

The tail flip escape response of the brown shrimp *Crangon crangon* (L.) in the context of predator-prey interactions

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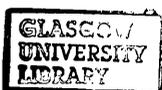
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Crangon crangon

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SUMMARY

This investigation has used high speed and conventional video techniques to investigate the tail flip escape behaviour of the brown shrimp *Crangon crangon* (L.) in the context of predator-prey interactions.

Shrimp length has a significant effect upon the displacement, velocity and acceleration achieved during a tail flip. Displacement per tail flip increases from approximately 12 mm in small (10 mm) shrimps, to 90 mm in large (> 60 mm) shrimps. Mean velocity, maximum velocity and maximum acceleration increase from approximately 0.4 m.s⁻¹, 0.6 m.s⁻¹ and 70 m.s⁻² respectively in small shrimps, to 1.1 m.s⁻¹, 1.8 m.s⁻¹ and 160 m.s⁻² in shrimps of between 50-60 mm, but performance in shrimps larger than this declines slightly.

The body flexion movement of *Crangon crangon* during tail flips is relatively symmetrical, with the result that both the head region and the tail region are moved through the water with respect to the shrimp's centre of mass. This is associated with the use of a head fan (formed by expansion of the antennal scales) as well as a tail fan (formed by expansion of the uropods) for generating thrust. Removal of the head fan results in a decline in tail flip velocity by 35 %, compared with a 58 % decline when the tail fan is removed.

Escapes by *Crangon crangon* have been found to consist of either a single tail flip, or a series of tail flips which together constitute an escape swimming bout. The first flexion phase of an escape translates the shrimp laterally or vertically depending on whether its body is rotated about the longitudinal axis during the initial stages of an escape. If the first flexion is vertical, a lateral roll often occurs during the following re-extension phase. Consequently, subsequent tail flips of an escape occur with the shrimp swimming on its side, and steering in the horizontal plane is achieved by modifying the angle of rotational pitch between one tail flip and the next. This tail flip mechanism is in direct contrast to that of many other types of larger decapods, which instead tend to tail flip in an upright body position.

Horizontal escape trajectories of shrimps have been investigated in an arena with a hard substratum (preventing shrimps from burying) using both a natural stimulus (juvenile cod, *Gadus morhua*) and an artificial stimulus (a wooden rod) to evoke tail flip responses. Both types of stimuli result in the first tail flip of a response being laterally (rather than vertically) directed, and generate similar escape trajectories. When a shrimp is attacked from either head-on or tail-on, the probability of an escape occurring to the left side of the shrimp is

approximately equal to an escape occurring to the right side. If an attack occurs from the side of a shrimp, escapes are directed preferentially to the contralateral side of the stimulus. Also, if the shrimp is exposed to a lateral sub-threshold pre-stimulus before being attacked from the front or the rear, escapes are directed preferentially to the contralateral side of the pre-stimulus.

The escape angle of the first tail flip of a response (with respect to the shrimp's body axis, where the head = 0°) changes significantly with attack direction, but always lies between 75° and 156° to the shrimp's left or right. This region defines a pair of 'escape envelopes' to each side of the shrimp. It is suggested that these escape envelopes reflect anatomical constraints on the shrimp. In addition to this, the first tail flip of an escape is never directed at an angle of less than 63° to either side of the stimulus (where the attack direction = 0°). The region defined by angles of less than 63° has been termed the 'exclusion envelope', and it is suggested that this represents a behavioural choice by the shrimp. The interaction of the anatomical and behavioural 'escape rules' for any given attack-escape angle can be represented by a graphic overlay of the escape and exclusion envelopes.

At the end of the first tail flip of an escape, shrimps sometimes perform a sudden change of direction by as much as $70-80^\circ$. Subsequent tail flips of an escape are usually directed away from the direction of an attack, but a proportion may be steered to the side of, and then behind the attacker. The frequency with which this occurs is dependent upon the direction of attack.

During both the initial and latter stages of an escape, the trajectory followed by a shrimp displays certain elements of unpredictability (protean behaviour) which may operate to reduce the ability of a predator to predict and compensate for the direction of an escape.

Further laboratory experiments under artificial (small arena with a hard substratum) and semi-natural (larger arena with a sediment substratum) conditions have revealed that as shrimps increase in length, the probability of being caught by a cod of a given size decreases. Correspondingly, the pursuit duration and the number of strikes within a pursuit increase. An experiment in which only infra-red illumination was provided suggests that the probability of juvenile cod capturing *Crangon crangon* declines in the absence of visible light.

