at room temperature (20-22 C), and a 16L:8D photoperiod to induce breeding behaviour (Wootton, 1984). They were fed frozen *Artemia* sp. twice a day. All these fish died within two weeks due to a fungal infection, (*Saprolegnia* sp.). It was suggested, (J. Barry, pers.com) that a treatment of the water with 0.1ppm malachite green would remove the fungus. This was found to be the case. More adults were captured, brought into the laboratory and successfully brought into breeding condition. Males showing the breeding coloration, which was a bluish coloration to the dorsal area of the body and red pigmentation on the lower jaw and pectoral region, were placed in separate aquaria with a constant flow of air, malachite green treated water, a small tray (14 x 14 x 2 cm containing stones and gravel and short

pieces (1-6 cm.) of green string. The males were successful in building their nests out of these materials. When a nest was completed, a gravid female (one with a distended abdomen) was placed in an aquarium with a nested male. When they had mated (determined either by observing mating behaviour or observing the female periodically to determine if her abdomen was no longer distended), the female was removed and placed in the holding tank. The male would then fan the nest for a period of seven days, after which the eggs would hatch. If the male was left with the eggs longer than six days, he would sometimes eat them (pers. obs.). Therefore, all eggs were removed from the nest on day six of development to avoid cannibalism. The nest was torn apart and the eggs removed with forceps. The eggs were then placed in a small mesh net suspended in a five litre aquarium with an airstone beneath the net to supply the eggs with a constant flow of aerated water. The first two batches of eggs succumbed to Saprolegnia infection. A 1500 ppm malachite green dip for 10 seconds was recommended (J. Barry pers.com.), however the larvae which hatched from these treated eggs died on the day of hatching. After this, the water in the hatching aquarium was treated with 0.1 ppm Malachite Green. This treatment was successful in preventing infection. When larvae hatched, they were held in the net for three to four days during which time they rested on the surface of the net. After three to four days they began to swim and were released into the aquarium.

Initially, the larvae were fed marine rotifers for the first couple of days free-swimming and two-day-old Artemia sp. nauplii thereafter. However, I later found that stickleback larvae were capable of capturing and ingesting Artemia sp. nauplii at first feeding, so marine rotifers were deleted from the diet. The predators chosen for the experiments were conspecific adults and dragonfly nymphs (Aeschna sp.) because both were present in the pond from which the adults were obtained and both are predators of stickleback larvae (pers. obs.; Reimchen, 1980; Foster et al., 1988). Initially, salmonid predators were to be used instead of the conspecifics, however, due to the relatively high water temperature during observations (20-22 C), which would be lethal to the salmonids, and the lack of small salmonids at the O.S.C. during the study, the conspecific predator was chosen over the salmonid.

Collecting and Rearing Larvae

The protocol for collecting and rearing larvae during 1989 was developed during the previous summer, with some improvements. When males started to develop breeding coloration they were removed from their holding tanks and placed in mating chambers. These chambers were 75 litre aquaria divided in half by an opaque barrier. One male was placed on each side of the barrier with a tray full of nesting material. The induction of mating behaviour and the

subsequent care of eggs were as previously described. After the larvae hatched they remained in the net until free swimming, three to four days post-hatch. At four to five days post-hatch the larvae were released into the five litre aquaria which now served as a holding tank. They were fed twice a day ad libitum with two-day-old Artemia sp., nutritionally enhanced with Selco (Artemia Systems, Belgium). Each brood of larvae was held in a separate aquarium to avoid mixing larvae of different ages.

Experiments

Two experiments were designed to test the following hypotheses:

1) With increasing predator size, feeding activity and the amount of time larvae spend adjacent to the predator will decrease, and predator-escape behaviour of larvae will increase.

2) As the larvae approach the size of the predators (predator to larvae size ratio decreases), feeding activity of the larvae will increase and predator-escape behaviour of the larvae will decrease.

3) Larvae in the presence of an active predator compared to those in the presence of a non-active, ambush predator will feed less, spend less time adjacent to an active predator, and perform more predator-escape behaviour in the presence of an active predator.

All experiments were carried out in 37 litre aquaria (50 x 25 x 30 cm.) divided into two chambers, one measuring 17 x 25 x 30 cm. (predator chamber), and one measuring 33 x 25 x 30 cm. (larvae chamber). These two chambers were separated by two partitions, one removable and opaque and the other being non-removable and transparent. The larvae chamber was divided into three 11 cm grids by drawing vertical lines on the front and back of the aquarium. Twenty- four hours prior to observations, three larvae were placed in the larval chamber and a predator placed in the predator chamber. Neither the larvae nor the predator were fed during this twenty-four hour period. Prior to observations, approximately 600 live, two day old Artemia sp. nauplii were placed in the feeding chamber in order to observe the feeding behaviour of the larvae, and the opaque partition removed. The observer sat motionless approximately 15 cm. from an aquarium and observed each larvae for one minute, recording the number of Artemia sp. captured and the number of turns performed by a larvae in each grid, the amount of time in each grid, the total amount of time the larvae were active, the type and occurance of any predator escape behaviour and a categorization of the general activity of the predator. A capture was defined as the intake of a food item into the mouth of the larvae. A turn was a rotation of the lonitudinal body axis that resulted in a change in the orientation of the body. After an observation period the larvae were removed and placed in a holding aquarium. Larvae

were tested only once to avoid any effect that prior experience with a predator may have on the larvae's behaviour. The experimental aquaria, breeding chambers, larval rearing and holding tanks, and predator holding tanks were all kept in an isolated room to control for unnecessary visual disturbance. Two experiments were carried out. Protocols for these experiments were identical, but the predators and study periods differed. In Experiment One, different sizes of conspecific predators were used. These were classified as small (X = 4.15 cm total length), medium (X = 5.0 cm tl.), and large (X = 6.4 cm tl.). A total of eight experimental aquaria were used per day in Experiment One, two for each of the three predator sizes and two for controls containing no predators. Experiment One lasted for 26 days with observations being carried out every second day from day four post-hatch to day 30 post-hatch, resulting in a total of 14 days of observations. In Experiment Two, two different types of predators were used: medium sized conspecific predator (X = 5.0 cm tl.) and a dragonfly nymph. A total of six observation aquaria were used per day, two for each of the predator types and two for controls containing no predator. Experiment Two lasted for 28 days, with observations carried out every second day from day three post-hatch to day 31 post-hatch, resulting in a total of 15 days of observations.

Predation on Larvae in the Laboratory

To determine the age and size at which the larval sticklebacks were no longer taken by the various predators, larvae were placed in aquaria with predators. Larvae were exposed to predators at day one and day five post-hatch and every five days after until 30 days post-hatch. During exposure, two larvae of the same age were placed in a 17 litre aquaria and then one of the laboratory predators were added. After one hour the number of larvae remaining were noted.

Clearing and Staining of Larvae

A clearing and staining technique was performed on a sample of stickleback larvae in order to describe the development of the dorsal and pelvic spines. This technique clears the tissues of all pigment so that the muscle becomes transparent and stains the cartilage blue and the bone red (Potthoff, 1984). A detailed description of this process is available in Potthoff (1984). The following is a brief summary of my protocol. Two larvae on day one post-hatch, three days post-hatch and every three days after until 30 days post-hatch were over-anesthetised with MS222 and placed in 10% formalin. After approximately a month in the formalin, the larvae were removed and washed in several changes of distilled water. The larvae were then placed in alcian blue stain until the stain was taken up by the larvae. The larvae were then put through an alcohol series of 95% alcohol, 75%, 40%, 15%, and finally,

distilled water. Following this they were placed in a solution of sodium borate and trypsin enzyme. The larvae remained in this solution until the bones and cartilage were clearly visible. They were then placed in a solution of 0.5% potassium hydroxide and alizarin red stain until the stain was absorbed by the sample. The final step was a series of potassium hydroxide/glycerine solutions, the last of which was a solution of 100% glycerine in which the sample is kept. A few crystals of thymol were added to inhibit the growth of molds and/or bacteria.

Field Observations

During July of 1989, two males guarding nests and larvae were observed from the shoreline of the pond where adults were captured. I would approach the area of the shoreline where a nest was located and sit motionless on the shore and observe the males and larvae. Observations were performed for a period of six days, after which both the males and larvae had left the nest area. Observations were usually performed mid-afternoon when the fish were most visible. The number of days that the larvae remained with the male was determined and any interactions among the larvae and the male or predators noted. Some larvae were removed from the nest area with a 60cc Syringe attached to a one ml. pipette. This apparatus was preferential to a net because it disturbed fewer fish and took a small sample size. These larvae were over anesthetised

with MS222 and preserved in 10% formalin in preparation for the cleaning and staining procedure.

Statistical Analysis

Prior to statistical analysis, the data were checked for homogeneity of variance and normality of distribution. Homogeneity was checked using the F-max test (Sokal and Rohlf, 1981) and normality checked using the Kolmogorov-Smirnov goodness of fit test. Because certain of the frequency and time distributions were not normal, the frequency data were square root transformed and the time data arcsine transformed to achieve normality. Two-way analysis of variance was used to determine if the predator or age treatments influenced the activities of the larvae. If the predator treatment was found to significantly influence any activities, a Duncan's multiple range test was performed to determine which predator treatments influenced the performance of the activity. The Student's T-test was then performed within each week amongst pairs of predator treatments found to be significantly different in order to determine the ages of larvae which differed significantly in their activities.

RESULTS

Predator-Escape Behaviour

Larval sticklebacks displayed three distinct predator escape Modal Action Patterns (MAPs) when confronted with an active predator. These were Freeze, Flee, and Flee-Approach. Freeze was defined as a cessation of all locomotive movement, resulting in the larvae remaining motionless in the water column. Flee was a very quick (<1 sec.) swimming movement directed away from the predator. Flee-Approach was considered a single MAP because the approach component was only observed following a Flee. The larvae would flee, stop, turn towards the predator and slowly swim back towards it, fixating on the predator during the entire approach sequence.

These MAPs were observed only in the grid closest to the predator. No predator escape MAPs were observed in the control aquaria (lacking predators) or in the two grids not adjacent to the predator. The grid closest to the predator was the only grid where predators directed attacks at the larvae, though the transparent barrier rendered all of the attacks unsuccessful.

Predator-Escape Behaviour: Experiment One

The data used for this section was obtained by lumping the occurrence of a particular MAP from all predator sizes. The

lack of direct attacks by each predator size class made it difficult to determine if certain predator escape MAPS were used selectively against different sized predators. Seventy four percent (20/27) of larvae receiving attacks responded with the MAPs freeze, flee, or flee-approach (Table 1). Only 1.5% (3/207) of larvae performed these MAPs to an active, non-attacking predator

Fleeing was observed throughout the five week study, appearing most in Week Three (Fig.1a). Freezing was not observed after Week Three (Fig.1b) while flee-approach was first observed in Week Three and remained in the repertoire until the end of the observation period (Fig.1c). There was no clear trend in the number of larvae that did not show any predator-escape responses to the direct attacks of the predator (Fig.1d).

Predator-Escape Behaviour: Experiment Two

During Experiment Two, the dragonfly nymph was inactive during 88 of 89 exposures to the larvae. One active, direct attack was observed, resulting in the larva fleeing. In those cases where the stickleback was used as a predator, 88% (8/9) of the larvae receiving direct attacks responded with either of the three predator-escape MAPs (Table 2). Only 5.4% (3/55) of the larvae responded with predator-escape to an active, non-attacking predator.

Fleeing was observed during Weeks Two, Four and Five

(Fig.2a). Freezing was observed during Weeks Two and Three (Fig.2b), while flee-approach was observed during Weeks Three and Four (Fig.2c). There was only one occurrence (Week Four) of a larva not responding to a direct attack.

Feeding Behaviour

Feeding behaviour in larval sticklebacks consisted of two MAPs; Turn and Capture. Turn was defined as a rotation of the longitudinal body axis which resulted in a change in the orientation of the body. Capture was defined as the intake of a food item into the mouth of the larvae. Typically, larvae would turn towards the food item, approach it and then capture it.

In Experiment One, the weeks treatment had a significant influence on the frequency of feeding activity, captures, turns, capture rate and turning rate (Tables 3 and 4). Figures 3 through 20 indicate that this influence is due to an overall increase in the various feeding behaviours and rates from the Week One to Week Five post-hatch.

In Experiment Two, the weeks treatment did not have the same overall influence on the various feeding activities noted in Experiment One (Tables 5 and 6). Figures 23 through 40 show no overall increase in feeding behaviours and rates over the five week period.

Feeding behaviour: Experiment One

The number of captures and turns performed per larvae were added together, to create a variable termed feeding which represented overall feeding activity. Larvae in the grid farthest from the predator chamber (Fig.3) and those in the middle grid (Fig.4) did not show a significant difference in the amount of feeding activity performed in the presence of the different sized predators (Table 3). Larvae in the grid adjacent to the predator chamber (Fig.5) however, showed significant differences in the feeding activity when exposed to the different sized predators (Table 3). Given this, only the feeding activity of larvae in the grid adjacent to the predator were examined in detail.

Larvae exposed to the large predator performed less feeding activity overall than larvae not exposed to a predator (Duncan's multiple ranges test; $p<0.05$, Fig.5). Examining the data on a weekly basis, larvae exposed to the large predator performed significantly less feeding than control larvae during Weeks Four (Student's T-test; $t=2.18$, $p<0.05$) and Five ($t=2.69$, $p<0.05$). Larvae exposed to the medium sized predator also performed less feeding overall than control larvae ($p<0.05$, Fig.5). On a weekly basis, there were significant differences during Weeks Two ($t=2.20$, $p<0.05$) and Four ($t=2.10$, $p<0.05$). Larvae exposed to the large predator performed less feeding activity overall than those larvae exposed to a small predator ($p<0.05$, Fig.5), with a

significant difference existing during Week Four ($t=2.80$, $p<0.05$). No significant differences in feeding activity existed between those larvae exposed to a small predator and those exposed to a medium predator ($p>0.05$), between larvae exposed to the small predator and the control larvae ($p>0.05$) and between larvae exposed to the large predator compared to the larvae exposed to the medium sized predator ($p>0.05$).

To examine the differences in feeding activity in more detail the mean number of captures and turns were analysed separately. The results were very similiar to those found for overall feeding activity. Within the grid adjacent to the predator there was a significant difference in the mean number of captures performed in the presence of the different sized predators (Table 3., Fig.6). Specifically, larvae exposed to the large predator performed significantly less captures overall than control larvae ($p<0.05$, Fig.6), with a significant difference in the mean number of captures performed during Week Five ($t=2.49$, $p<0.05$). Larvae exposed to the large predator also performed significantly less captures overall than larvae exposed to the small predator ($p<0.05$, Fig.6). In this case there were no weekly significant differences. Larvae exposed to the medium sized predator did not perform an overall significantly different number of captures than larvae exposed to the large ($p>0.05$) or small ($p>0.05$) predators or the control larvae ($p>0.05$). As well, larvae in the presence of the small predator did not

perform a significantly different number of captures than control larvae ($p>0.05$).

Larvae in the middle grid showed no significant difference in the mean number of captures performed in the presence of different sized predators (Table3, Fig.7), while larvae in the grid farthest from the predators did show a significant difference in the mean number of captures performed when exposed to different sized predators (Table3, Fig.8). Specifically, larvae exposed to the small predators performed significantly fewer captures than larvae exposed to the other predators during Week Two: large predators ($p<0.05$, Fig.8), medium sized predators ($p<0.05$, Fig.8) or no predators ($p<0.05$, Fig.8).

Larvae in the grid closest to the predator also showed a significant difference in the mean number of turns performed when exposed to the different sized predators (Table 3, Fig.9), while larvae in the middle (Fig.10) and farthest (Fig.11) grids did not (Table 3). Data from the larvae in the grid adjacent to the predator were analysed in more detail. Overall, larvae exposed to the large predator performed significantly less turns than control larvae ($p<0.05$, Fig.9) with significant differences during weeks Four ($t=2.61$, $p<0.05$) and Five ($t=2.53$, $p<0.05$). Larvae exposed to the large predator also performed significantly fewer turns overall than larvae exposed to the small predator ($p<0.05$, Fig.9), with a significant difference during Week Four

(t=2.54, p<0.05). Larvae in the presence of the medium sized predator also performed fewer turns than control larvae (p<0.05, Fig.9), with significant differences within Weeks Three (t=2.93, p<0.05) and Four (t=2.38, p<0.05). There were no overall significant differences in the number of turns performed between larvae exposed to the medium and small predators (p>0.05), the medium and large predators (p>0.05), or the larvae exposed to the small predators and the control larvae (p>0.05).

During observations, larvae would swim within the aquaria, spending varying amounts of time in each of the three grids. Only in the grid adjacent to the predator did the amount of time larvae spent within the grid differ significantly among the predator size-classes (Table 4, adjacent grid: Fig.12, middle grid: Fig.13, farthest grid: Fig.14). Both the larvae exposed to the large predator and those exposed to the medium predator spent significantly less time overall in the grid adjacent to the predator than the control larvae (p<0.05 in both cases, Fig.12). On a weekly basis, these differences were significant during Weeks One (t=2.10, p<0.05) and Three (t=2.23, p<0.05) between larvae exposed to the large predator and the control larvae, and also between Weeks One (t=2.85, p<0.05) and Three (t=2.50, p<0.05) between larvae exposed to the medium predator and the control larvae. Larvae in the presence of the large predator also spent less time overall in the grid adjacent to the predator than larvae exposed to the

small predator ($p<0.05$, Fig.12) although none of the weekly differences were significant. Larvae exposed to the medium predator also spent significantly less time overall in the grid adjacent to the predator than did those larvae exposed to the small predator ($p<0.05$, Fig.12), with a weekly significant difference existing during Week Four ($t=2.34$, $p<0.05$). Larvae exposed to the small predator did not differ from control larvae in the amount of time spent in the grid adjacent to the predator ($p>0.05$). This was also the case for larvae exposed to the medium sized predator when compared to the larvae exposed to the large predator ($p>0.05$).

To determine if larval sticklebacks differed in the number of captures and turns they performed per unit time in the presence of different sized predators, the number of captures and turns per minute were calculated. The total number of captures or turns performed by a larva in a grid was divided by the total amount of time the larva spent in that grid (in seconds). This number was then multiplied by 60 to give the number of captures or turns per minute. There were no significant differences in the mean number of captures per minute performed by larvae in the farthest (Fig.15) or middle grids (Fig.16, Table 4), however the size of the predator did appear to have a significant influence on the capture rate in the adjacent grid (Fig.17, Table 4). Although no two predator treatments were significantly different overall, larvae exposed to the large and medium predators had significantly

lower capture rates than the rate shown by control larvae during Week Two (large/control: $t=2.36$, $p<0.05$; medium/control: $t=2.98$, $p<0.05$, Fig.17). Larvae exposed to the large predator had a lower capture rate than those larvae exposed to the small predator, though none of these weekly differences were significant (Fig.17). The same can be said for the capture rate of larvae exposed to the medium predator when compared to the rate shown by larvae exposed to the small predartor (Fig.17). There were no significant differences between the capture rate of larvae exposed to the small predator compared to the control larvae and no differences in capture rate between the larvae exposed to the medium predator and those in the presence of the large predator.

The size of the predator did not influence the turning rate in the furthest (Fig.18) and middle grids (Fig.19, Table 4), however size of the predator did appear to influence the turning rate in the grid adjacent to the predator (Fig.20, Table 4). As with the capture rates, no two predator treatments were significantly different overall. However, on a weekly basis, larvae in the presence of the large predator had a significantly lower turning rate than control larvae during Week Four ($t=2.51$, $p<0.05$), while larvae exposed to the predator had significantly lower turning rates than control larvae during Weeks Three ($t=3.52$, $p<0.05$) and Four ($t=2.29$, $p<0.05$). Larvae in the presence of the medium predator had a significantly lower turning rate than larvae

exposed to the small predator during Week Three ($t=2.93$, $p<0.05$). There was also a significant difference in turning rate between larvae exposed to a large predator and those exposed to a small predator during Week Four ($t=2.28$, $p<0.05$). There were no significant differences in turning rate between larvae exposed to a small predator and the control larvae, or between larvae exposed to the medium predator and those exposed to a large predator.

Predator/Larvae Size Ratio and Feeding

The observed reduction in the number of turns or captures performed in the presence of a small predator compared to a larger predator leads to the question of whether this reduction is due to the absolute size of the predator or the relative size of the larvae to the predator. To address this question a ratio of predator size to larvae size was calculated by dividing the length of the predator by the mean length of the larvae for each week. This resulted in three ratio values per week, one for each of the three predator sizes, over the five week period. These values were then compared to the weekly mean number of captures and turns performed in the grid adjacent to the predator. Spearman's Rank Order Correlation Coefficient indicated that this ratio was negatively associated with the mean number of captures ($r_s= -0.5832$, $p<0.05$, Fig.21) and the mean number of turns ($r_s= -0.5682$, $p<.05$, Fig.22). Generally, the smaller the ratio the

more captures and turns performed as the larvae approach the size of the predator.

Feeding Behaviour: Experiment Two

In this experiment the responses of larvae to different types of predators were compared. The treatments were a medium sized stickleback, a dragonfly nymph and controls (no predator). The type of predator did not have a significant influence on feeding activity performed by larvae in the three grids (Table 5, farthest grid: Fig.23; middle grid: Fig.24; adjacent grid: Fig.25).

The type of predator also did not significantly influence the number of captures performed by larvae within the three grids (Table 5, farthest grid: Fig.26; middle grid: Fig.27; adjacent grid: Fig.28). This was also the case for the mean number of turns (Table 5, farthest grid: Fig.29; middle grid: Fig.30; adjacent grid: Fig.31).

The type of predator also did not affect the amount of time spent by the larvae within the three grids (Table 6, farthest grid: Fig.32; middle grid: Fig.33; adjacent grid: Fig.34).

As well, the type of predator also did not influence the capture rate within either of the three grids (Table 6, farthest grid: Fig.35; middle grid: Fig.36; adjacent grid: Fig.37). The type of predator appears to have influenced the turning rate within the grid adjacent to the predator (Table 6, Fig.38) and the grid furthest from the predator (Table 6,

Fig.39), but not the middle grid (Table 6, Fig.40). Within the grid adjacent to the predator, no two predator treatments were significantly different overall, however, during Week Three both the larvae exposed to the dragonfly and the larvae exposed to the conspecific predator had a significantly lower turning rate than control larvae (dragonfly/control: $t=2.81$, $p<0.05$; conspecific/ control: $t=2.46$, $p<0.05$, Fig.38). Within the grid furthest from the predator larvae exposed to the dragonfly nymph had a lower turning rate overall than larvae exposed to the conspecific predator ($p<0.05$, Fig.39). On a weekly basis, this difference was significant during Week Two ($t=4.49$, $p<0.05$). Neither the larvae exposed to the dragonfly nymph nor the conspecific predator had turning rates significantly different than the turning rates of control larvae (dragonfly/control: $p>0.05$; conspecific/ control: $p>0.05$).

Spine Development

On day 15 post-hatch (X Total length = 11.8mm, week 3) the dorsal and pelvic spines were visible, however no stain was absorbed by them (Fig.41). On day 18 (X tl. = 11.2mm, Week 3) the spines absorbed the alcian blue stain, indicating that the spines were composed of cartilage at this point in development (Potthoff,1984). The spines retained the blue dye through day 21 (X tl. = 14.0mm, week 4). By day 24 (X tl. = 14.4mm, week 4), the spines absorbed the alizarin red stain

and appeared purple. This indicated that the spines were composed of bone. The spines retained the purple color for the rest of the sampling period.

Predation

Both small and medium sized predators captured and consumed larvae at ages one, five (Week One), and ten days (Week Two) post-hatch (Fig.42). At day ten post-hatch, larvae attained a mean total length of 9.8mm. From day 15 (Week Three)(X tl.= 11.8mm.) to day 30 (Week Five) post-hatch (X tl.= 16.1mm.) none of the larvae were captured or consumed by the small and medium sized predators. Large predators captured and consumed larvae from day one to day 25 (Week Four) post-hatch (X tl. = 14.4mm.). On day 30 post-hatch (X tl. = 16.1mm.) no larvae were taken by the large predator. Day 20 post-hatch (Week Three)(X tl. = 14.0mm.) larvae were the only larvae captured and consumed by the dragonfly nymph.

Field observations

Two males were observed guarding their free-swimming larvae for a period of six days each, however the exact age of the larvae could not be determined. After six days, the larvae dispersed from the nest area and could not be followed. On the second and sixth day of observation, three larvae from each nest were captured. The mean total length of both groups on the second day was 7.7mm., while on the sixth day the mean

lengths were 8.1 and 8.6mm.. If the growth rates of lab and field larvae are similiar, the larvae would be three to six days old (Fig.41) when I began observations and 9-12 days old when they left the nest area.

Males would swim around and through the cluster of larvae, occasionally leaving the nest area to chase away adult conspecifics and other intruders. I did not observe larvae fleeing from their male guardians, nor did I observe direct attacks of the father on the larvae. The larvae would remain in a small cluster approximately 10 cm. in diameter near the nest. Larvae moved independently, not as a school. Most of their movements were comprised of swimming and turning, and were probably associated with feeding behaviour.

DISCUSSION

Predator-Escape Behaviour

The concept of threat-sensitive, anti-predator behaviour predicts that a prey is able to assess the immediate threat posed by a predator and then respond in a manner appropriate to the magnitude of the threat (Helfman, 1989). The larval sticklebacks used in this study, which were less than 30 days post-hatch and predator naive, were found to be threat sensitive to the predators they encountered. This conclusion is based on the observation that larvae used the flee, or flee-approach, predator-escape MAPs only when directly attacked and that larvae spent less time adjacent to large predators and fed less when adjacent to larger predators.

The three predator-escape MAPs performed were freeze, flee and flee-approach. Flee and flee-approach were performed only when the larvae were attacked and not only when the predator was active. Freeze was the only MAP used towards active, non-attacking predators, but was also performed when larvae were attacked. Thus, direct attacks, which may be considered the strongest threat, elicited the strongest response, in the form of the flee MAPs. An active, non-attacking predator was less threatening and the larvae responded with the freeze MAP, a weaker response, or no response at all. This is similar to the interaction between damselfish (*S. planifrons*) and trumpetfish (*A. maculatus*), where damselfish show a strong

escape response to a strong threat from the trumpetfish and a weak response to a weak threat (Helfman, 1989). This gradation in response to predator threat is based on the hypothesis that it is non-adaptive to perform a maximum escape response to a non-threatening predator because other important activities such as feeding or mating may be jeopardized (Coates, 1980; Dill, 1987; Licht, 1989). Animals that are able to assess degrees of threat posed by a predator and respond appropriately should be selected for. For larval sticklebacks, it may be more adaptive to freeze or show no response to a non-attacking predator so the larva does not have to give up its present foraging area.