After being caught, shrimps with a shrimp:cod (S:C) length ratio of greater than 0.19 sometimes escape by tail flipping out of a cod's mouth. The handling time required by a cod to consume a shrimp increases exponentially with S:C ratio such that shrimps with a ratio of

between 0.15 and 0.20 have the highest profitability (in terms of dry weight consumed per handling time).

In a field study, *Crangon crangon* was found to constitute a low proportion of the diet of juvenile cod collected from Tralee Beach on the west coast of Scotland. For those cod that did feed upon *C. crangon*, small (40-80 mm) individuals consumed shrimps with an S:C ratio of 0.10 in greatest numbers, whilst large (80-110 mm) cod fed mainly upon shrimps with an S:C ratio of 0.15-0.20.

This study has found that the tail flip escape response of *Crangon crangon* provides these animals with an effective secondary defence against predation. The success of this strategy operates in a size-dependent manner, and is probably influenced by prevailing habitat conditions. Differences between the tail flip behaviour of *C. crangon* and larger decapod crustaceans offer scope for further work on this species.

Chapter 1
General Introduction

1.1 Interactions between animals, and associated adaptations

Animals interact with each other in a variety of ways. Some types of interactions, such as commensalism, mutualism and symbiosis, involve partnerships in which one or more animals benefit without harming the other participants of the association (Gotto, 1969; Burton, 1969). However, many types of interactions involve conflict between individuals. For example, animals are vulnerable to an array of parasite species, which, if not fatal, may nevertheless impose significant energetic and reproductive costs (e.g. Dobson *et al.*, 1992). Animal species must also compete with each other for limited resources such as food, shelter and mates (Krebs & Davies, 1993), and in the case of carnivores, must be able to catch and consume prey whilst at the same time avoiding being eaten themselves by larger predators (Edmunds, 1974). The last two of these relationships come under the heading of predation, which Malcolm (1992, p.459) considers as:

“.....an inextricably linked interaction between prey defences and predator foraging”.

Defensive adaptations protect animals against attack by other animals, and are distinct from protective adaptations, which protect animals from hostile physical, chemical and biological factors in the environment (Edmunds, 1966). This thesis is primarily concerned with the defensive adaptations of prey in the context of predator-prey interactions.

Predation is often considered to consist of a series of events (e.g. O'Brien, 1979; Endler, 1986; Bailey & Houde, 1989; Fuiman & Magurran, 1994), and at a simple level can be broken down into the sequence: prey detection → attack → capture. For a prey animal to survive, it must use one or more defence mechanisms to interrupt this sequence. Primary (or indirect) defences are those which operate regardless of whether or not there is a predator in the vicinity of the prey (Kruuk, 1972; Edmunds, 1974), or before a predator initiates any prey-catching behaviour (Robinson, 1969). Examples of this include mechanisms which attempt to minimise the likelihood of an animal being detected, such as crypsis, or living within a crevice or burrow (anachoresis). Secondary (or direct) defences operate when a prey detects a predator, and have the function of increasing the prey's chances of survival once it has been detected (Edmunds, 1974). This is usually achieved through resistive (fight) or escape

behaviour (Vermeij, 1987; Malcolm, 1990). Weihs & Webb (1984) further sub-divide escape into avoidance and evasion. Avoidance is an active response by the prey which reduces the chances of an attack occurring once it has been detected; the prey either moves out of the predator's field of detection (type I), or moves into a position which optimises its future evasion chances (type II). Evasion (often referred to as an escape response) removes the prey from the predator's interception path once an attack has occurred, and counteracts further attacking behaviour of the predator. This usually results in the animal escaping at its maximum velocity, and often requires the use of large anaerobic muscles for intensive bursts of activity. Therefore, as defence mechanisms shift from primary (pre-detection) to secondary (post-detection), they generally become more energetically demanding (Endler, 1986; Malcolm, 1990, 1992).

The central theme of this study is the escape response from predators of the brown shrimp *Crangon crangon* (Linnaeus, 1758; formerly known as *Crangon vulgaris*). This species is preyed upon extensively by a large number of fish species (see section 1.2), and has evolved a rapid escape response to counteract the effects of this (Smith, 1993). Investigation of the shrimp's escape has wide interest because *C. crangon* is extremely common in many shallow marine communities throughout Europe, and is also fished extensively in various regions such as the Wadden Sea, the Severn Estuary, the Solway Firth, and the Loire Estuary. Furthermore, whilst considerable interest has been paid to the escape response of larger decapods such as crayfish and lobsters, knowledge of escape responses in smaller decapods is comparatively sparse. *C. crangon* are readily available, and their small size (< 90 mm) and hardness make them amenable to laboratory experimentation.