This may be particularly relevant for larval sticklebacks being guarded by a male. It is unknown if stickleback larvae are able to distinguish their guarding males from other conspecifics. If they cannot, then it would be advantageous for the larvae to respond with predator escape behaviour only to direct attacks. If the larvae responded to just the presence of a male, then they would needlessly reduce their feeding activity. Certainly, direct attacks from guarding males are the only behaviours which should elicit escape behaviour from the larvae. Such attacks occur when males capture wandering larvae in their mouths and spit them back into the nest area (Tinbergen, 1968). Tulley and Huntingford (1987 a,b) suggest that this form of larvae retrieving behaviour may facilitate predator avoidance in the larvae.

Both flee and freeze have been previously documented for adult sticklebacks (Wootton, 1984), however the MAP of flee-approach, to my knowledge, has not been documented. This MAP may be the precursor to predator inspection behaviour by adult sticklebacks (Wootton, 1984). The flee-approach MAP appeared in the behavioural repertoire of the larvae during their third week post-hatch, when the larvae had attained a total length of 11.8 - 12.5 mm. This corresponds to the size at which the dorsal and pelvic spines appeared on the larvae (11.8 mm tl.) and the week after the larvae have left the guarding males in the wild. The development of the spines as a form of morphological defense may allow an increased boldness towards the predators, thus the onset of the flee-approach MAP. As well, the approach component may be a form of agonism which may serve as a retaliation towards the attack or may serve to drive the predator away (Helfman, 1989).

Feeding Behaviour

The feeding behaviour of larval sticklebacks consists of two MAPs, turn and capture, which occurred consistently in the feeding repertoire from first feeding until the end of the 30 day observation period. This is a relatively simple repertoire which is similiar to that of the adults (Pers. obs.). In comparison, some larval fish have complex feeding repertoires that are very different from their adult counterparts. Brown and Colgan (1984, 1985) found that

centrarchid larvae have three MAPs that disappear from the feeding repertoire as the larvae grow in size. They hypothesised that species with larger, morphologically advanced larvae would use these MAPs less frequently and the MAPs would disappear from the repertoire of larger larvae sooner than small larvae. This was found to be the case. Relatively large smallmouth bass (Micropterus dolomieui) larvae (total length= 8.2mm) used the three MAPs less frequently and ceased using them sooner than the smaller black crappie (Pomoxis nigromaculatus) larvae (4.8mm tl.). The crappie larvae also used S-posture feeding for a longer period of time than the bass larvae (Brown and Colgan, 1985).

The stickleback larvae in this study do not support the hypothesis of Brown and Colgan (1985), as the relatively small stickleback larvae (5.4mm tl.) have a feeding repertoire almost identical to that of the adults. As well, there is no change in the repertoire as the larvae grow in size, and the S-posture feeding used by many larval fish is not used at all. In this case, as suggested by Brown (1986), an hypothesis that attempts to predict the ontogeny of feeding behaviour for larval fish may be more useful if the state of development of the larvae at hatching, along with their size, is used. At the free-swimming stage, larval sticklebacks are relatively well developed with large, functioning eyes, a functional mouth and well developed pectoral fins with cartilagenous fin rays. With the pectoral fins, the larvae are able to perform

the sculling style swimming used by the adults, and do not need to perform other MAPs, including the S-posture feeding.

As the larvae grew, there was an increase in the frequency of captures and turns performed by the control larvae in Experiment One. This was expected due to development of the musculature and sensory systems along with increased proficiency in feeding behaviour. However, in Experiment Two, there was a decrease in frequency of captures and no clear trend of either increase or decrease in the frequency of turns as the control larvae grew in size. This result was unexpected as conditions between both experiments were identical except for the predator treatments, which would have no effect on the control larvae.

In summary, stickleback larvae do not fit the hypothesis for the ontogeny of feeding behaviour proposed by Brown and Colgan (1985) due to their small size and unlarval-like feeding behaviour. It appears that the state of development of the larvae at hatching may therefore be more useful than size when trying to predict the ontogeny of feeding behaviour in larval fish.

Predator-Avoidance Behaviour: Experiment One

The distance and/or the amount of time a prey stays away from a threatening stimuli indicates how threatening that stimuli appears to the prey. Prey should keep a greater distance and spend more time farther away from a strong threat compared to a weak or non-existant threat. Larval sticklebacks in this study appeared to assess large and medium-sized predators as more threatening than small ones and spent less time adjacent to the large and medium sized predators compared to the time spent adjacent to the small predator. This is supported by the observation that larvae exposed to the small predator spent no less time in the grid adjacent to the small predator than control larvae in the grid adjacent to an empty predator chamber. Similiar results have been documented with other fish. Licht (1989) demonstrated that adult guppies (Poecillia reticulata) spent less time near hungry predators than near satiated predators. Although Licht's study was on adult fish, it does indicate that not all predators are treated as equal, but rather that prey are able to distinguish levels of threat within a predator type. The present study suggests that larval sticklebacks are able to do the same, using predator size as a criterion to evaluate threat.

The results of predation by the three size classes of predators indicate that large predators consumed larvae less than 16 mm total length and the medium and small predators

consumed larvae less than 11.8 mm total length. Based on this, I would expect larvae to cease to avoid the small and medium size predator shortly after the second week post-hatch, when these predators no longer preyed on the larvae. As well, the large predator did not prey on larvae in their fifth week post-hatch, so I would predict that larvae should stop avoiding the large predator after Week Four. The results partially support these predictions. Larvae exposed to the small predator spent less time, though not significantly, adjacent to the predator grid than control larvae during the first three weeks (with the exception of week two) compared to Weeks Four and Five. Larvae exposed to the large and medium predators spent significantly less time adjacent to the predator grid than control larvae during Weeks One and Three. The lack of a significant difference between the control larvae and those larvae exposed to the large and medium predators during Week Two cannot be explained. However, the data appear to support the hypothesis that the larvae behave appropriately towards a predator whose apparent threat may be size dependent. In this case larvae avoided predators when they were of a size to be dangerous, but spent less time avoiding the smaller predator.

Larvae also performed less feeding activity in the presence of the large and medium predators than to a small predator or no predator. The same predictions made for time adjacent to the predators may be made for feeding activity. That is,

shortly after the second week larvae exposed to the small and medium predators should have feeding activities similiar to the control larvae, whereas larvae exposed to the large predator should have feeding activities similiar to the control larvae during Week Five. Larave exposed to the small predator did have similiar feeding activity to the control larvae after Week Two. Those exposed to the medium predator, however, did not approach the level of feeding shown by the controls until Week Five and larvae exposed to the large predator maintained reduced feeding levels throughout the five weeks. The larvae behave more cautiously than predicted towards the large and medium predator. Nonetheless, larvae did reduce their foraging in the presence of the large and medium predators, indicating they assess these predators as more threatening than the small predator. This result is important to survival of the larvae because larvae exposed to more threatening predators feed less, should have reduced growth, and thus spend more time vulnerable to predators. In nature, larvae would be exposed to an assortment of predators of varying threat. If larvae do reduce their feeding in the presence of threatening predators, it is advantageous to reduce feeding as little as possible. This should be accomplished by adjusting this reduction according to the level of threat.

When the larvae were adjacent to the predators, the mean capture and turn rates for larvae exposed to large and medium

predators were less than the capture rate of control larvae for most weeks. Thus, the larvae exposed to the greater threat (ie. large predators) may be more vigilant than the control larvae and those larvae exposed to the lesser threat (ie. small predator). This was true for adult sticklebacks exposed to a cichlid predator (Milinski, 1986). When the sticklebacks were near the cichlid, they reduced their foraging rate and spent more time being vigilant. Helfman (1989) also noted a depression in feeding by damselfish when they encountered trumpetfish predators. Reduced foraging rate translates to a decrease in energy gain resulting in a decrease in growth. This is particularly important for larval fish which should grow as fast as possible in order to outgrow certain predators and increase their chances of survival. In this study the larval sticklebacks exposed to the small predator maintained a feeding rate similiar to that of the control larvae. These fish behave appropriately by not reducing their feeding rate in the presence of a less threatening predator.

Predator-avoidance: Experiment two

In this experiment, the larvae exposed to a dragonfly nymph and those exposed to the medium sized stickleback behaved like control larvae exposed to neither predator. Although there were no statistically significant differences, the larvae exposed to dragonfly nymphs fed consistently less and had capture and turning rates consistently lower than the control larvae over the five week period. Based on the predatory behaviour of dragonfly nymphs, it is easier to explain a similarity than a difference between the control larvae and those exposed to the dragonfly nymphs.

The dragonfly nymph, which is an ambush predator (Reimchen, 1980), remained motionless for all except one of the observation periods, as expected from an ambush predator. Therefore, because of the lack of motion by the nymph, the stickleback larvae did not detect its presence and behaved as if no predator were present. Foster et al. (1988) found that stickleback fry 5-25mm long would avoid vegetation inhabited by dragonfly nymphs. If this is the case, then the fry must have been responding to failed attacks from the nymphs and learning to avoid the vegetation because the results from my study indicate that larvae do not respond to just the presence of nymphs. Larvae may also have been responding to olfactory cues in the study by Foster et al. (1988), however the ability of larval sticklebacks to respond to olfactory cues is undetermined. It would be interesting to determine if the

larvae are threat-sensitive to nymphs that they have detected. If they were threat-sensitive, larvae should approach a nymph closer than a pursuit predator because the nymph can only make successful attacks within the short distance of its feeding palps (Reimchen, 1980), whereas the pursuit predator can attack the larvae from a greater distance.

If the consistently lower feeding values of the larvae exposed to the dragonfly nymph are due to the presence of the predator, then this is not easily explained. If a motionless ambush predator such as the dragonfly nymph should gives no visual cues for the larvae to detect, the larvae should behave as if no predator were present.

I did not expect the same behaviour between the larvae exposed to the medium sized predator and the control larvae, because in Experiment One larvae avoided this size predator. Close examination of the data do, however, indicate a lower mean frequency of feeding, captures and turns but no difference for time adjacent to the predator and feeding rates during Weeks Two through Four. The reason for the difference in behaviour of larvae exposed to the same predators under the same conditions in the two different experiments is not clear.

Based on the differences in the predatory behaviour of the two predators used in this experiment, I predicted that larval sticklebacks would not respond to the dragonfly nymph due to its lack of motion and thus behave as the control larvae. I also predicted that the larvae exposed to the active, medium

sized conspecific predator would perform less feeding activity, spend less time adjacent to the predator grid and have a lower feeding rate than control larvae. The results of this experiment are inconclusive and fail to reject or support my predictions.

Predator/Larvae Size Ratio

Size, and its importance in predator-prey interactions can be considered at two levels: the absolute size of the predator and the prey, and or the relative size of the predator to the prey (the ratio between the two). The absolute size should only be considered important in a situation when the predator is so large, or the prey so small, that no matter how large the prey grows, it remains vulnerable to predation by that predator. For instance, most copepods, no matter how large they grow, will still be vulnerable to predation by adult planktivorous fish.

The relative size, or ratio of predator size to prey size, has been suggested to be an important factor when considering predator-prey interactions because in this situation it is possible for the prey to grow to a size where it is no longer possible for the predator to capture or ingest the prey (Brown, 1984; Miller et al., 1988; Helfman, 1989). Miller et al. (1988) looked at predator/prey size ratios in terms of capture success of larval fish predators and found that the capture success of small predators is more dramatically

influenced by changes in prey size than is the success of large predators. This makes sense because it is easier for a prey to outgrow a smaller predator than a larger one. Helfman (1989) suggested that agonistic attacks by prey towards their predators may be influenced by the size ratio between the two, with the prey attacking predators that are marginally too small to capture the prey. Such behaviour would occur when the prey is territorial and is attempting to drive the predator away.

In this study, the ratio between predator size and larve size could be a more important indicator of predator threat than the absolute size of either the larvae or the predators. This is indicated by the observed increase in feeding activity as the ratio decreases (larvae bigger relative to the predator). This increase in feeding behaviour in the presence of the predators indicates an increased boldness towards the predators. For instance, when the predators are only three times larger than the larvae, they perform more feeding activity than when the predators are eight times larger than the larvae. Therefore, stickleback larvae may somehow be aware of their size relative to the size of a predator and use this to assess the threat of predation.

Summary

The concept of threat-sensitive predator-avoidance behaviour arose from the idea that it would be non-adaptive for a prey to give up feeding and/or mating opportunities to predators which pose little to no threat (Sih, 1987; Helfman, 1989; Licht, 1989). Rather, prey should be able to use cues to distinguish harmful from harmless predators and behave appropriately to both (Sih, 1987; Helfman, 1989; Licht, 1989).

In the case of young animals, one possible strategy to avoid some predators would be to outgrow them (Werner and Gilliam, 1984; Milinski, 1986). To do this, young animals should feed as efficiently as possible, which includes not giving up feeding opportunities to harmless predators, such as small predators. Therefore, threat-sensitive predator-avoidance behaviour should be particularly important to young animals.

From these studies on larval sticklebacks it appears that sticklebacks less than 16 mm tl. (30 days post-hatch) are capable of assessing the threat posed by different sized conspecific predators and modifying their feeding behaviour in an appropriate fashion to the level of threat encountered. As well, the relative size of the predators to the larvae appears to be an important cue used to assess the threat of the predator.

Further research into the field of threat-sensitive predator-avoidance with larval fish should concentrate on

determining how important the ratio between predator and larvae size is to the larvae in determing the level of threat posed by the predator. A detailed investigation into the cues used by larvae to determine the predatory intentions of a predator such as olfaction, predator size, and activity level of the predator would also be profitable.

Table 1. The number of larvae performing predator-escape MAPs in response to predator activity during Experiment One.

Larval Response	Predator Activity			
	No predator	Predator not active	Predator active, no direct attack	Predator active, direct attack
No response	78	18	207	07
Freeze	00	00	03	04
Flee	00	00	00	12
Flee-approach	00	00	00	04

Table 2. The number of larvae performing predator-escape MAPs in response to predator activity during Experiment Two.

Larval Response	Predator Activity			
	No predator	Predator not active	Predator active, no direct attack	Predator active, direct attack
No response	89	25	52	01
Freeze	00	00	03	03
Flee	00	00	00	02
Flee-approach	00	00	00	03

Table 3. Results of two-way ANOVA analysis on the frequency of feeding behaviour over five weeks by larvae exposed to the predator size treatments during Experiment One. p significant at <0.05.

Dependent variables	Independent variables	df	F value	p
Feeding in furthest grid	Predator size	3	1.276	0.287
	Weeks	4	5.186	0.001
	Interaction	12	0.626	0.816
Feeding in middle grid	Predator size	3	0.109	0.955
	Weeks	4	11.524	0.001
	Interaction	12	0.703	0.747
Feeding in adjacent grid	Predator size	3	8.511	0.001
	Weeks	4	9.442	0.001
	Interaction	12	0.387	0.967
Captures in furthest grid	Predator size	3	3.180	0.027
	Weeks	4	5.931	0.001
	Interaction	12	0.734	0.715
Captures in middle grid	Predator size	3	0.064	0.979
	Weeks	4	8.786	0.001
	Interaction	12	0.348	0.979
Captures in adjacent grid	Predator size	3	4.355	0.005
	Weeks	4	6.159	0.001
	Interaction	12	0.611	0.831
Turns in furthest grid	Predator size	3	0.500	0.683
	Weeks	4	4.530	0.002
	Interaction	12	0.755	0.694
Turns in middle grid	Predator size	3	0.155	0.927
	Weeks	4	10.952	0.001
	Interaction	12	1.115	0.350
Turns in adjacent grid	Predator size	3	9.207	0.001
	Weeks	4	10.078	0.001
	Interaction	12	0.372	0.972

Table 4. Results of two-way ANOVA analysis on the rate of feeding behaviour and amount of time spent in each grid over five weeks by larvae exposed to the predator size treatments during Experiment One. p significant at <0.05.

Dependent variables	Independent variables	df	F value	p
Captures per minute in the furthest grid	Predator size	3	1.180	0.321
	Weeks	4	13.068	0.001
	Interaction	12	1.291	0.236
Captures per minute in the middle grid	Predator size	3	0.110	0.954
	Weeks	4	14.936	0.001
	Interaction	12	0.531	0.893
Captures per minute in the adjacent grid	Predator size	3	3.164	0.026
	Weeks	4	12.772	0.001
	Interaction	12	0.644	0.802
Turns per minute in the furthest grid	Predator size	3	0.974	0.408
	Weeks	4	11.100	0.001
	Interaction	12	1.144	0.334
Turns per minute in the middle grid	Predator size	3	0.786	0.503
	Weeks	4	26.446	0.001
	Interaction	12	1.675	0.076
Turns perin minute in the adjacent grid	Predator size	3	5.416	0.001
	Weeks	4	28.837	0.001
	Interaction	12	0.884	0.564
Time (seconds) in the furthest grid	Predator size	3	1.899	0.130
	Weeks	4	2.702	0.031
	Interaction	12	0.877	0.571
Time (seconds) in the middle grid	Predator size	3	0.315	0.814
	Weeks	4	1.697	0.151
	Interaction	12	0.738	0.714
Time (seconds) in the adjacent grid	Predator size	3	4.779	0.003
	Weeks	4	1.883	0.113
	Interaction	12	1.203	0.280

Table 5. Results of two-way ANOVA analysis on the frequency of feeding behaviour over five weeks by larvae exposed to the various predator type treatments during Experiment Two. p significant at <0.05.

Dependent variables	Independent variables	df	F value	p
Feeding in furthest grid	Predator type	3	1.690	0.190
	Weeks	4	2.990	0.022
	Interaction	12	2.487	0.017
Feeding in middle grid	Predator type	3	2.423	0.092
	Weeks	4	3.492	0.009
	Interaction	12	1.253	0.272
Feeding in adjacent grid	Predator type	3	3.063	0.051
	Weeks	4	2.036	0.094
	Interaction	12	0.711	0.681
Captures in furthest grid	Predator type	3	1.531	0.221
	Weeks	4	1.850	0.125
	Interaction	12	1.744	0.097
Captures in middle grid	Predator type	3	2.319	0.102
	Weeks	4	0.957	0.433
	Interaction	12	0.549	0.818
Captures in adjacent grid	Predator type	3	2.240	0.111
	Weeks	4	1.959	0.105
	Interaction	12	0.567	0.803
Turns in furthest grid	Predator type	3	1.025	0.362
	Weeks	4	2.880	0.026
	Interaction	12	2.473	0.017
Turns in middle grid	Predator type	3	1.802	0.168
	Weeks	4	5.474	0.001
	Interaction	12	1.589	0.132
Turns in adjacent grid	Predator type	3	2.676	0.073
	Weeks	4	2.344	0.059
	Interaction	12	0.737	0.659

Table 6. Results of two-way ANOVA analysis on the rate of feeding behaviour and amount of time spent in each grid over five weeks by larvae exposed to the various predator type treatments during Experiment Two. p significant at <0.05.

Dependent variables	Independent variables	df	F value	p
Captures per minute in the furthest grid	Predator type	3	3.054	0.051
	Weeks	4	1.666	0.164
	Interaction	12	2.337	0.024
Captures per minute in the middle grid	Predator type	3	2.750	0.067
	Weeks	4	1.361	0.250
	Interaction	12	0.230	0.985
Captures per minute in the adjacent grid	Predator type	3	1.719	0.184
	Weeks	4	2.087	0.087
	Interaction	12	0.627	0.754
Turns per minute in the furthest grid	Predator type	3	3.259	0.042
	Weeks	4	5.127	0.001
	Interaction	12	1.596	0.135
Turns per minute in the middle grid	Predator type	3	1.412	0.247
	Weeks	4	6.134	0.001
	Interaction	12	1.496	0.163
Turns per minute in the adjacent grid	Predator type	3	3.486	0.034
	Weeks	4	5.099	0.001
	Interaction	12	1.236	0.284
Time (seconds) in the furthest grid	Predator type	3	0.251	0.778
	Weeks	4	6.879	0.001
	Interaction	12	1.652	0.111
Time (seconds) in the middle grid	Predator type	3	1.593	0.206
	Weeks	4	0.298	0.879
	Interaction	12	0.913	0.507
Time (seconds) in the adjacent grid	Predator type	3	0.721	0.488
	Weeks	4	1.240	0.295
	Interaction	12	1.171	0.317

Fig.1. Weekly number of larvae performing the predator-escape MAPs flee (a), freeze (b), flee-approach (c), and no response (d) to direct attacks from predators during Experiment One.

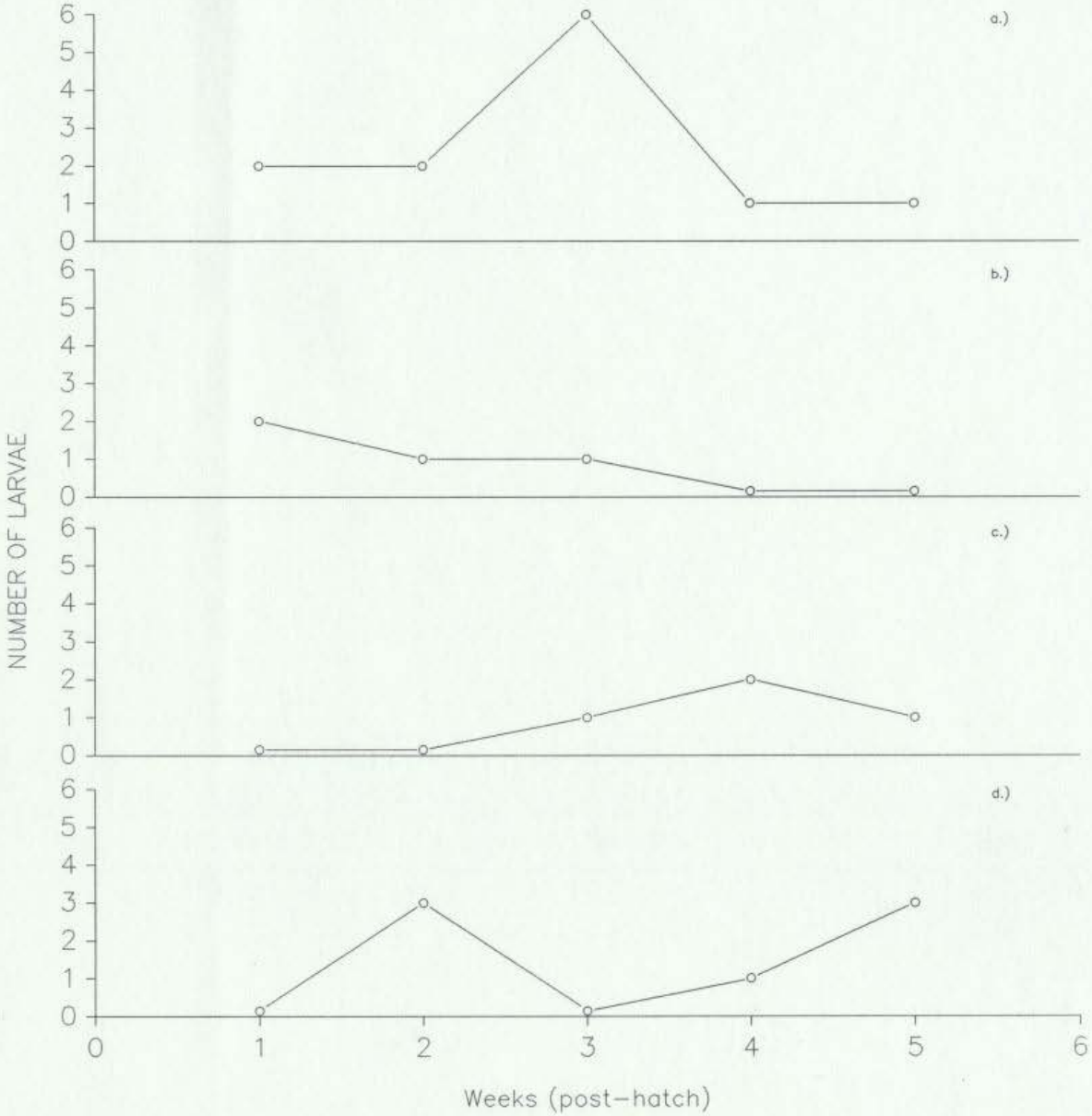

a.)
b.)
c.)
d.)
NUMBER OF LARVAE
0
1
2
3
4
5
6
Weeks (post-hatch)

Fig.2. Weekly number of larvae performing the predator-escape MAPs flee (a), freeze (b), and flee-approach (c) to direct attacks from predators during Experiment Two.

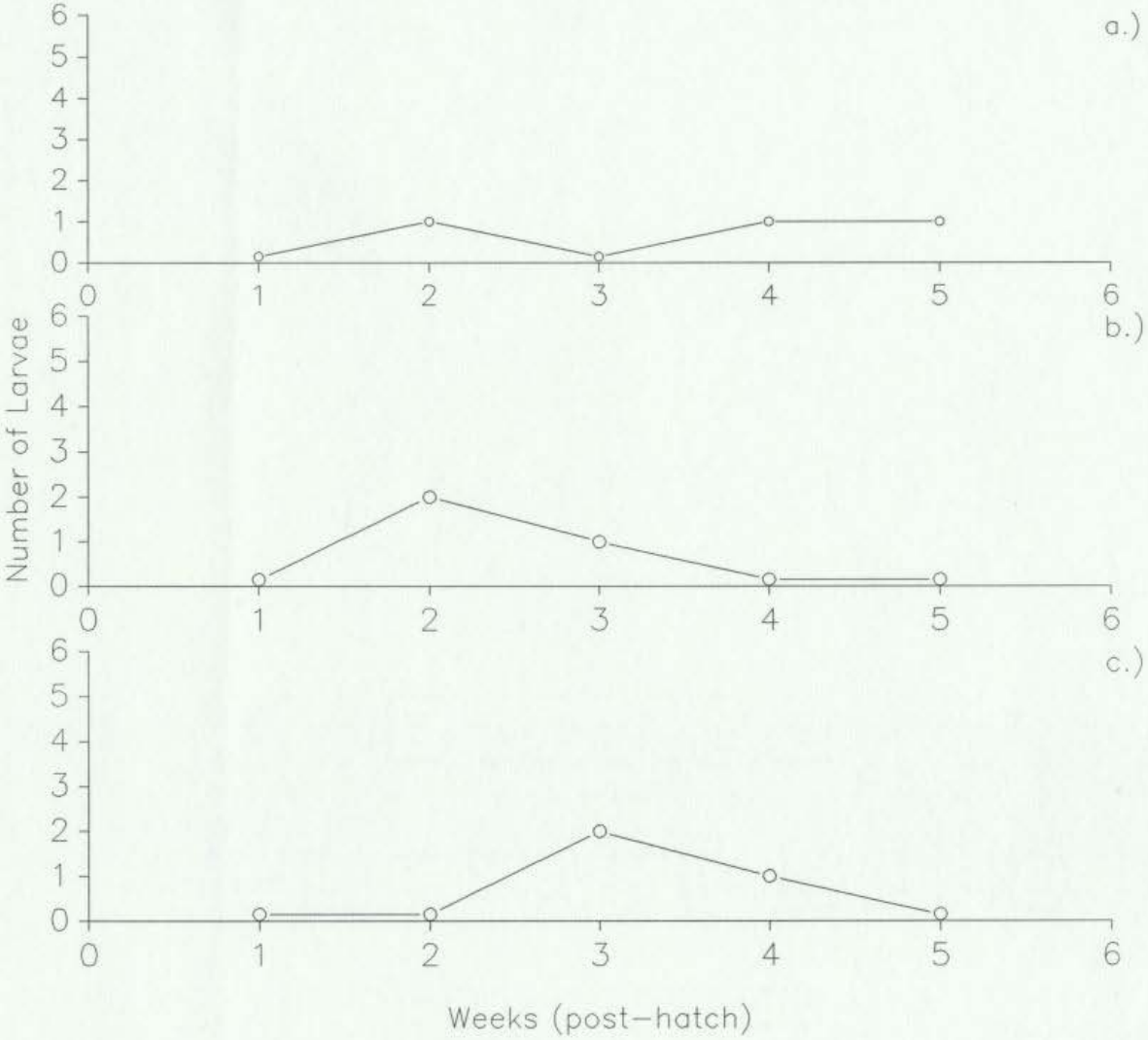

a.)
b.)
c.)
Number of Larvae
Weeks (post-hatch)
0
1
2
3
4
5
6

Fig.3. Mean frequency of feeding performed each week in the grid furthest from the predator by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

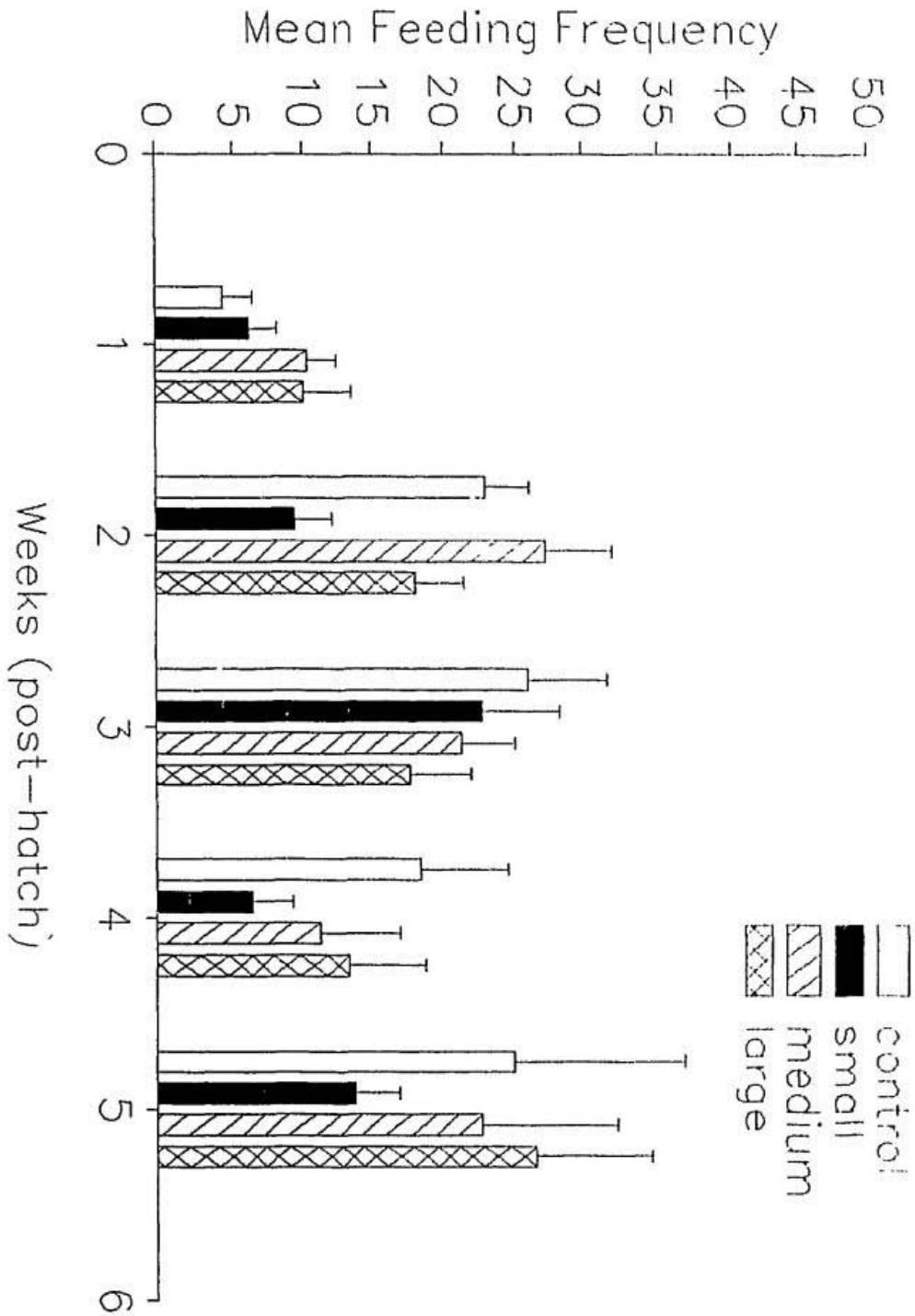

Mean Feeding Frequency
0
5
10
15
20
25
30
35
40
45
50
Weeks (post-hatch)
0
1
2
3
4
5
6
control
small
medium
large

Fig. 4. Mean frequency of feeding performed each week in the middle grid by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

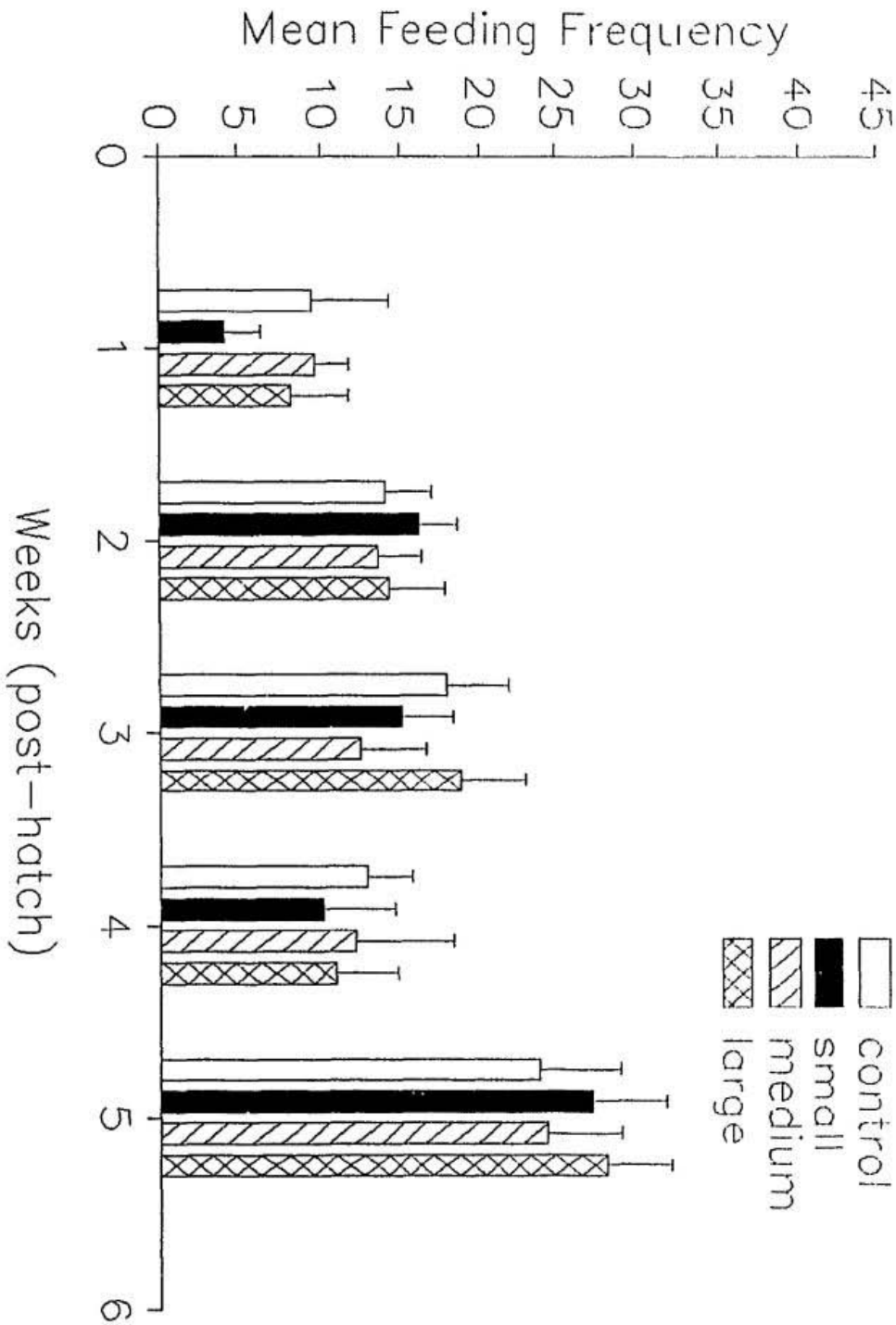

Mean Feeding Frequency
0
5
10
15
20
25
30
35
40
45
Weeks (post-hatch)
0
1
2
3
4
5
6
control
small
medium
large

Fig.5. Mean frequency of feeding performed each week in the grid adjacent to the predator by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

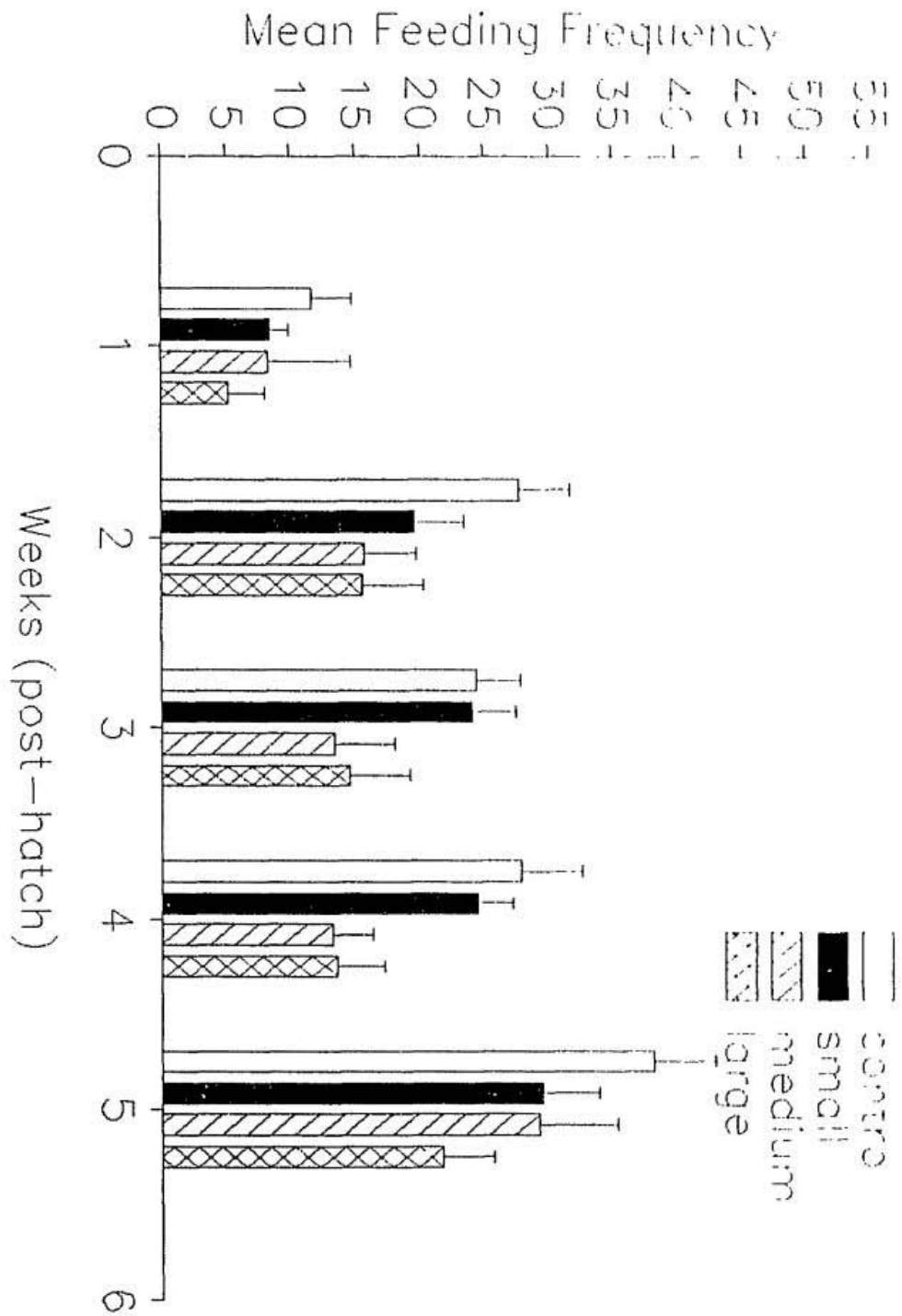

Mean Feeding Frequency
0
5
10
15
20
25
30
35
40
45
50
55
Weeks (post-hatch)
0
1
2
3
4
5
6
control
small
medium
large

Fig.6. Mean number of captures performed each week in the grid adjacent to the predator by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

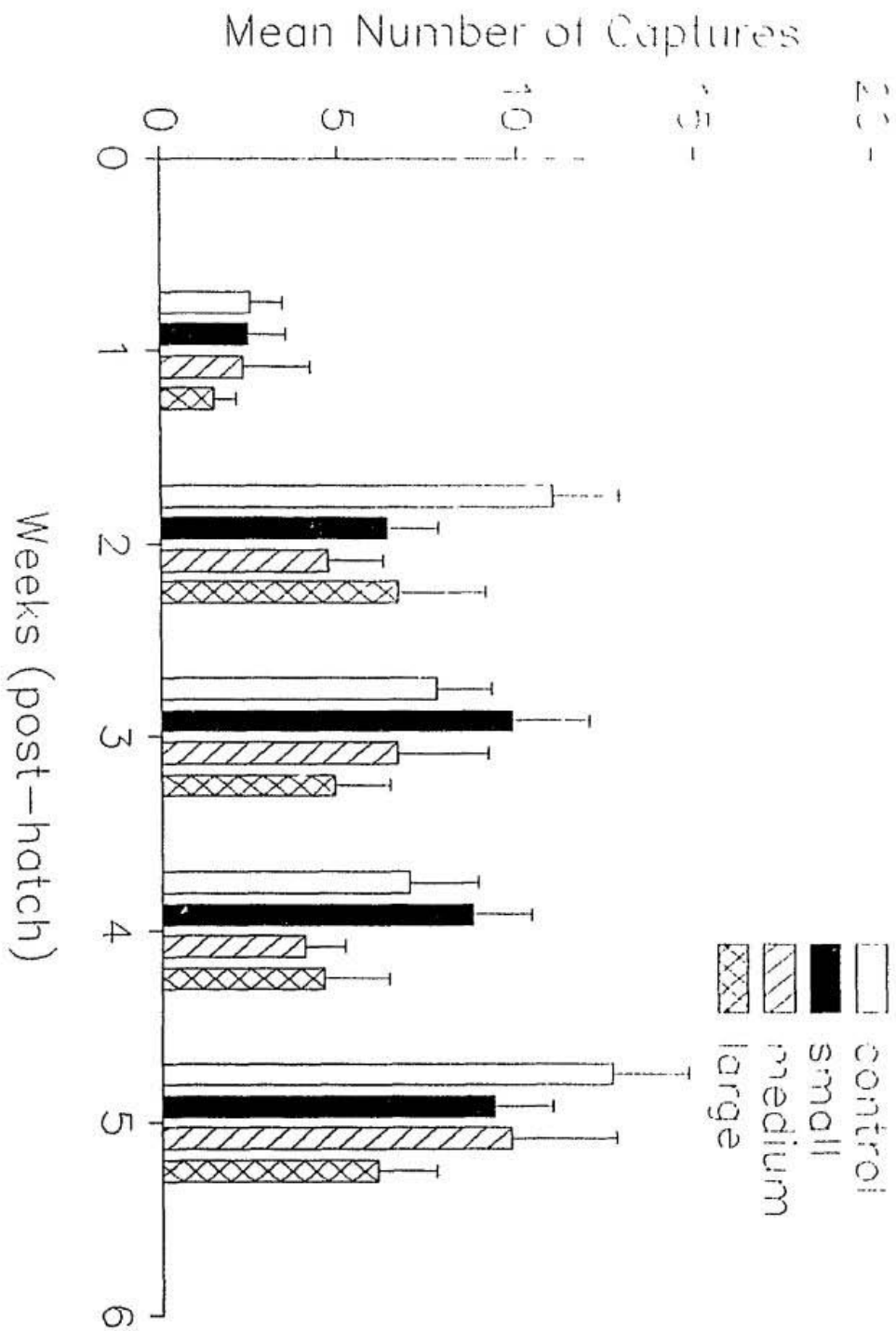

Mean Number of Captures
0
5
Weeks (post-hatch)
0
1
2
3
4
5
6
large
medium
small
control

Fig.7. Mean number of captures performed each week in the middle grid by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

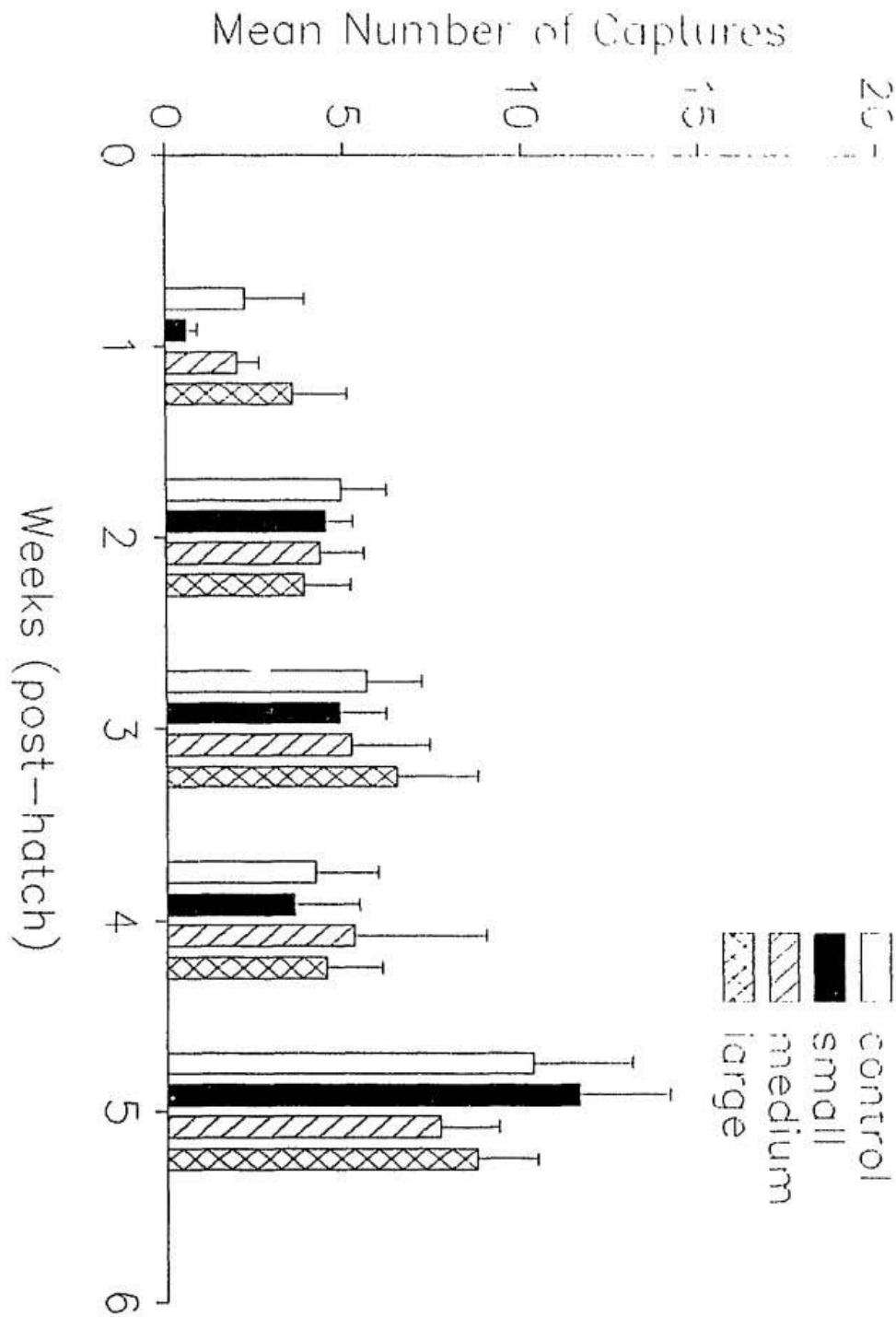

Mean Number of Captures
0
5
10
15
20
Weeks (post-hatch)
0
1
2
3
4
5
6
control
small
medium
large

Fig.8. Mean number of captures performed each week in the grid furthest from the predator by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

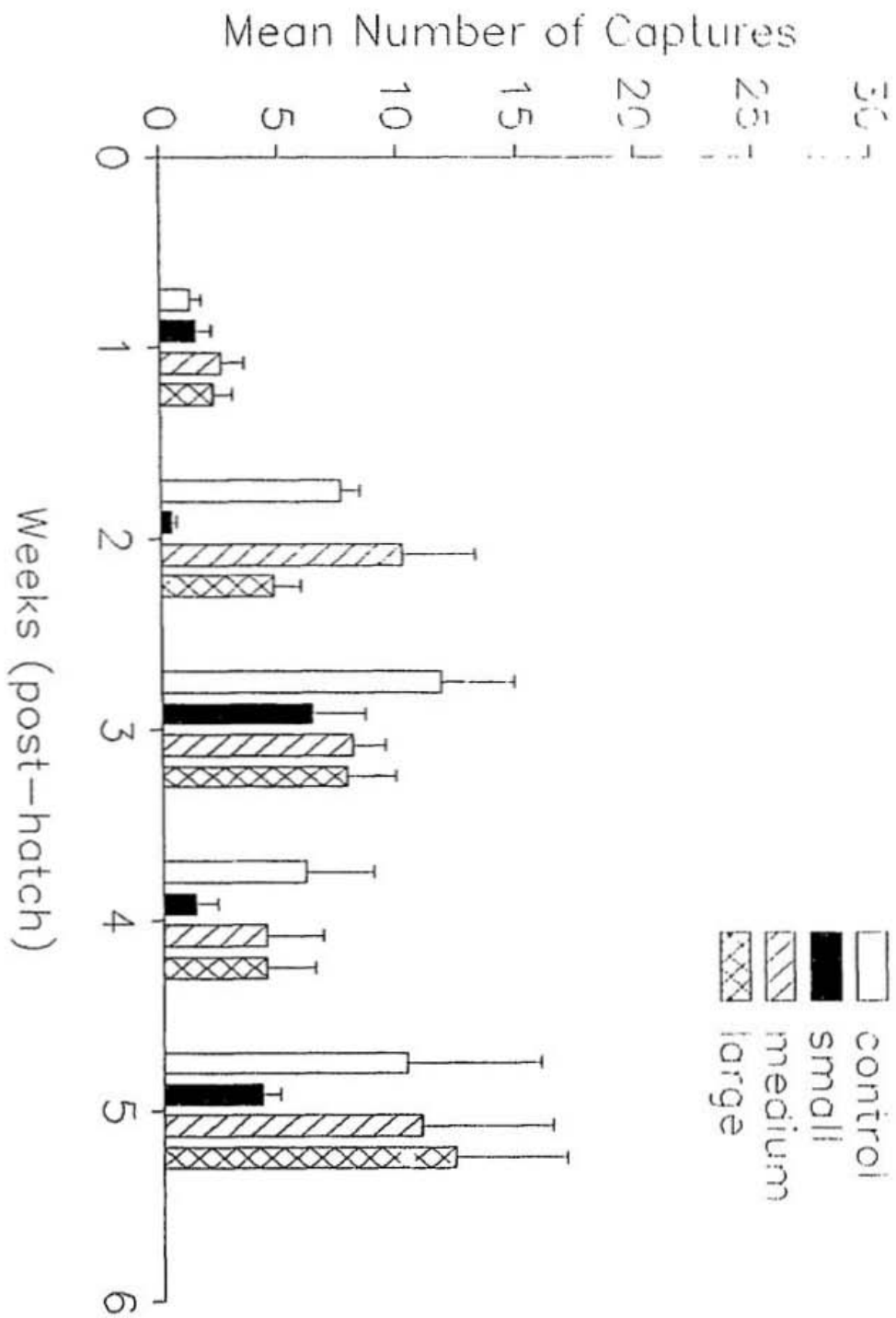

Mean Number of Captures
0
5
10
15
20
25
30
Weeks (post-hatch)
0
1
2
3
4
5
6
control
small
medium
large

Fig.9. Mean number of turns performed each week in the grid adjacent to the predator by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

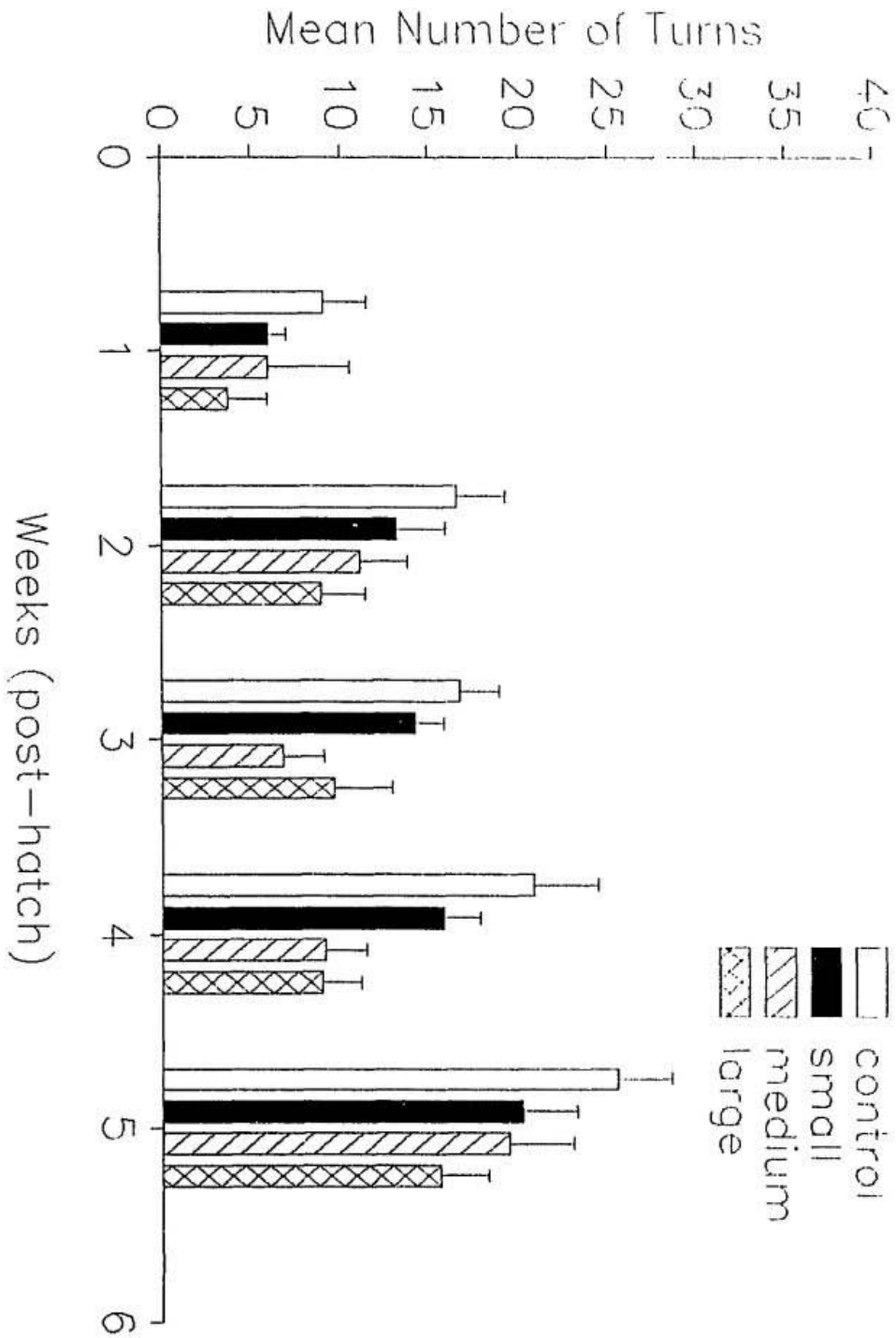

Mean Number of Turns
0
5
10
15
20
25
30
35
40
Weeks (post-hatch)
0
1
2
3
4
5
6
control
small
medium
large

Fig.10. Mean number of turns performed each week in the middle grid by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

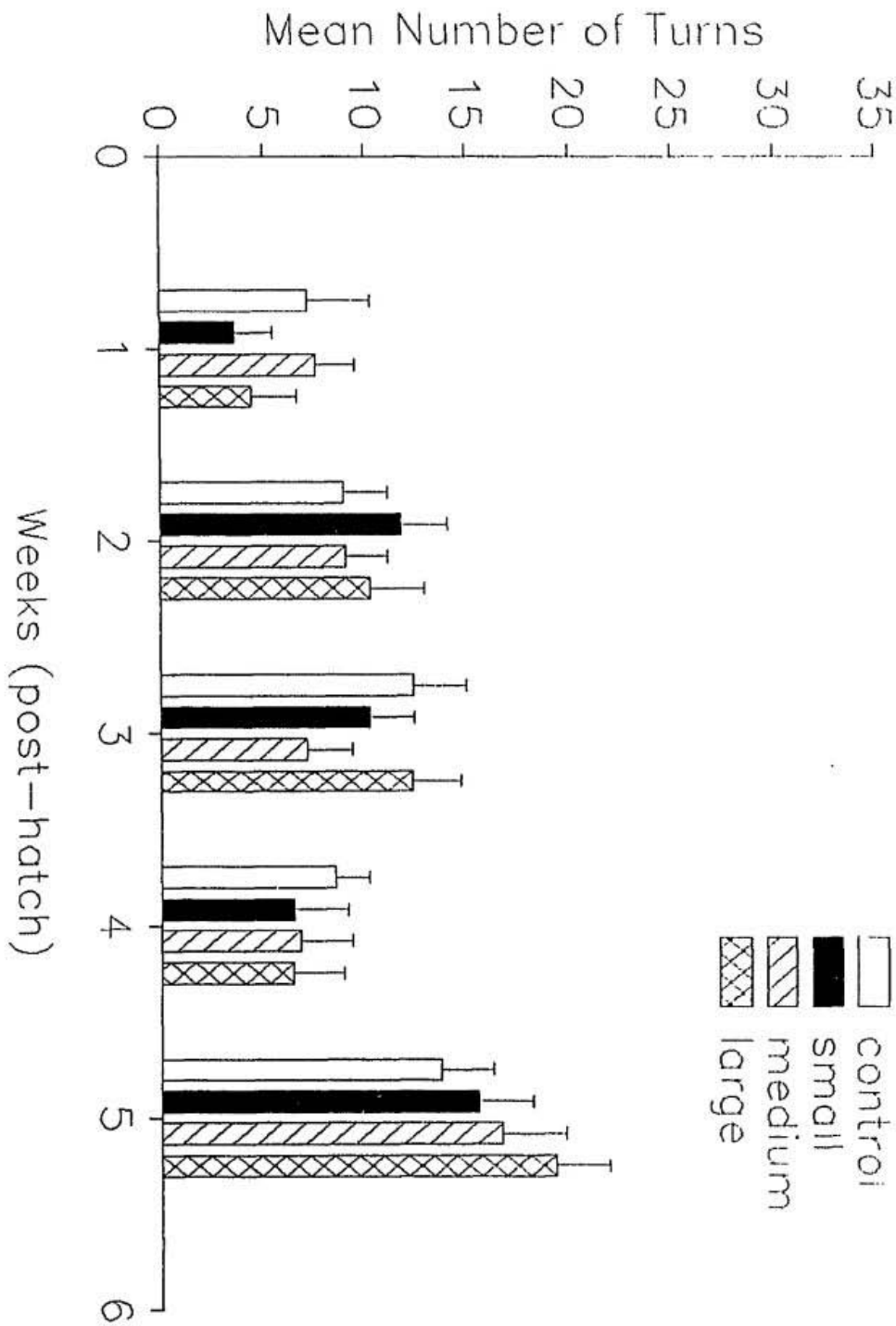

Mean Number of Turns
0
5
10
15
20
25
30
35
Weeks (post-hatch)
0
1
2
3
4
5
6
control
small
medium
large

Fig.11. Mean number of turns performed each week in the grid furthest from the predator by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

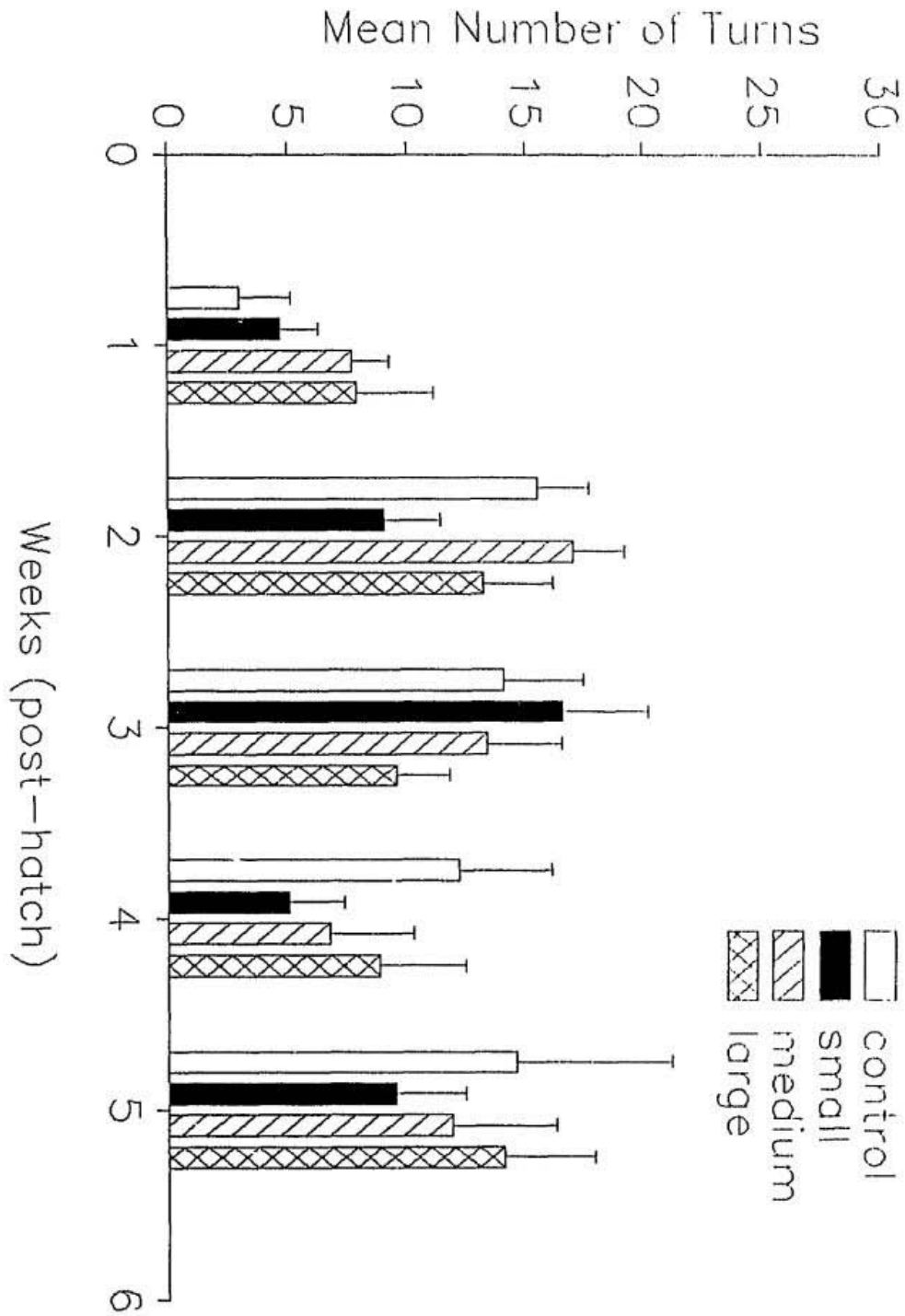

Mean Number of Turns
0
5
10
15
20
25
30
Weeks (post-hatch)
0
1
2
3
4
5
6
control
small
medium
large

Fig.12. Mean time (seconds) spent per week in the grid adjacent to the predator by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

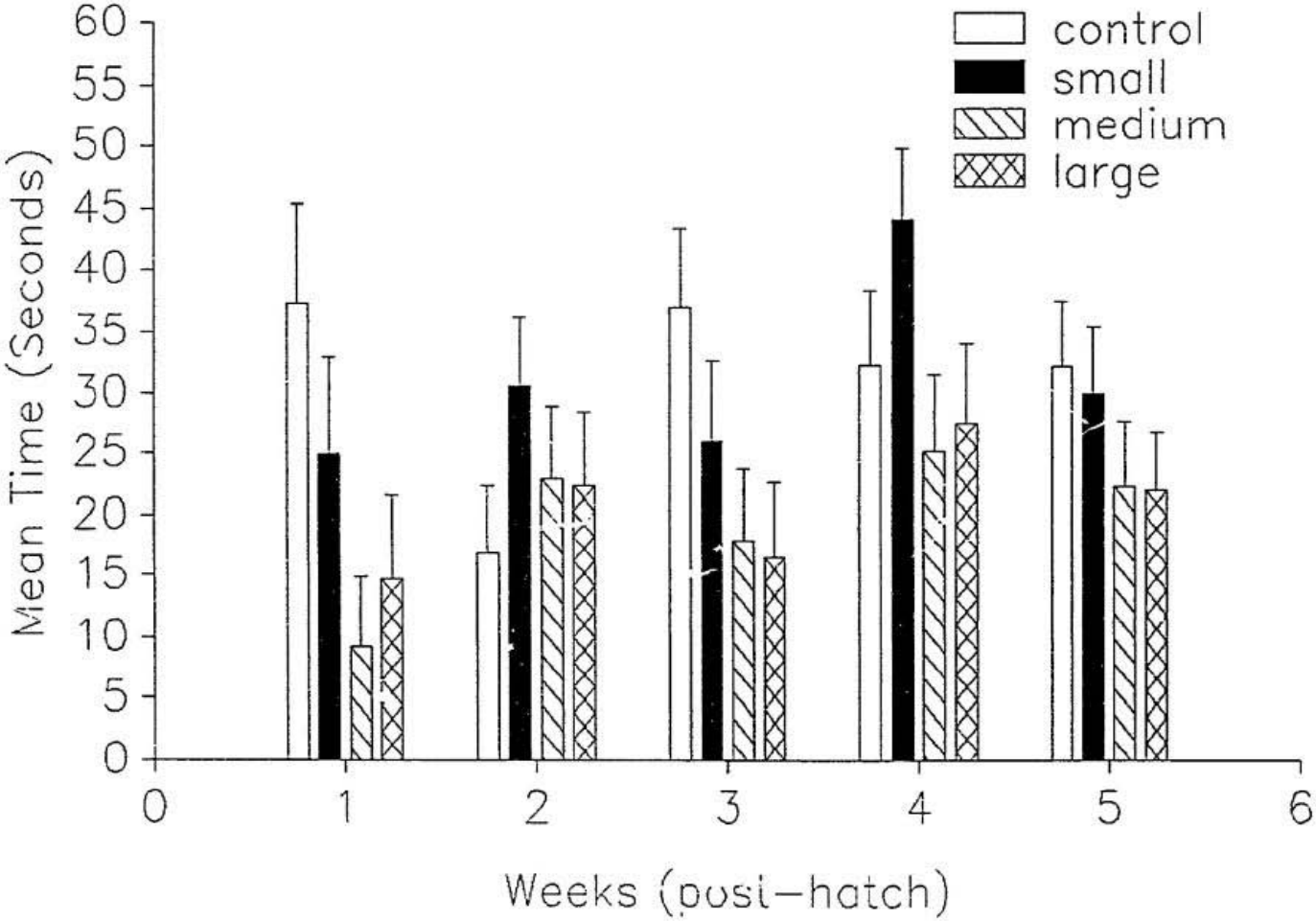

control
small
medium
large
Mean Time (Seconds)
60
55
50
45
40
35
30
25
20
15
10
5
0
0
1
2
3
4
5
6
Weeks (post-hatch)

Fig.13. Mean time (seconds) spent per week in the middle grid by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

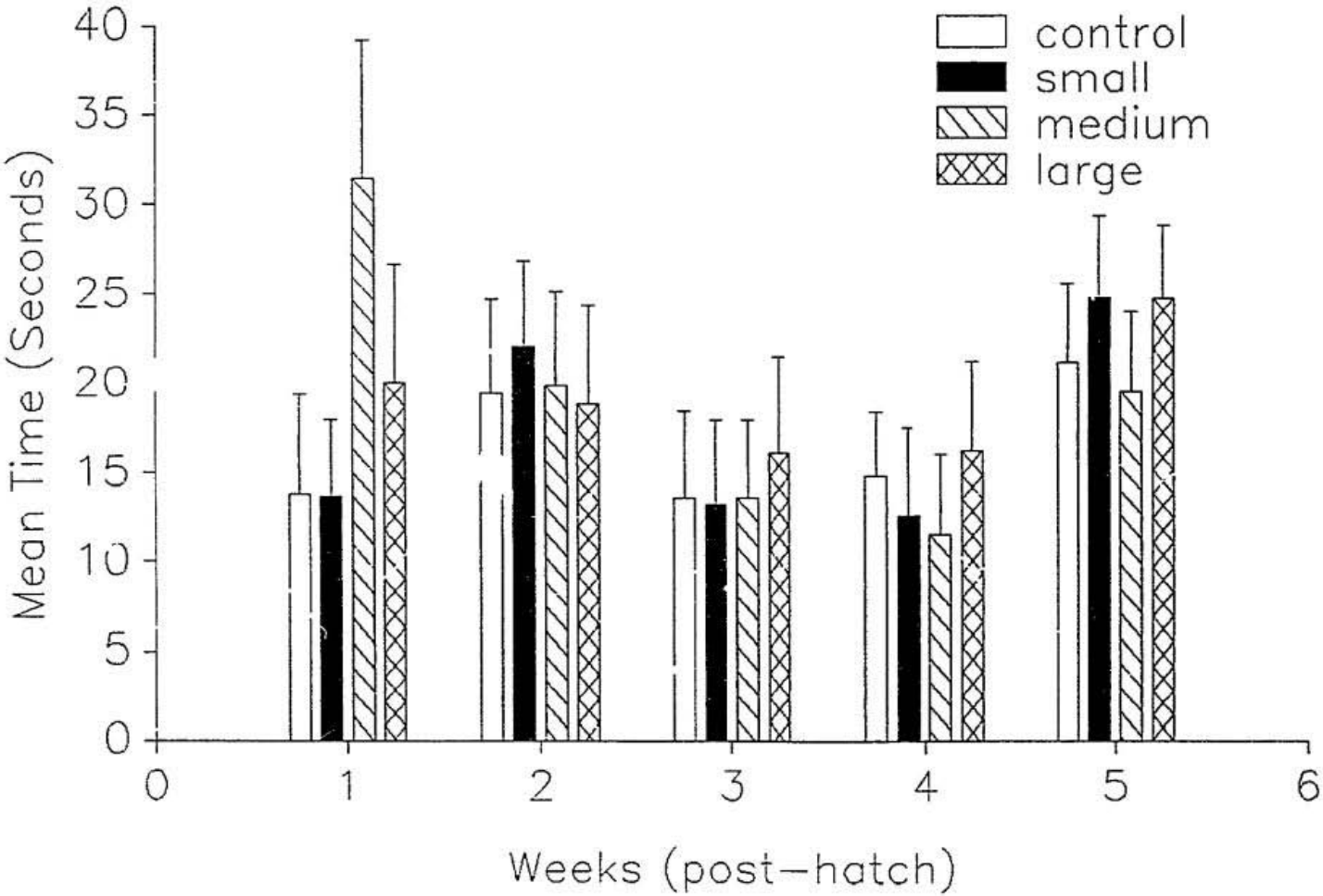

control
small
medium
large
Mean Time (Seconds)
0
5
10
15
20
25
30
35
40
0
1
2
3
4
5
6
Weeks (post–hatch)

Fig.14. Mean time (seconds) spent per week in the grid furthest from the predator by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

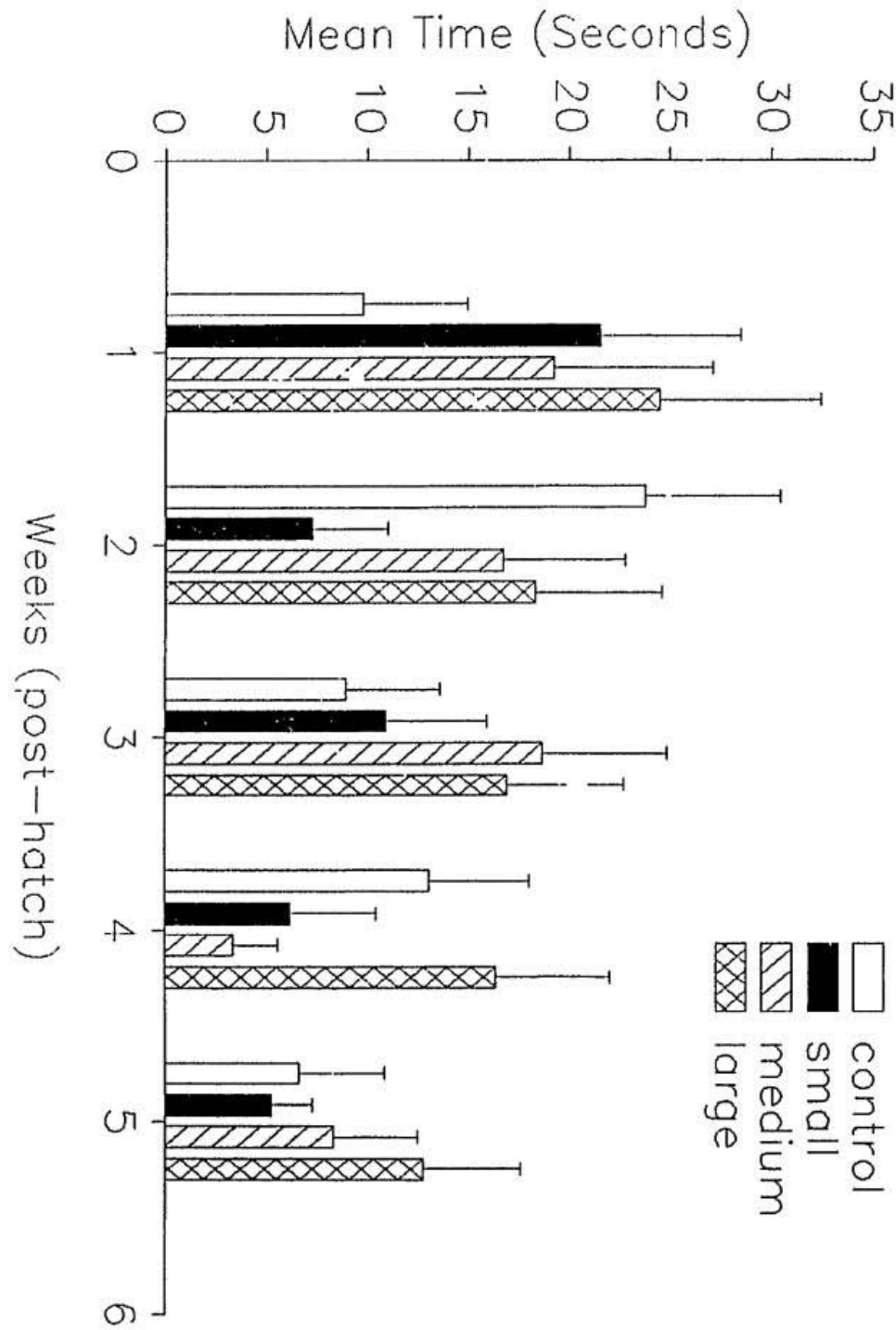

Mean Time (Seconds)
0
5
10
15
20
25
30
35
Weeks (post-hatch)
0
1
2
3
4
5
6
control
small
medium
large

Fig.15. Mean number of captures per minute performed each week in the grid furthest from the predator by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

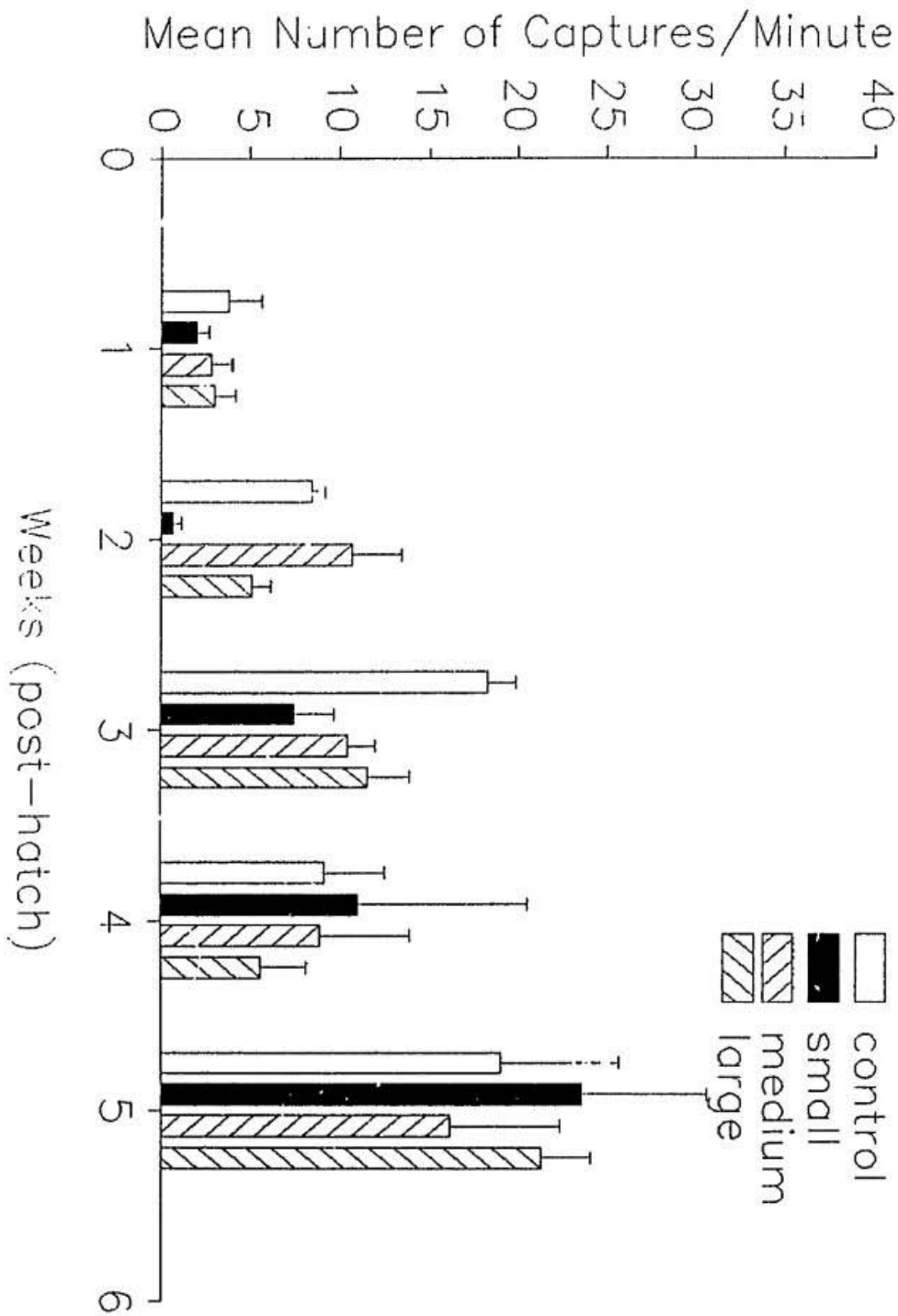

Mean Number of Captures/Minute
0
5
10
15
20
25
30
35
40
Weeks (post-hatch)
0
1
2
3
4
5
6
control
small
medium
large

Fig.16. Mean number of captures per minute performed each week in the middle grid by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

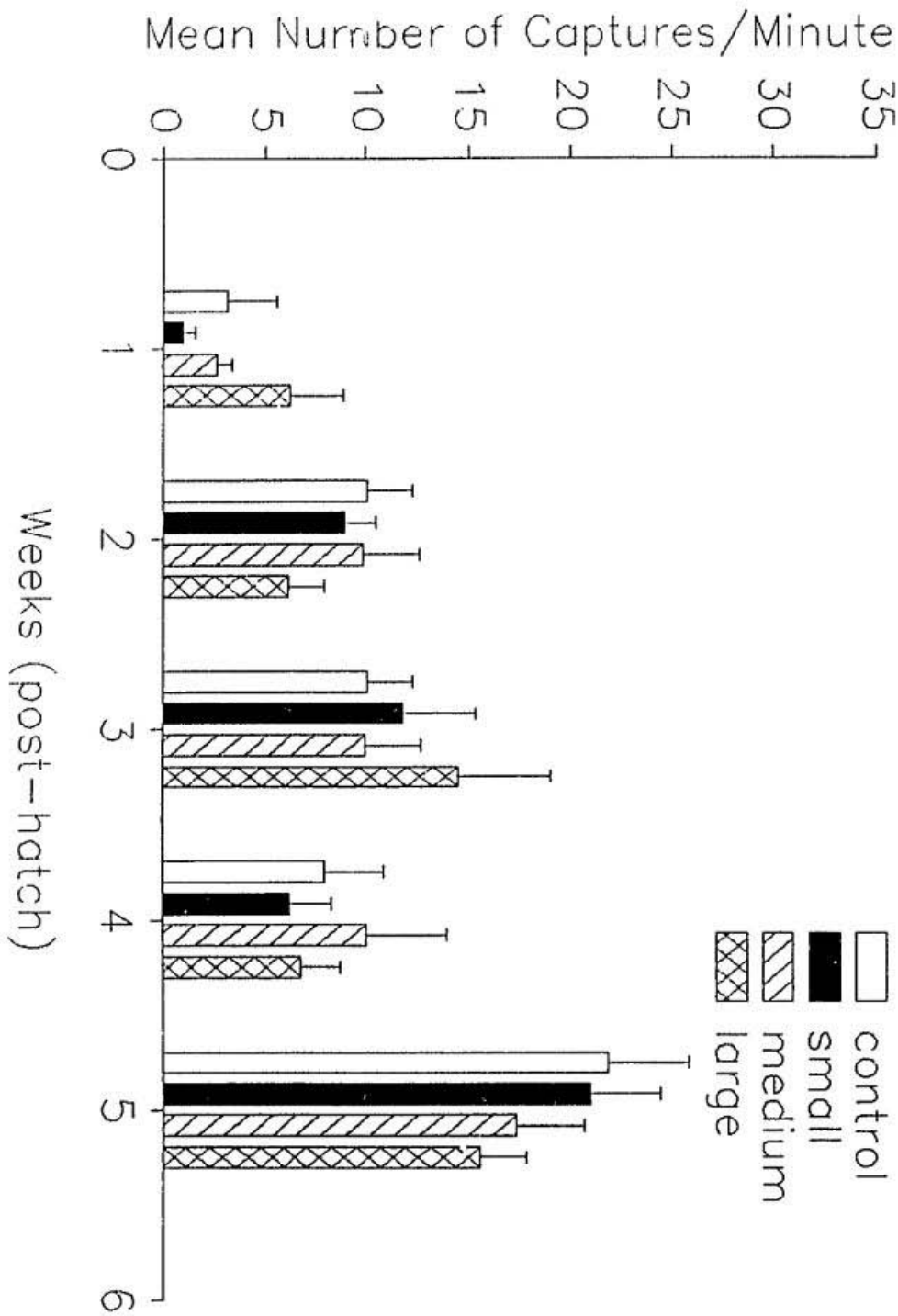

Mean Number of Captures/Minute
0
5
10
15
20
25
30
35
Weeks (post-hatch)
0
1
2
3
4
5
6
control
small
medium
large

Fig.17. Mean number of captures per minute performed each week in the grid adjacent to the predator by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

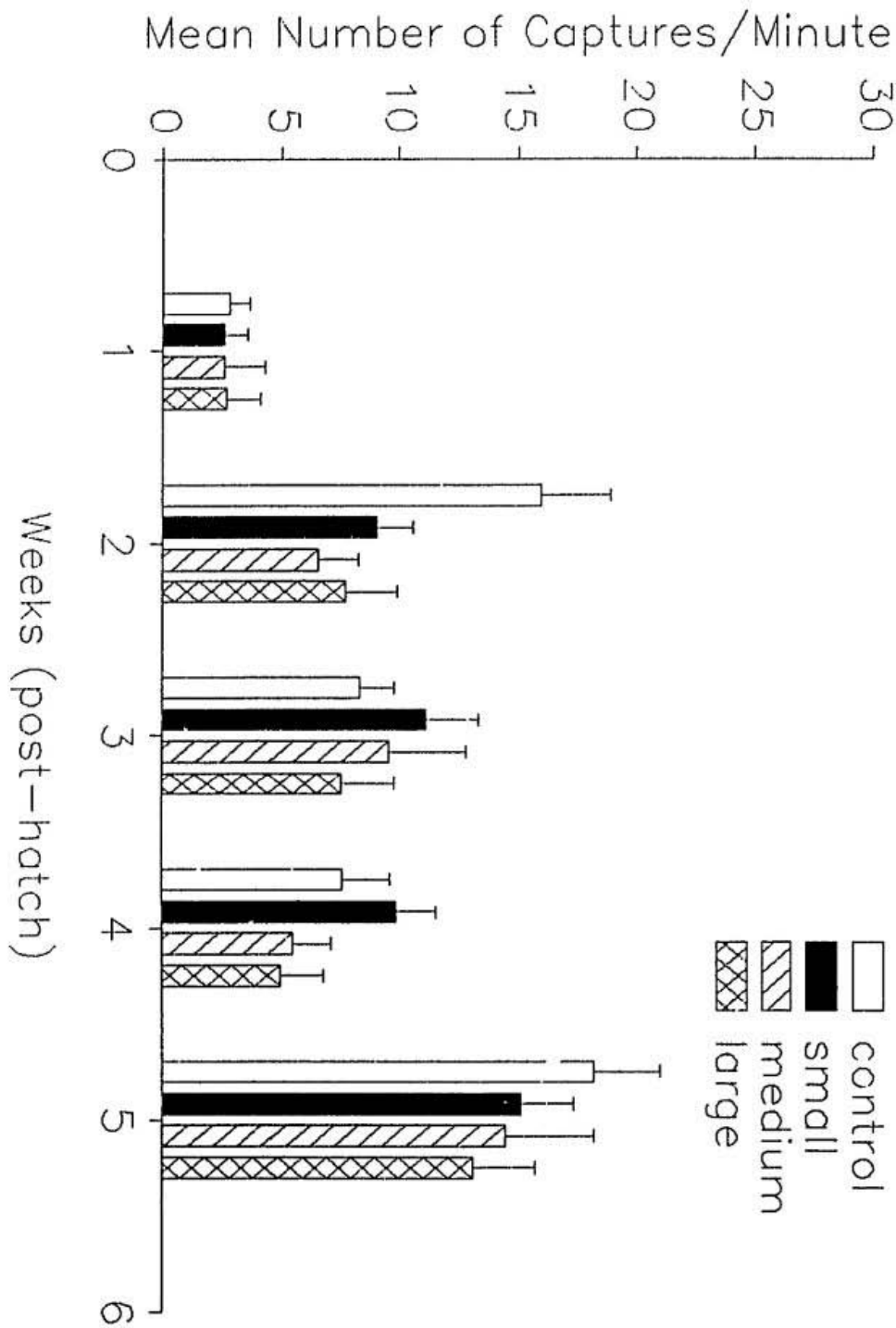

Mean Number of Captures/Minute
0
5
10
15
20
25
30
Weeks (post-hatch)
0
1
2
3
4
5
6
control
small
medium
large

Fig.18. Mean number of turns per minute performed each week in the grid furthest from the predator by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

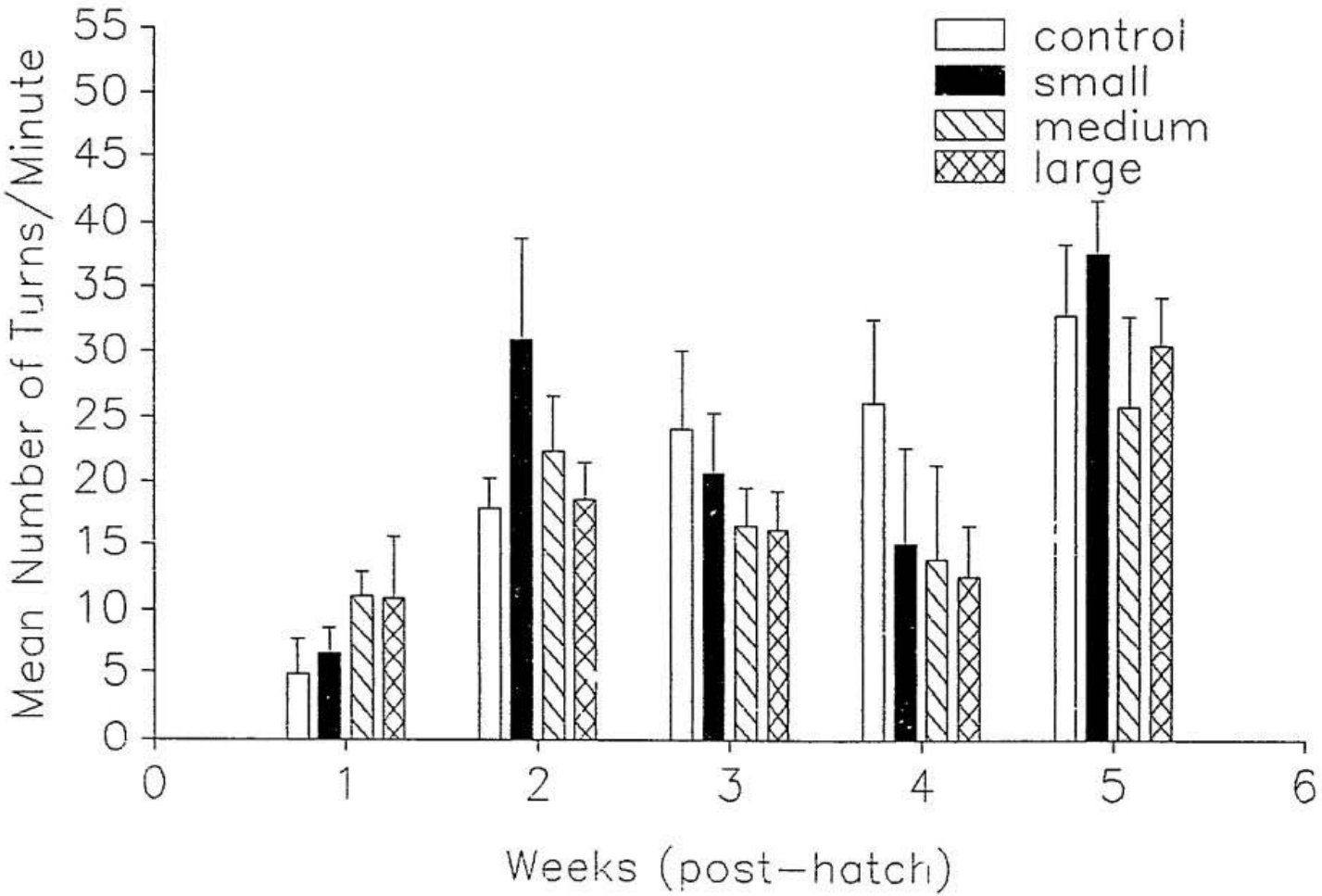

control
small
medium
large
Mean Number of Turns/Minute
0
5
10
15
20
25
30
35
40
45
50
55
0
1
2
3
4
5
6
Weeks (post-hatch)

Fig.19. Mean number of turns per minute performed each week in the middle grid by larvae exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

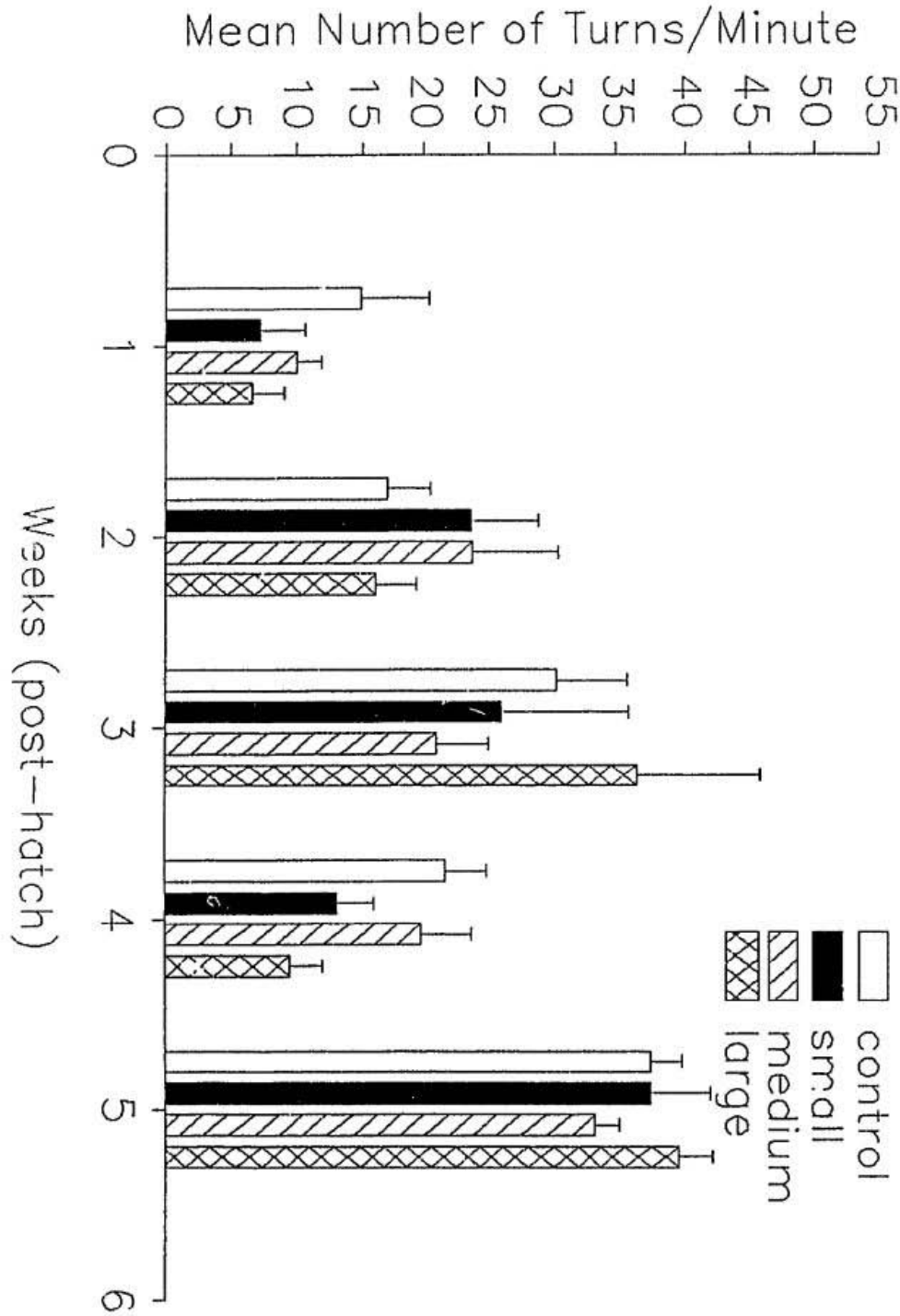

Mean Number of Turns/Minute
0
5
10
15
20
25
30
35
40
45
50
55
Weeks (post-hatch)
0
1
2
3
4
5
6
control
small
medium
large

Fig.20. Mean number of turns per minute performed each week by larvae in the grid adjacent to the predator exposed to the large (cross-hatched bar), medium (hatched bar), small (solid bar) and no predator (open bar) during Experiment One. Vertical bar = standard error. n = 12 larvae per treatment for week one, 18 larvae per treatment for weeks 2-5.

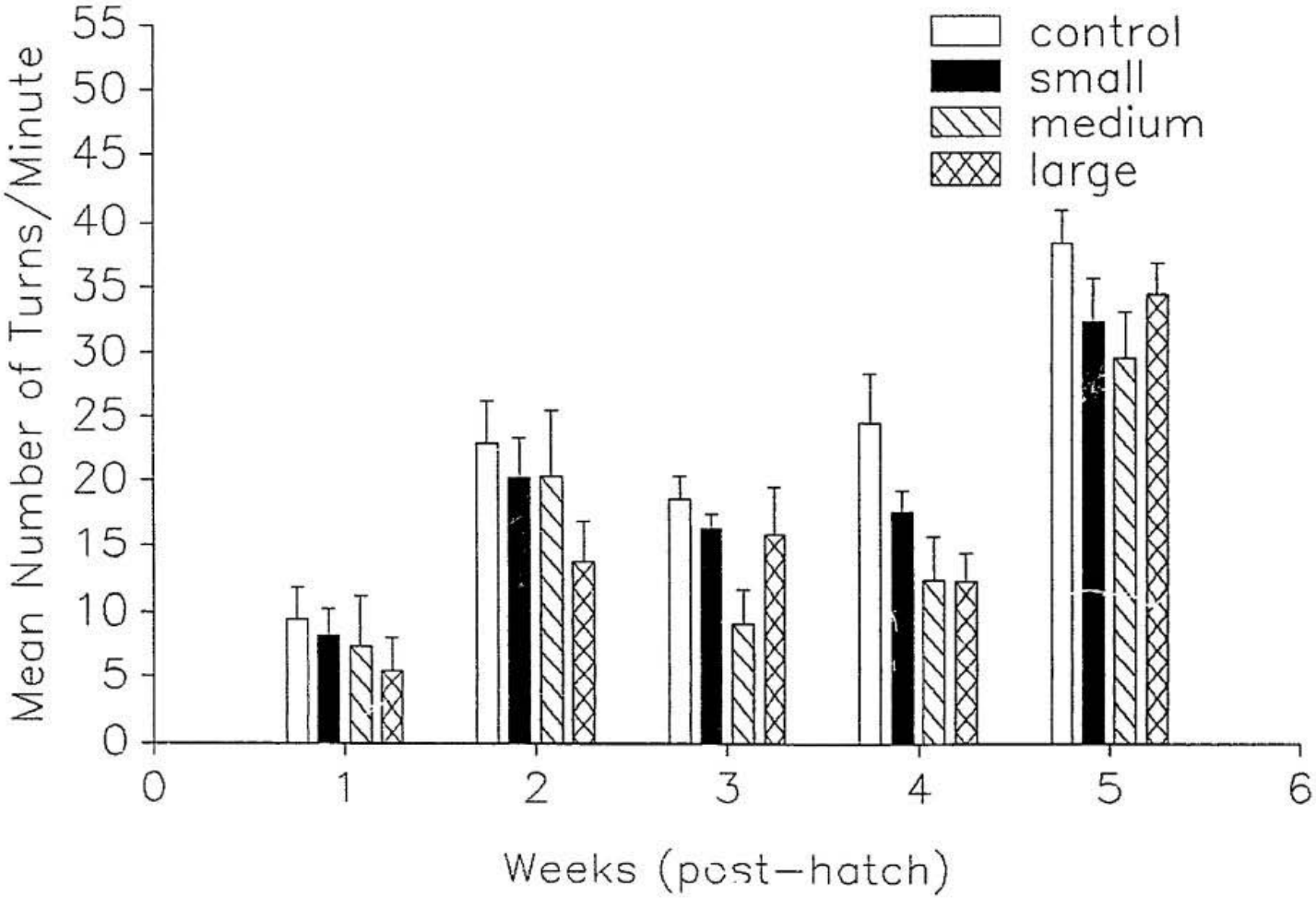

control
small
medium
large
Mean Number of Turns/Minute
0
5
10
15
20
25
30
35
40
45
50
55
0
1
2
3
4
5
6
Weeks (post-hatch)

Fig.21. Mean number of captures performed each week in the grid adjacent to the predator by larvae exposed to the large (square), medium (inverted triangle), small (circle) predator during Experiment One in relation to the predator/larvae size ratio.

Mean Number of Captures
0
2
4
6
8
10
Predator/Larvae Size Ratio
2
4
6
8
10
small
medium
large

Fig.22. Mean number of turns performed each week in the grid adjacent to the predator by larvae exposed to the large (square), medium (inverted triangle), small (circle) predator during Experiment One in relation to the predator/larvae size ratio.

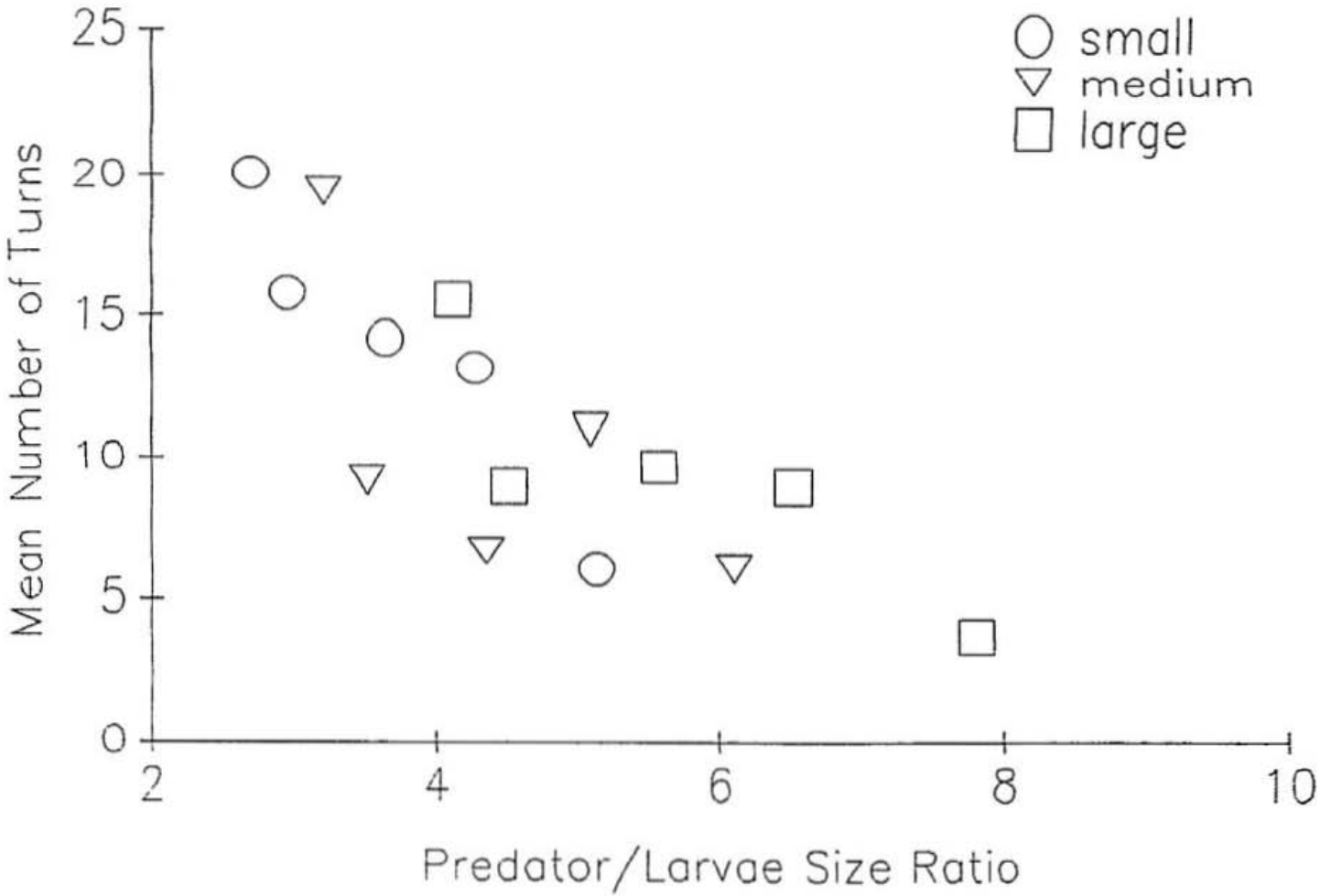

small
medium
large
Mean Number of Turns
25
20
15
10
5
0
2
4
6
8
10
Predator/Larvae Size Ratio

Fig.23. Mean frequency of feeding performed each week in the grid furthest from the predator by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

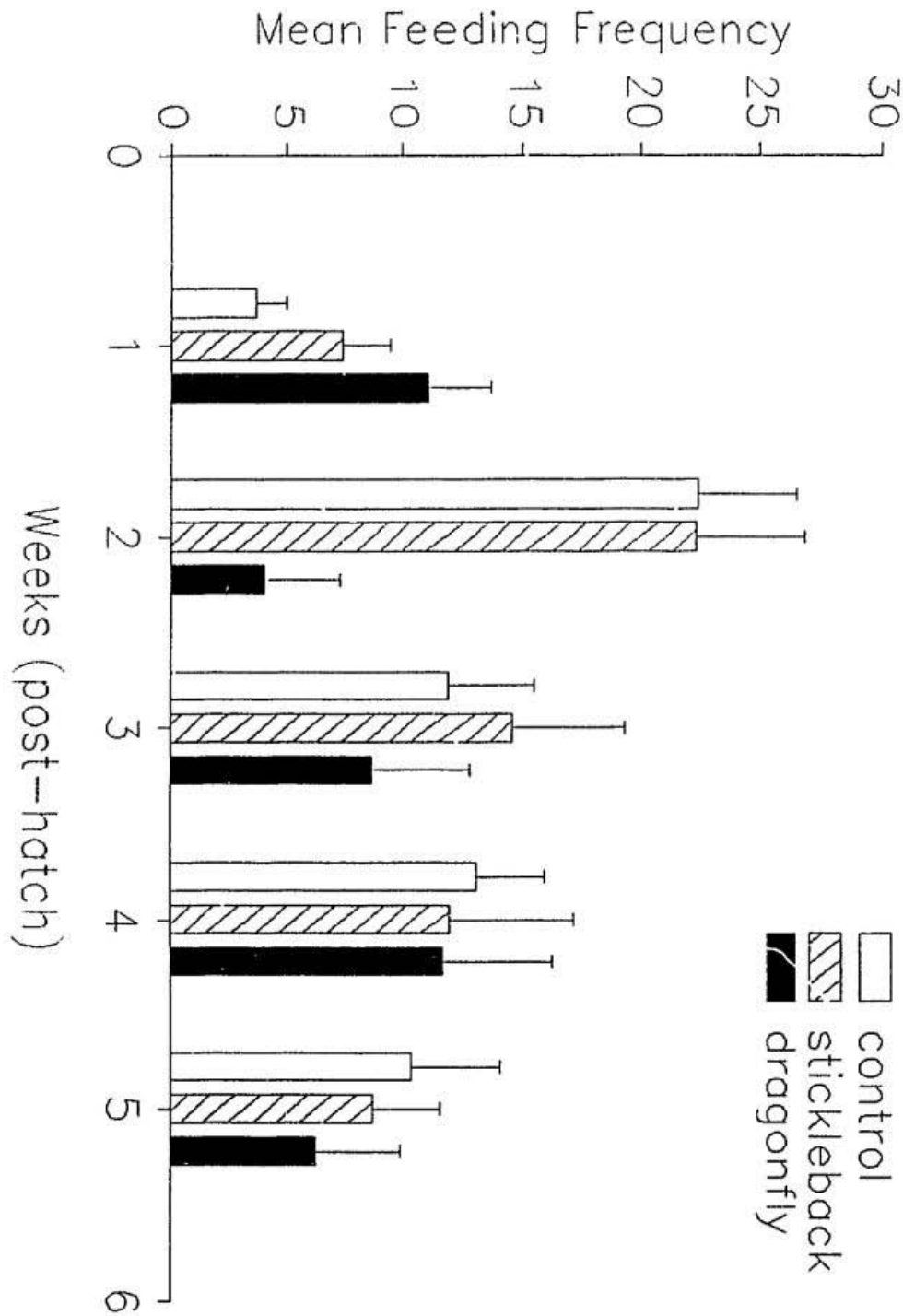

Mean Feeding Frequency
0
5
10
15
20
25
30
Weeks (post-hatch)
0
1
2
3
4
5
6
control
stickleback
dragonfly

Fig.24. Mean frequency of feeding performed each week in the middle grid by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

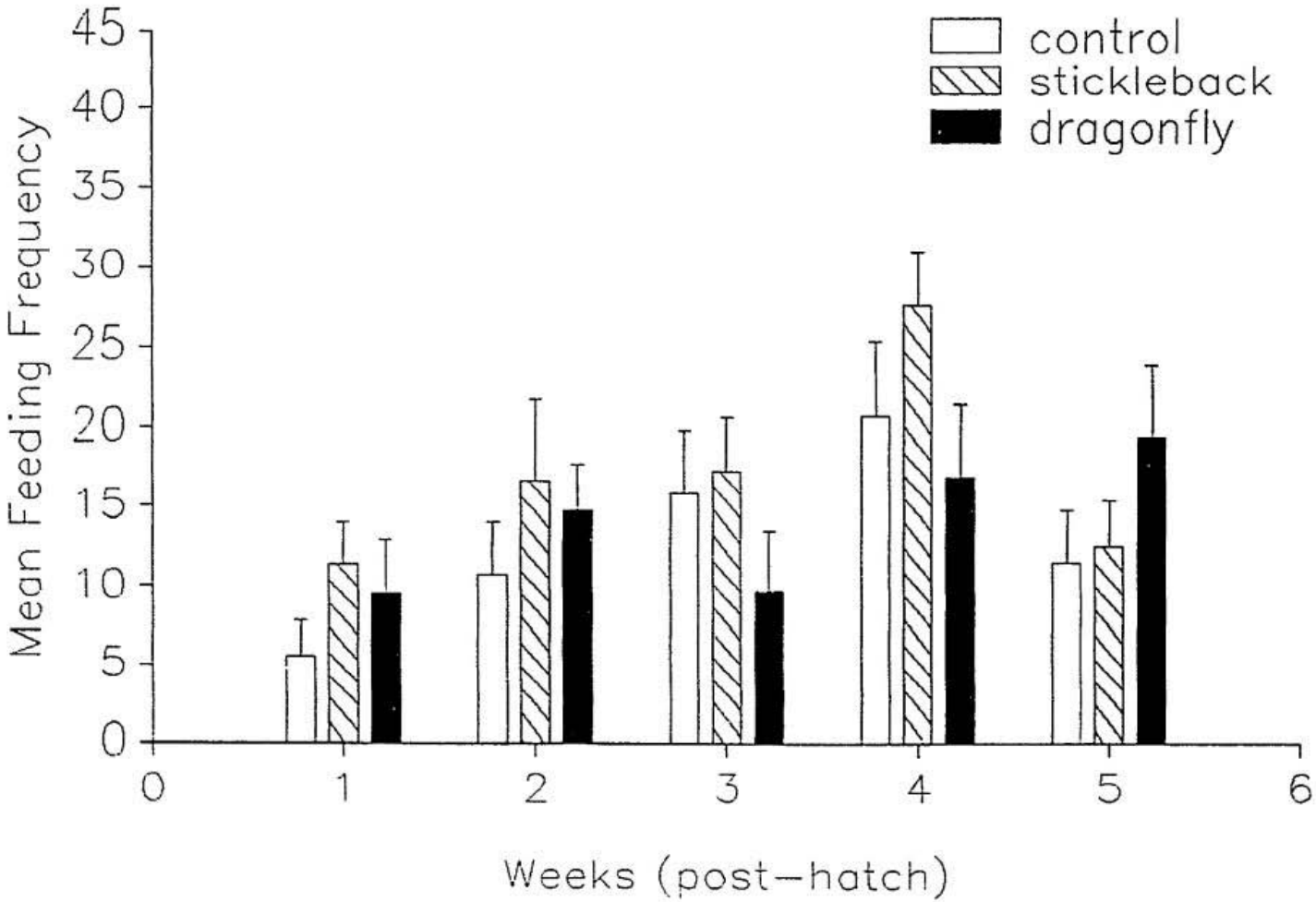

Mean Feeding Frequency
45
40
35
30
25
20
15
10
5
0
0
1
2
3
4
5
6
Weeks (post-hatch)
control
stickleback
dragonfly

Fig.25. Mean frequency of feeding performed each week in the grid adjacent to the predator by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

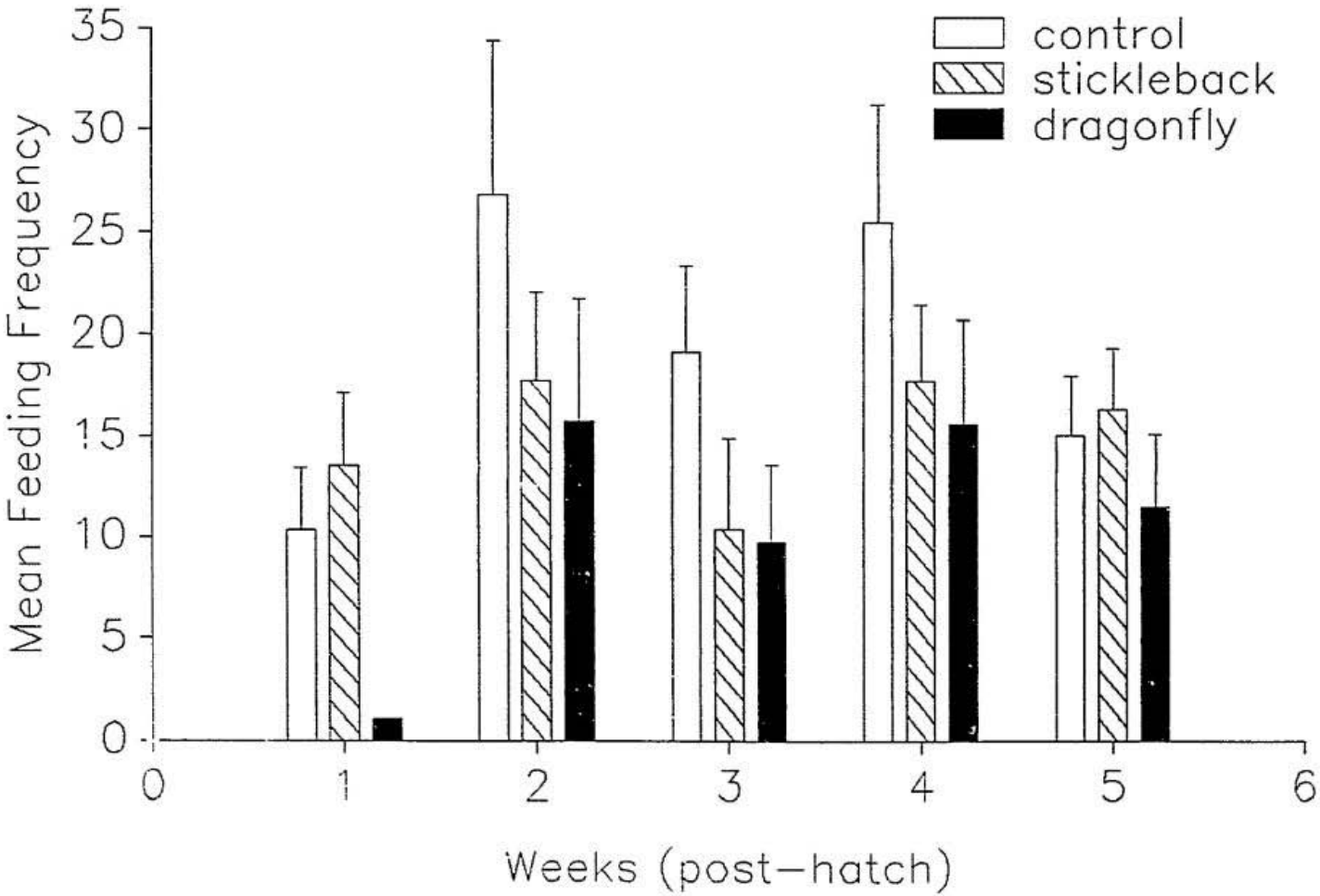

control
stickleback
dragonfly
Mean Feeding Frequency
35
30
25
20
15
10
5
0
0
1
2
3
4
5
6
Weeks (post–hatch)

Fig.26. Mean number of cacptures performed each week in the grid furthest from the predator by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

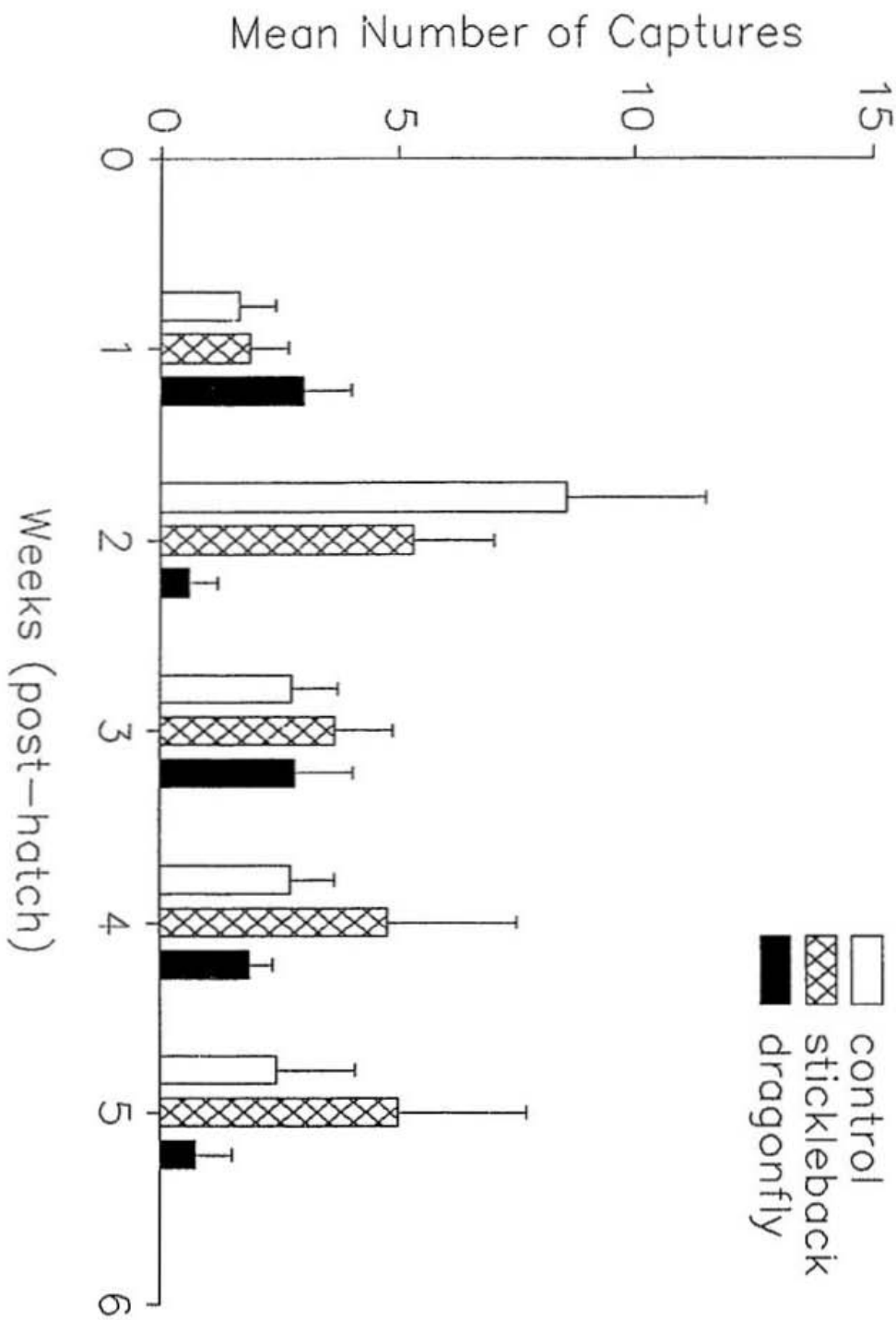

Mean Number of Captures
0
5
10
15
0
1
2
3
4
5
6
Weeks (post-hatch)
control
stickleback
dragonfly

Fig.27. Mean number of captures performed each week in the middle grid by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

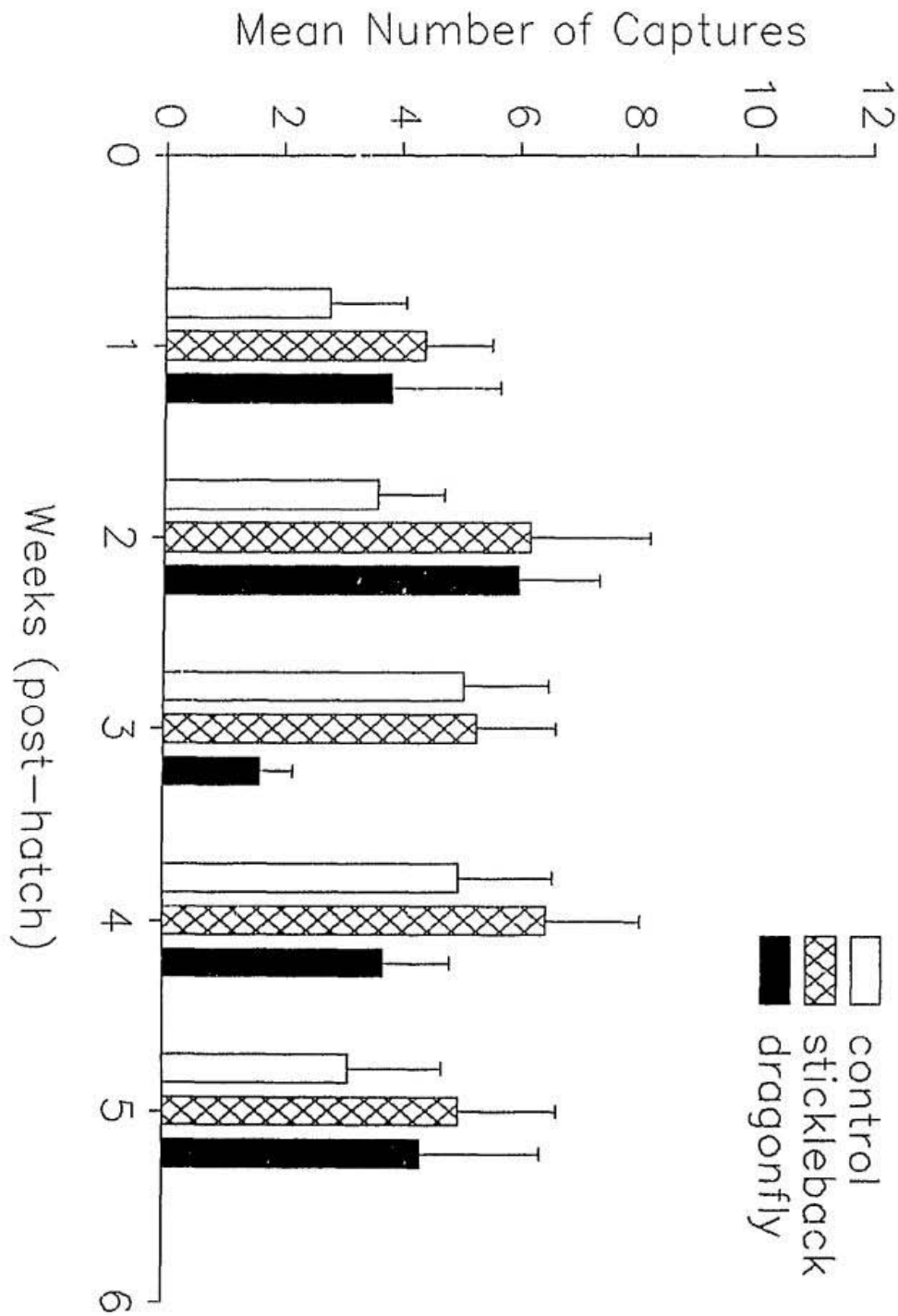

Mean Number of Captures
0
2
4
6
8
10
12
0
1
2
3
4
5
6
Weeks (post-hatch)
control
stickleback
dragonfly

Fig.28. Mean number of captures performed each week in the grid adjacent to the predator by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

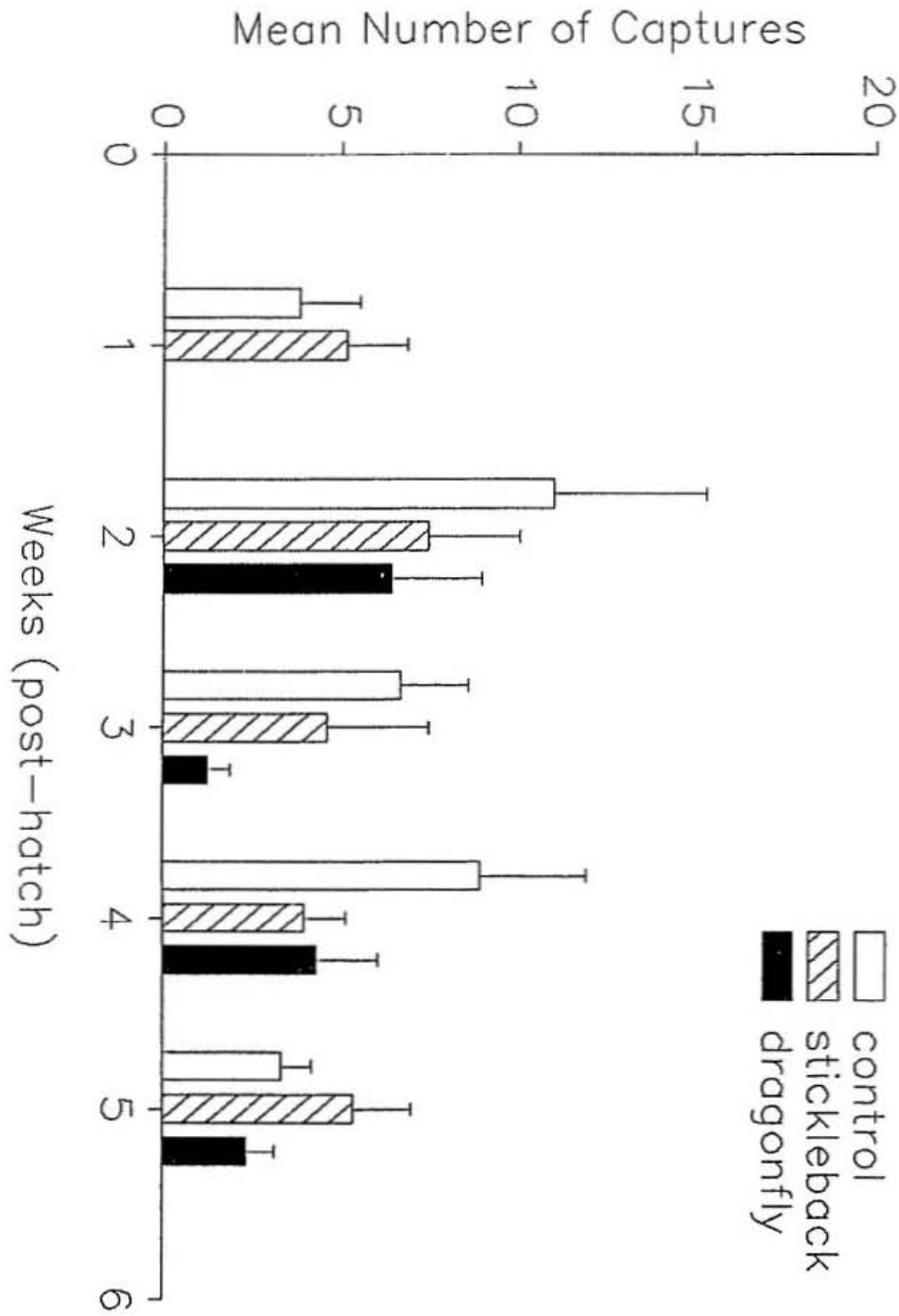

Mean Number of Captures
0
5
10
15
20
0
1
2
3
4
5
6
Weeks (post-hatch)
control
stickleback
dragonfly

Fig.29. Mean number of turns performed each week in the grid furthest from the predator by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar= standard error. n= 18 larvae per treatment per week.

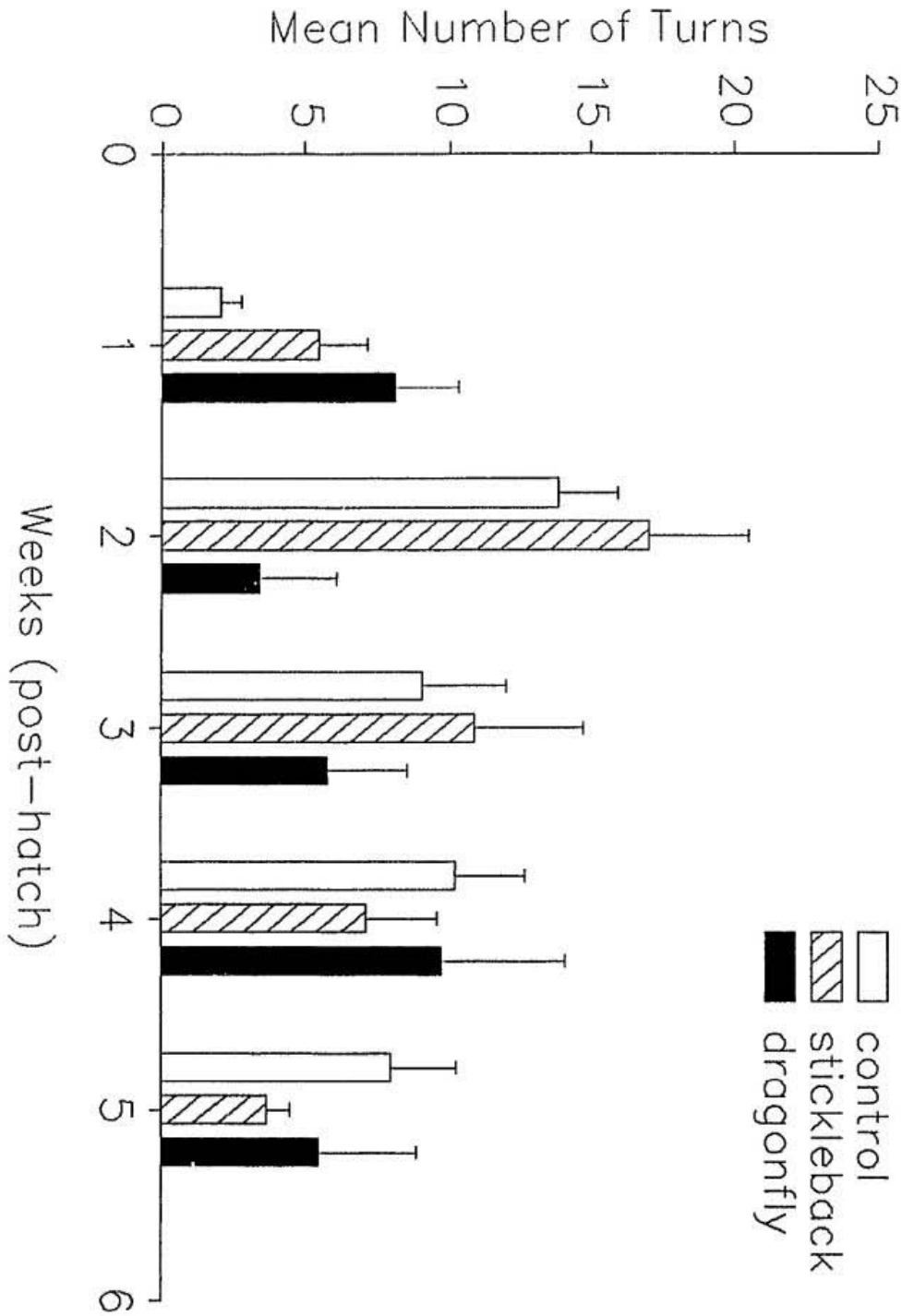

Mean Number of Turns
0
5
10
15
20
25
Weeks (post-hatch)
0
1
2
3
4
5
6
control
stickleback
dragonfly

Fig.30. Mean number of turns performed each week in the middle grid by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

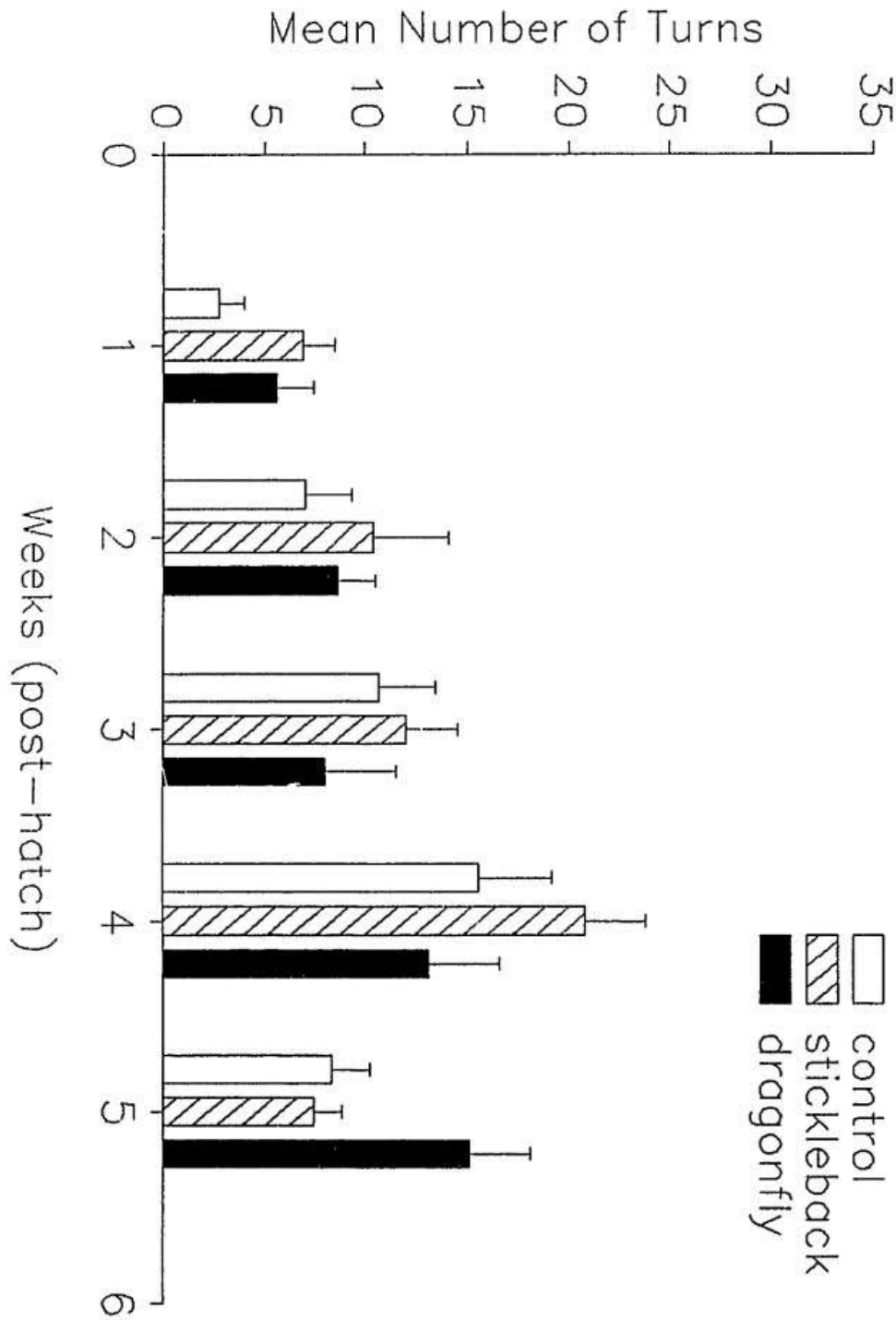

Mean Number of Turns
0
5
10
15
20
25
30
35
Weeks (post-hatch)
0
1
2
3
4
5
6
control
stickleback
dragonfly

Fig.31. Mean number of turns performed each week in the grid adjacent to the predator by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

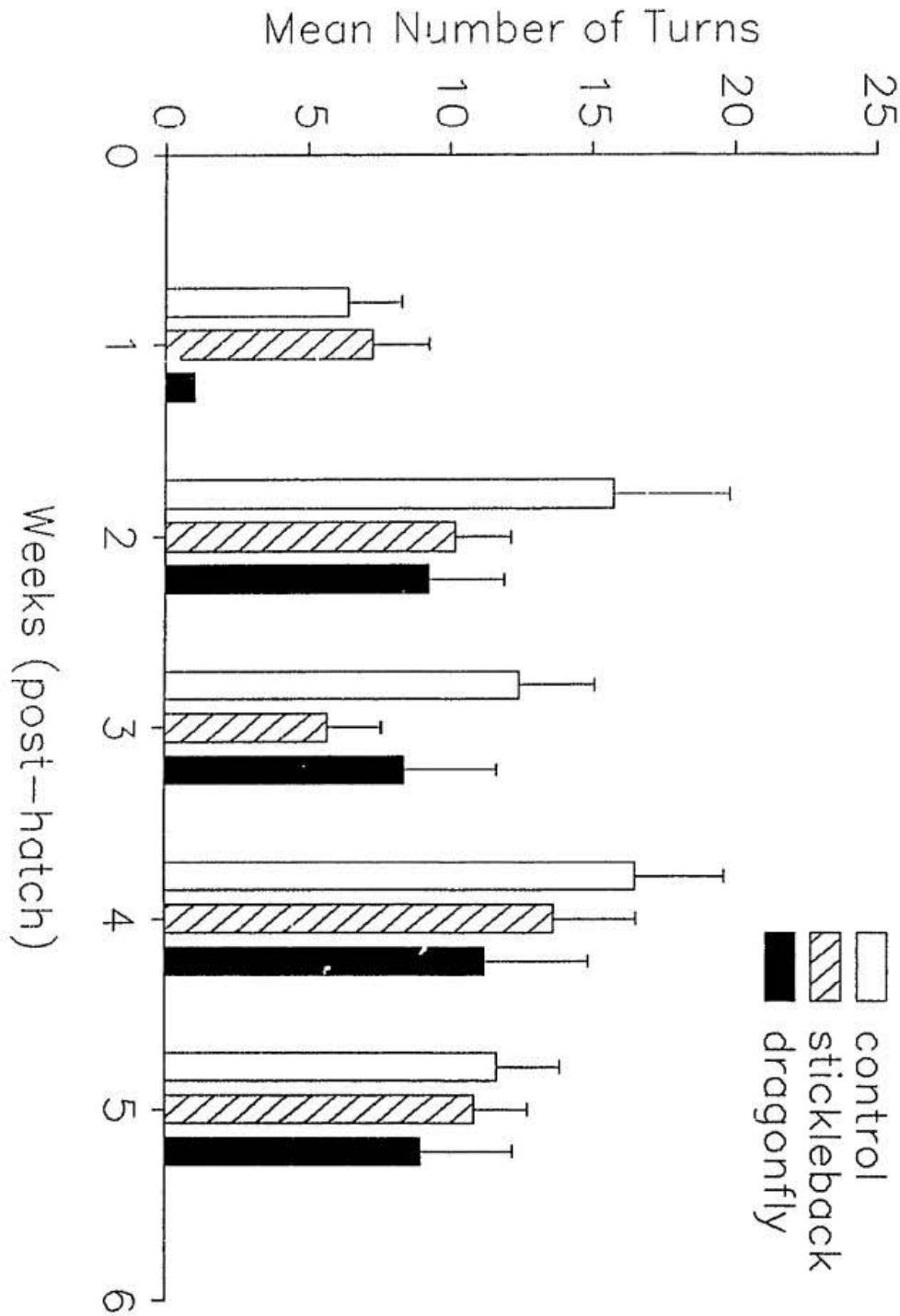
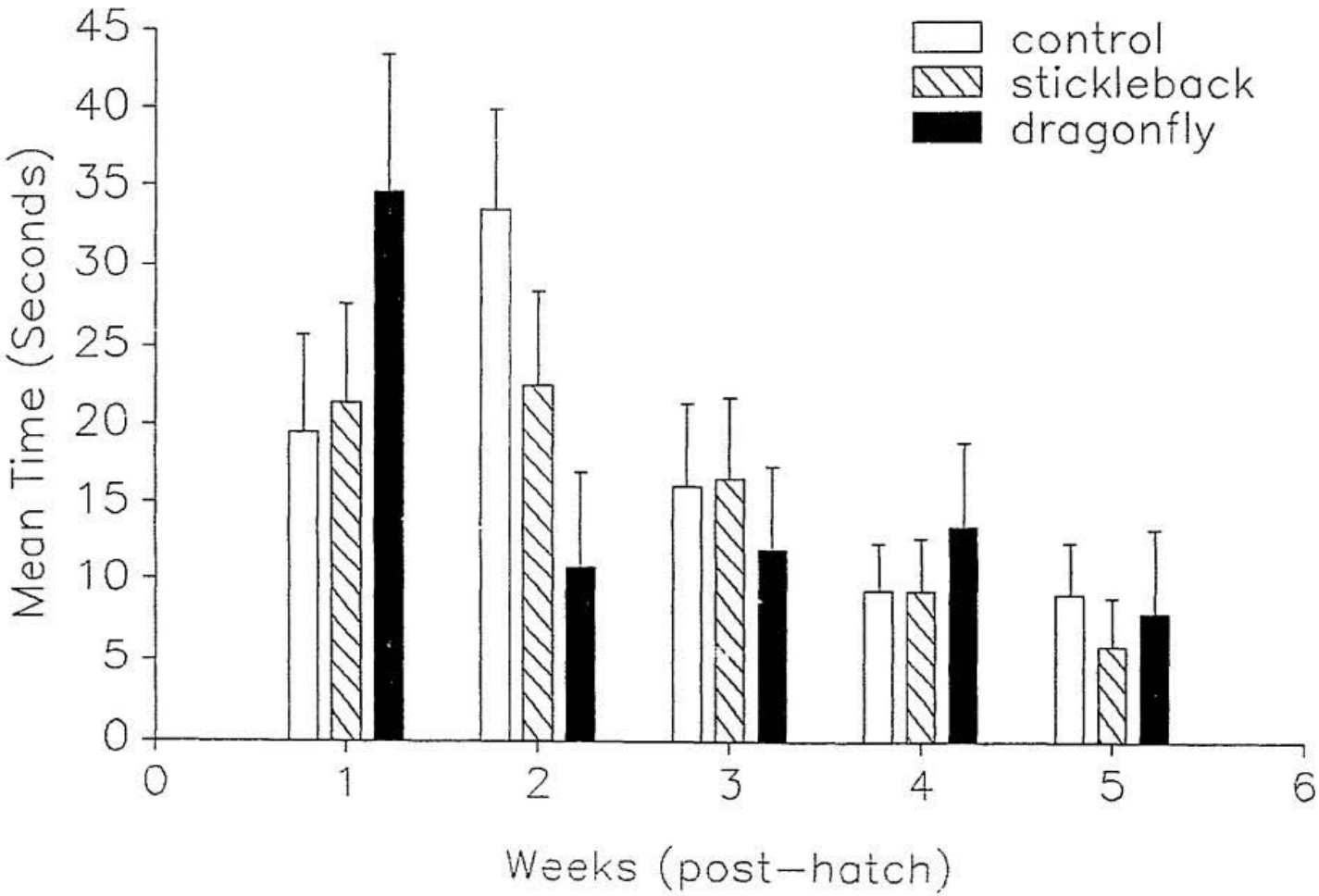

Mean Number of Turns
0
5
10
15
20
25
0
1
2
3
4
5
6
Weeks (post-hatch)
control
stickleback
dragonfly

Fig.32. Mean time (seconds) spent each week in the grid furthest from the predator by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.


control
stickleback
dragonfly
Mean Time (Seconds)
45
40
35
30
25
20
15
10
5
0
0
1
2
3
4
5
6
Weeks (post-hatch)

89a

Fig.33. Mean time (seconds) spent each week in the middle grid by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

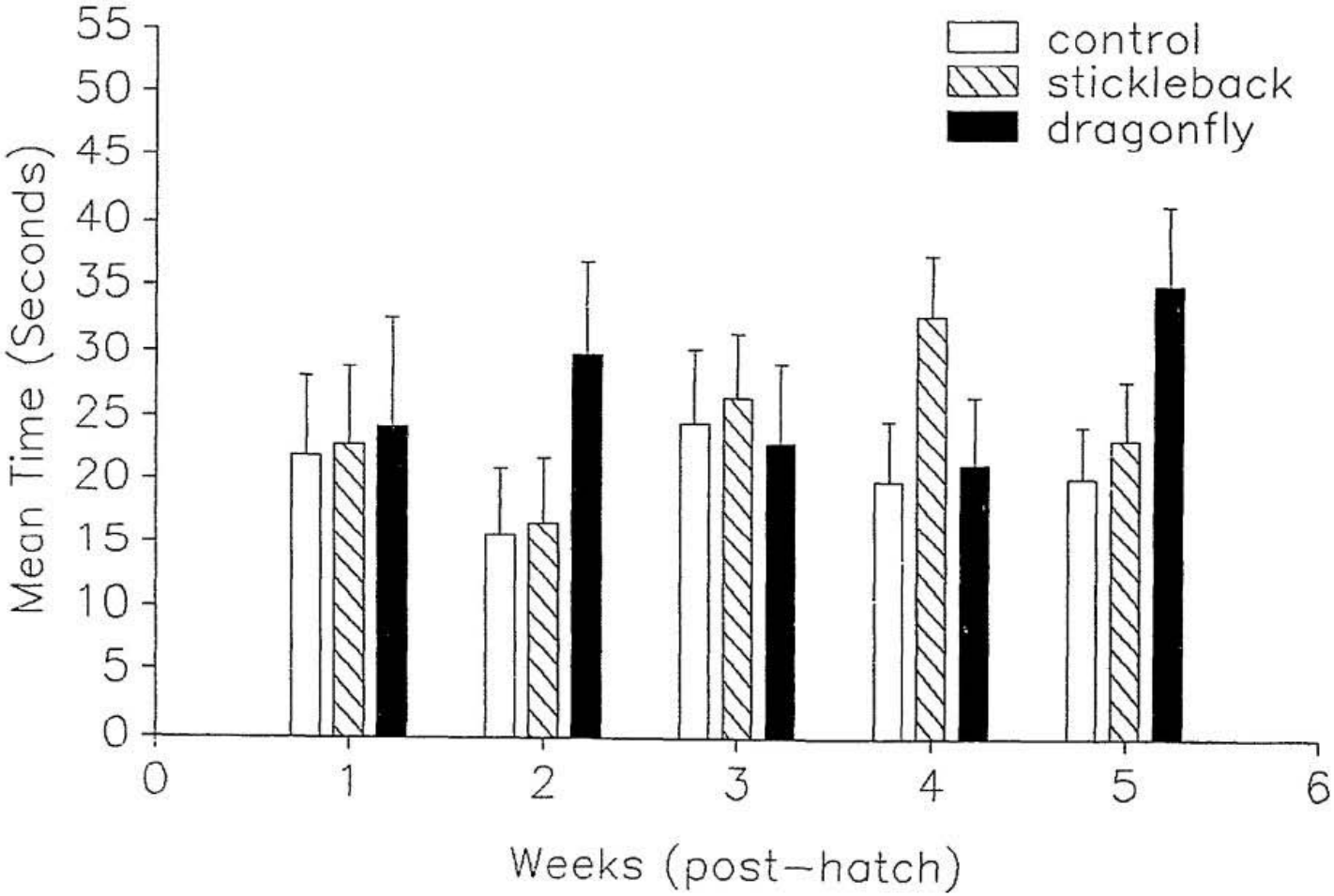

control
stickleback
dragonfly
Mean Time (Seconds)
55
50
45
40
35
30
25
20
15
10
5
0
0
1
2
3
4
5
6
Weeks (post-hatch)

Fig.34. Mean time (seconds) spent each week in the grid adjacent to the predator by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

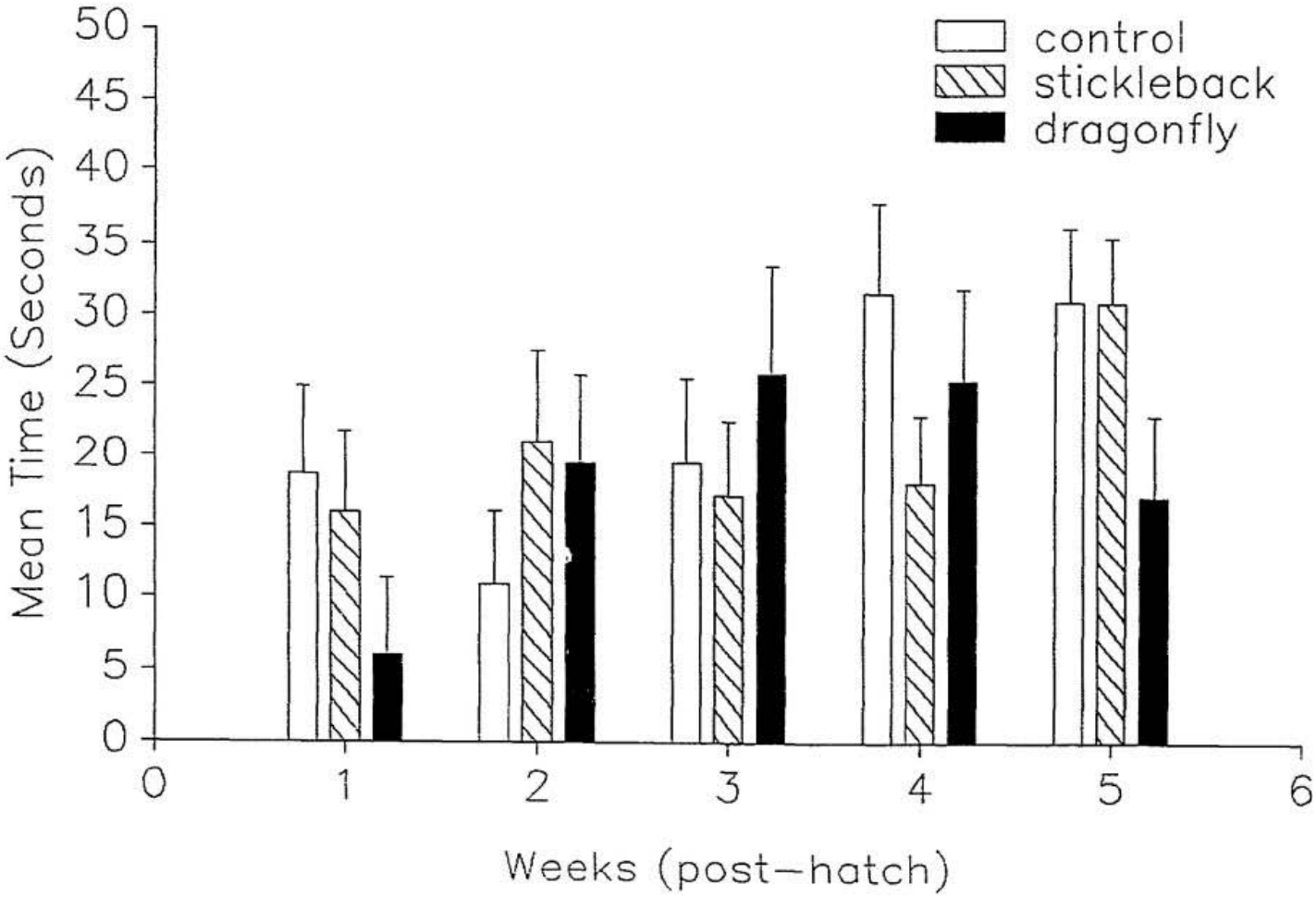
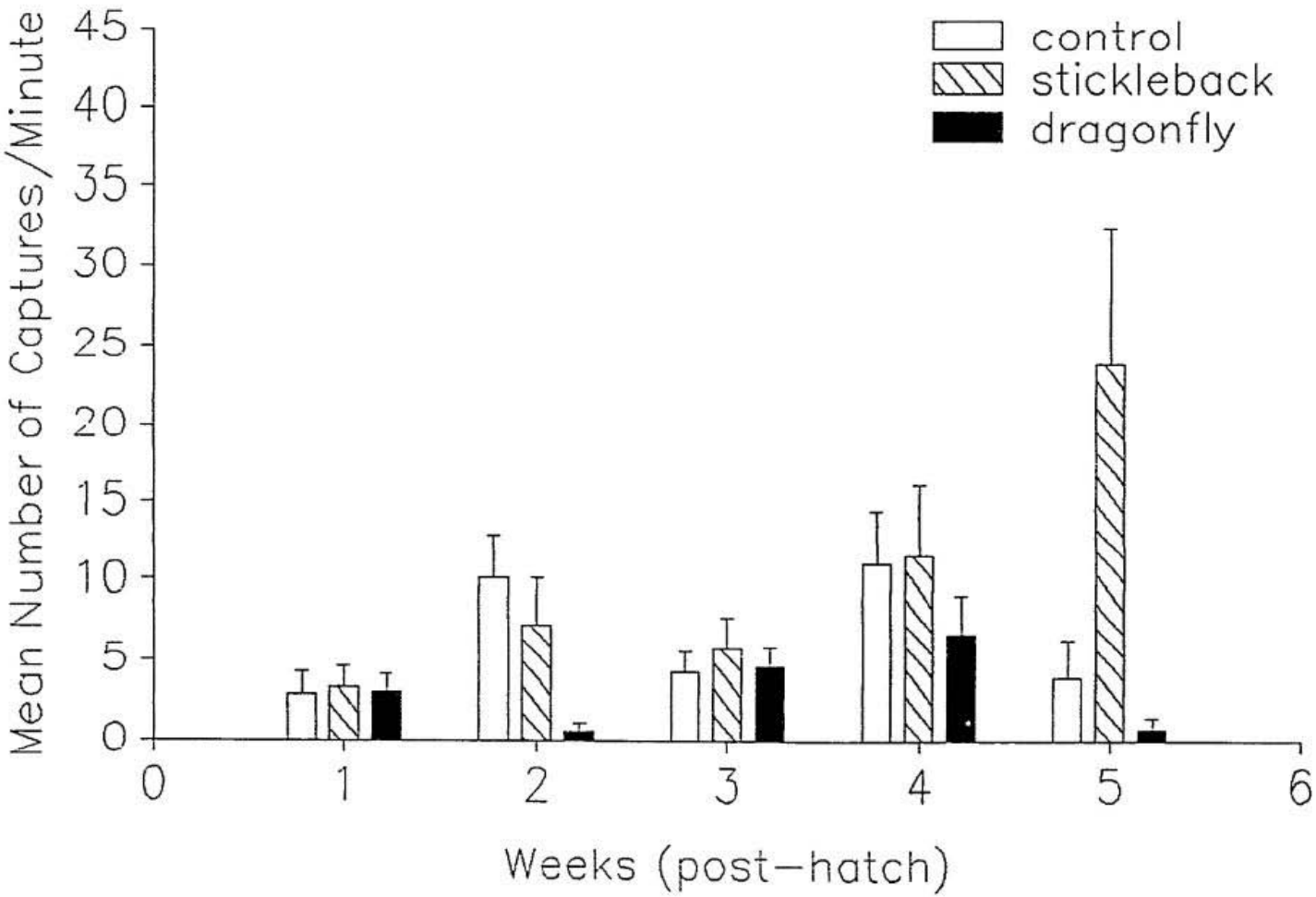

control
stickleback
dragonfly
Mean Time (Seconds)
0
5
10
15
20
25
30
35
40
45
50
0
1
2
3
4
5
6
Weeks (post—hatch)

Fig.35. Mean number of captures per minute performed each week in the grid furthest from the predator by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.


Mean Number of Captures/Minute
45
40
35
30
25
20
15
10
5
0
0
1
2
3
4
5
6
Weeks (post-hatch)
control
stickleback
dragonfly

92a

Fig.36. Mean number of captures per minute performed each week in the middle grid by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

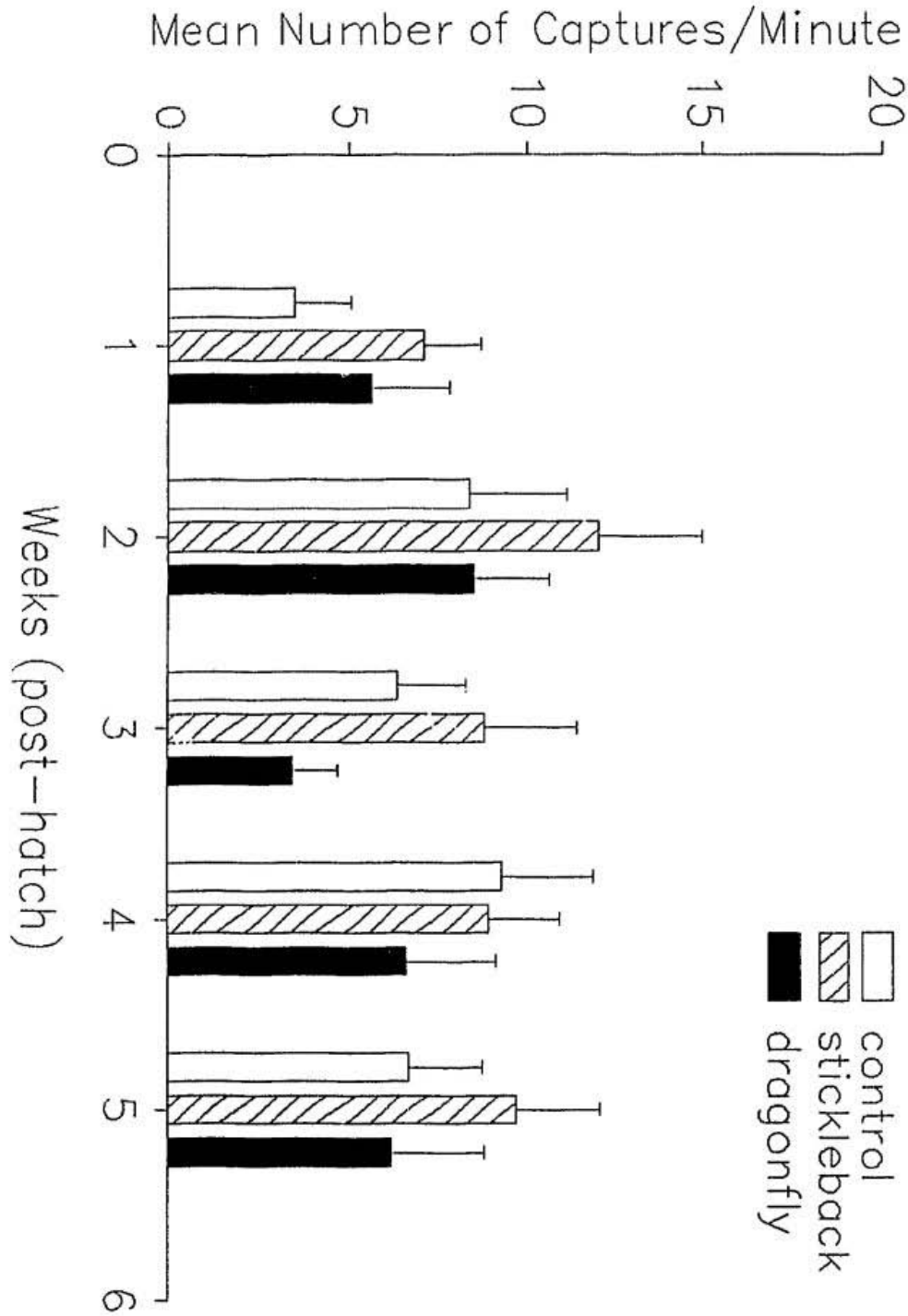

Mean Number of Captures/Minute
0
5
10
15
20
Weeks (post-hatch)
0
1
2
3
4
5
6
control
stickleback
dragonfly

Fig.37. Mean number of captures per minute performed each week in the grid adjacent to the predator by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

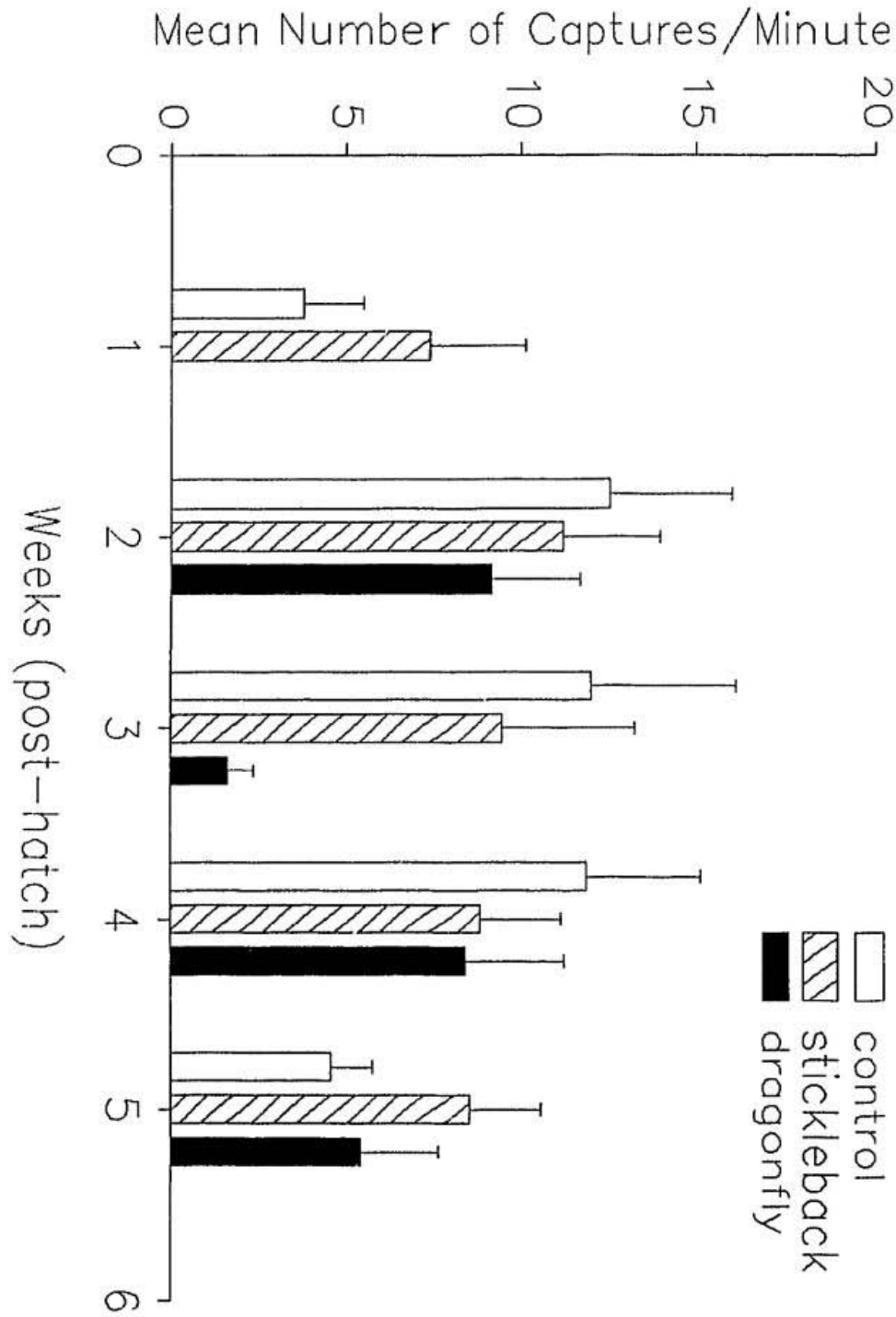

Mean Number of Captures/Minute
0
5
10
15
20
Weeks (post-hatch)
0
1
2
3
4
5
6
control
stickleback
dragonfly

Fig.38. Mean number of turns per minute performed each week in the grid adjacent to the predator by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

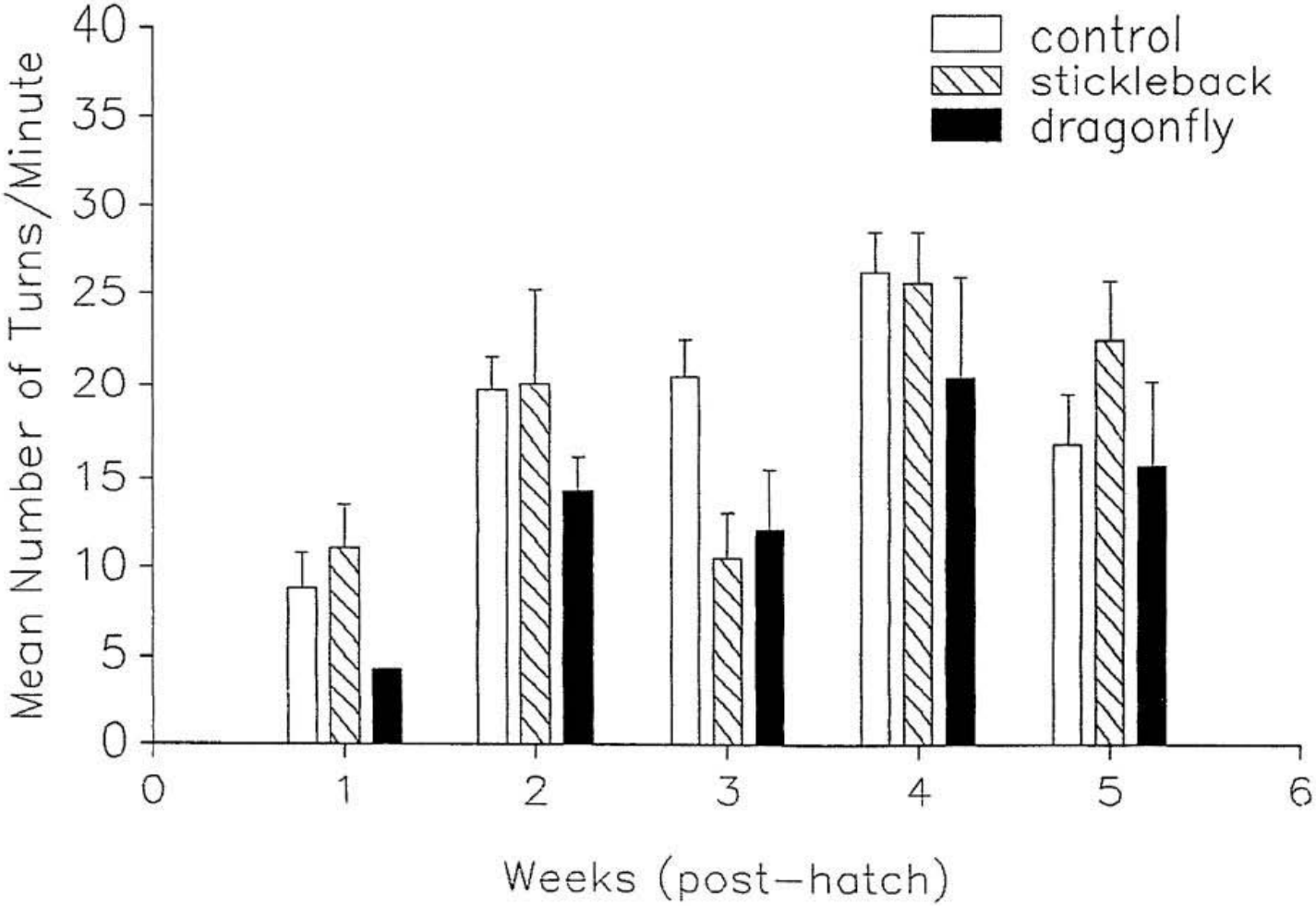

control
stickleback
dragonfly
Mean Number of Turns/Minute
0
5
10
15
20
25
30
35
40
0
1
2
3
4
5
6
Weeks (post-hatch)

Fig.39. Mean number of turns per minute performed each week in the grid furthest from the predator by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.

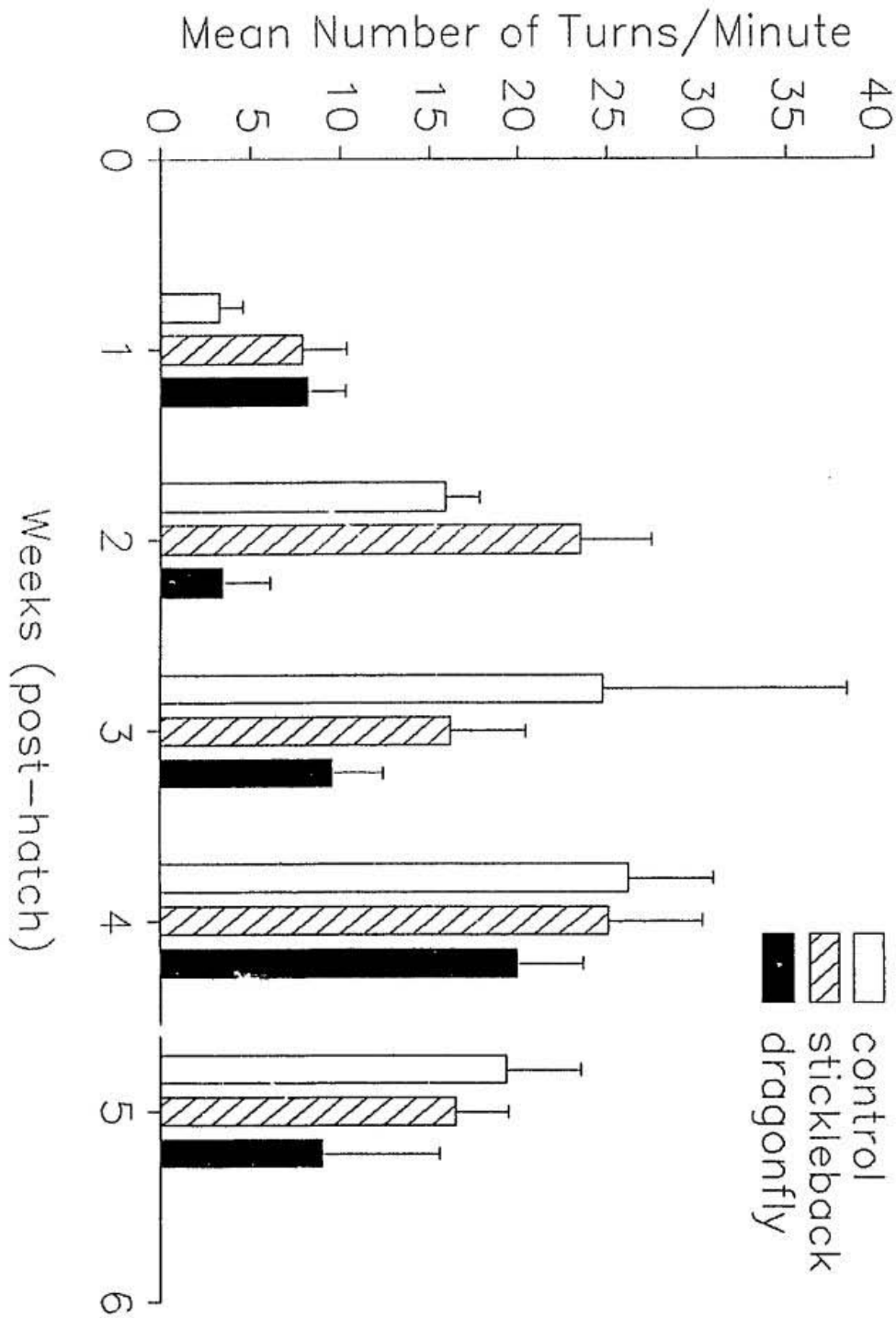
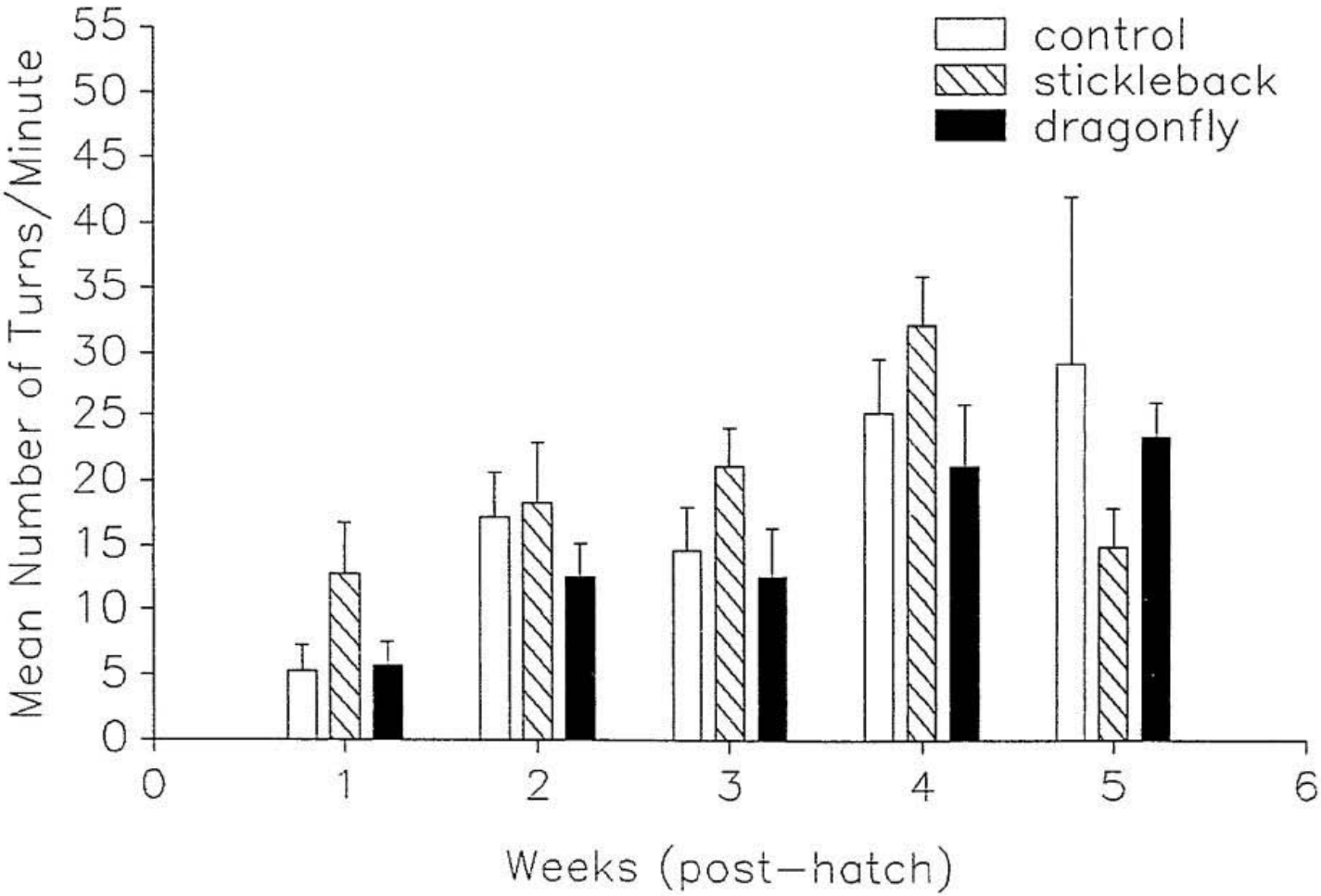

Mean Number of Turns/Minute
0
5
10
15
20
25
30
35
40
Weeks (post-hatch)
0
1
2
3
4
5
6
control
stickleback
dragonfly

Fig.40. Mean number of turns per minute performed each week in the middle grid by larvae exposed to the stickleback (hatched bar), dragonfly (solid bar) and no predator (open bar) during Experiment Two. Vertical bar = standard error. n = 18 larvae per treatment per week.


control
stickleback
dragonfly
Mean Number of Turns/Minute
55
50
45
40
35
30
25
20
15
10
5
0
0
1
2
3
4
5
6
Weeks (post–hatch)

97a

Fig.41. Mean total length (mm) at age (days post-hatch) of larval sticklebacks raised in the laboratory. No dorsal or pelvic spines (empty circle); dorsal and pelvic spines appear, no stain absorbed (hatched circle); spines absorbed blue stain indicating they are composed of cartilage (cross-hatched circle); spines absorbed red stain indicating they are composed of bone (Double circle).

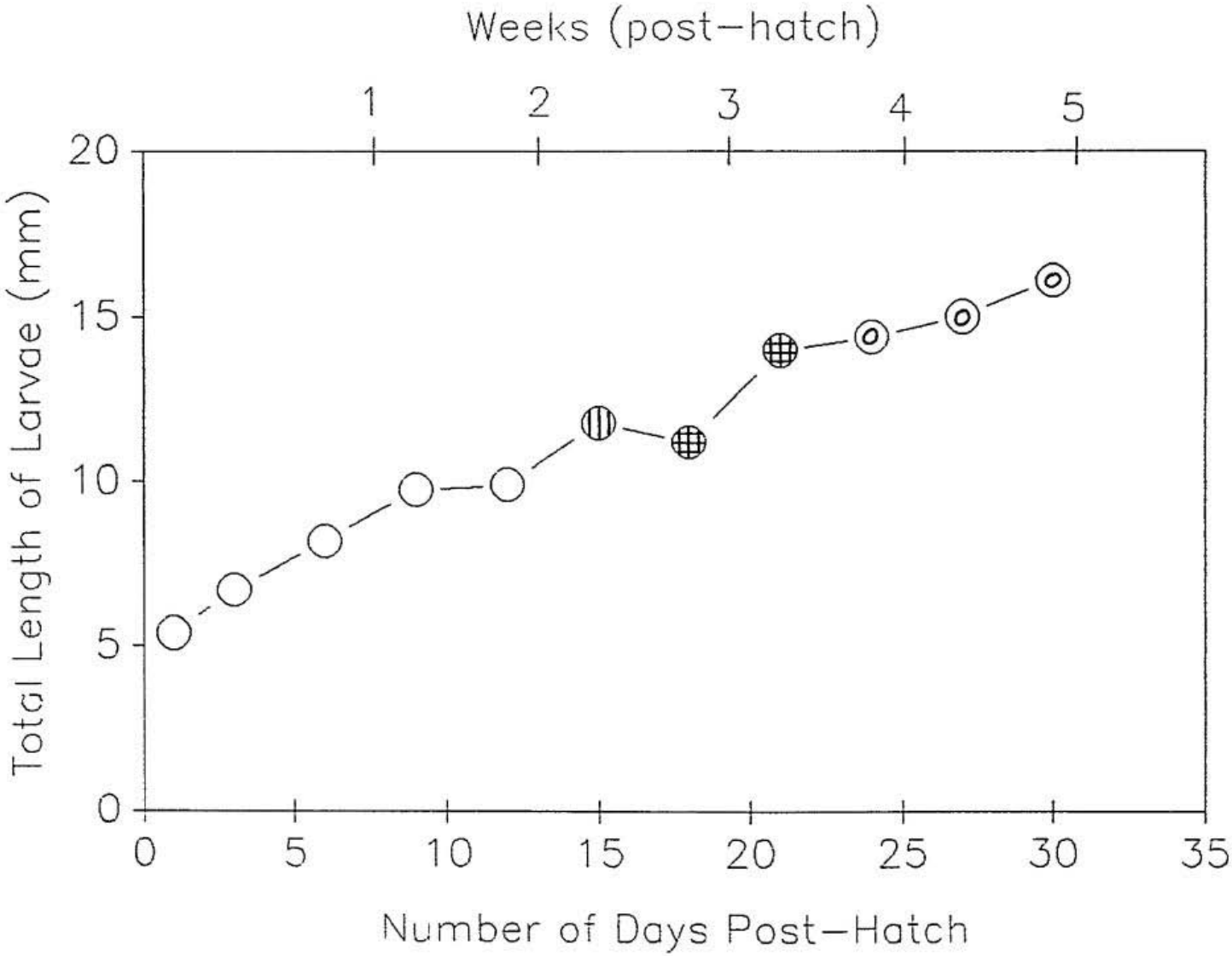
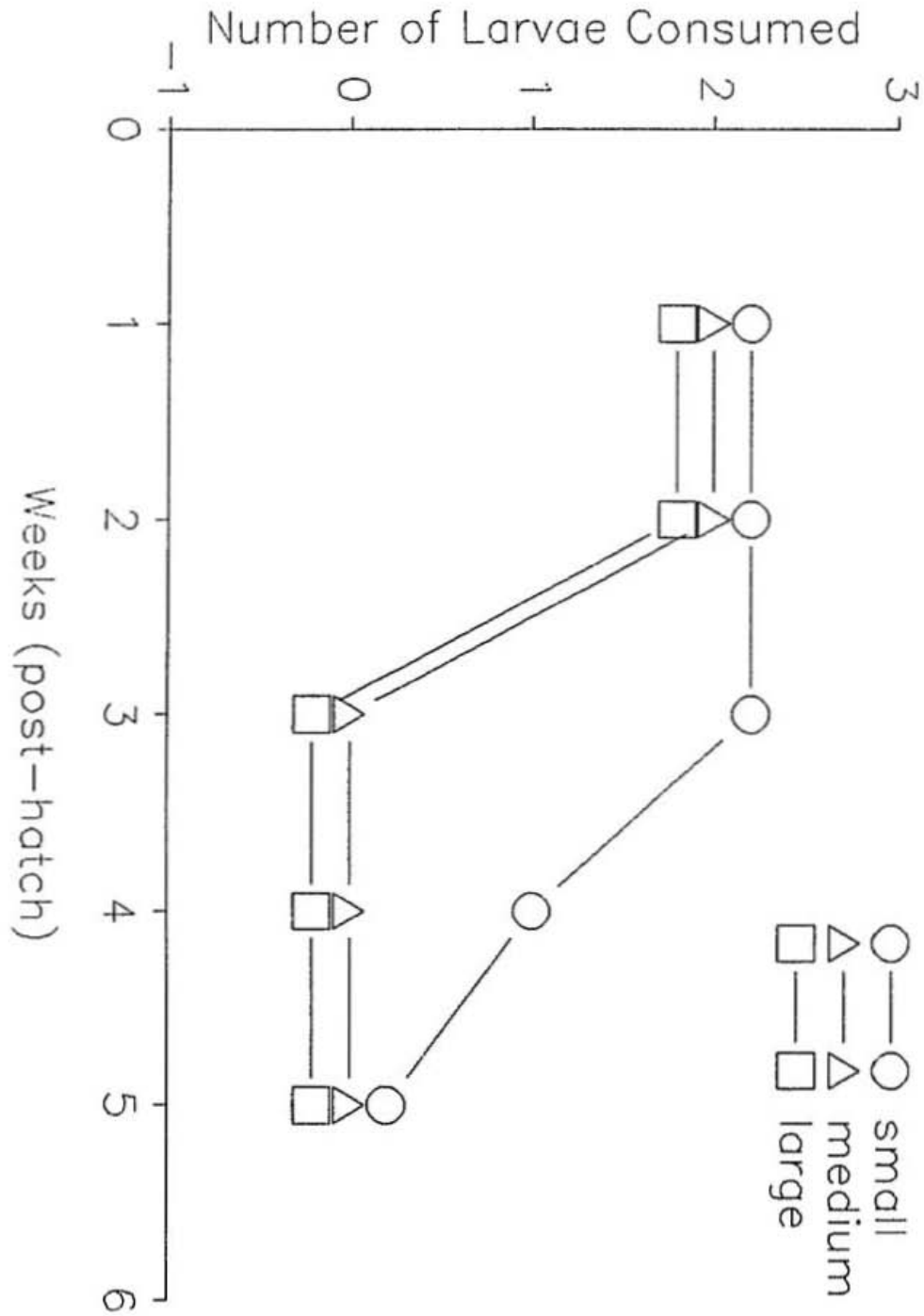

Weeks (post-hatch)
1
2
3
4
5
20
15
10
5
0
Total Length of Larvae (mm)
0
5
10
15
20
25
30
35
Number of Days Post-Hatch

Fig.42. The number of larval sticklebacks remaining after one hour in an enclosure with a small (triangle), medium (square), or large (circle) predator each week. The initial number of larvae is two.


Number of Larvae Consumed
-1
0
1
2
3
Weeks (post-hatch)
0
1
2
3
4
5
6
small
medium
large

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