1.2 The biology of *Crangon crangon*

Crangon crangon is a member of the infraorder Caridea, and the family Crangonidae (Barnes, 1987), of which 15 species are represented in British coastal waters (Allen, 1967). The genus *Crangon* has a world-wide distribution, and depending upon different authors, contains from 7 to more than 30 species (Tiews, 1970), 2 of which (*C. crangon* and *C. allmani*), occur in British waters (Allen, 1967).

In a comprehensive review of the biology of *Crangon crangon*, Tiews (1970) lists the species as being present from the fjords of Finland, to the North Sea, the Baltic Sea, the coasts of north and west Europe, and the Mediterranean. Vertically, their distribution ranges from

intertidal beaches down to depths of about 20 m (Allen, 1960; Tiews, 1970; Henderson & Holmes, 1989), although they also occur in deeper waters. Wollebaek (1908) reportedly collected a specimen from depths of greater than 800 m. *C. allmani* is a more boreal species, extending from the White Sea to the northern part of the Bay of Biscay, and usually occurs at depths of between 20 and 200 m (Allen, 1960). *C. crangon* and *C. allmani* are similar morphologically, the latter being distinguishable by its slightly narrower abdomen, different colouration, and a pair of ridges on the dorsal side of the 6th abdominal segment. Some early workers (Ortmann, 1891; Doflein, 1900) considered the two as belonging to the same species, but observations on the adults (Wollebaek, 1908) and larvae (Sars, 1890; Lebour, 1931) reveal that they are in fact distinct from one another. Recent genetic comparisons between the two species corroborate this. In two separate studies, they were found to have genetic identities with one another of 0.245 (11 enzyme loci compared; Abdullah & Shukor, 1993) and 0.262 (18 enzyme systems from 23 loci; Bulnheim & Schwenger, 1993), which suggests that the two may in fact be quite distantly related, since values of 0.5-0.8 are more typical of closely related species (Moyses *et al.*, 1982). Bulnheim & Schwenger (1993) were further able to distinguish genetic differences between populations of *C. crangon* collected from the North Sea/Baltic region, the north Atlantic, Portugal, and the Adriatic (the most divergent of all). Differences between *C. crangon* populations over a smaller zoogeographical scale have also been found by Henderson *et al.* (1990). Using morphometric analysis, they were able to identify 6 distinct populations off the English and Welsh coasts, and they suggest that these have arisen due to incomplete mixing of neighbouring water bodies with different physical characteristics. These act as partial barriers to the translocation of planktonic larvae.

Crangon crangon lives on sand and mud substrata, and occurs in greatest numbers in areas of brackish water and strong tidal currents. After passing through 5 planktonic larval stages (Tiews, 1970), the 1st post-larvae (4-5 mm total length) adopt an epibenthic lifestyle, often on inter-tidal sand or mud flats (Kuipers & Dapper, 1984; Beukema, 1992). Beukema (1992) estimated growth rates of 0.2-0.5 mm.day⁻¹ for newly settled juveniles in the Wadden Sea, and although maximum lengths of 80-90 mm may be achieved, shrimps of greater than 70 mm are comparatively rare. Estimates on the life-span vary between 3-5 years (Lloyd & Yonge, 1947; Tiews, 1970; Henderson & Holmes, 1987).

According to various authors (see Tiews, 1970), *Crangon crangon* is heterosexual, with females living longer, and growing larger than males (Lloyd & Yonge, 1947). However,

there is also evidence that, at least under some circumstances, they are protandrous hermaphrodites, changing from males into females at a length of between 42 and 46 mm after their first copulation (Boddeke, 1966, 1982; Boddeke *et al.*, 1988). During sexual maturation in females, the ovaries undergo an increase in size (Haefner & Spaargaren, 1993), and within 24 hours of mating, the eggs are released from the ovaries and carried on the ventral side of the 'berried' shrimp after attaching to the setae of the 1st-4th pleopods (Lloyd & Yonge, 1947). Development times of the eggs vary in different locations according to temperature. In the Severn Estuary and Bristol Channel, Lloyd & Yonge (1947) estimated that females carried their eggs for 5 weeks during the warmest periods of the year (July-August), but that this rose to 13 weeks during the coldest period (February). The larvae are planktonic for a period of approximately 5 weeks (Thorson, 1946) before adopting an epibenthic lifestyle. Recruitment of post-larval juveniles in north European waters occurs from spring to late autumn, and is generally later in the year in more northerly locations (e.g. Thorson, 1946; Lloyd & Yonge, 1947; Tiews, 1970; Kuipers & Dapper, 1984; Henderson & Holmes, 1987; Beukema, 1992; Cattrijsse *et al.*, 1994). Females are able to breed more than once a year, and generally spawn both in spring, and again later in the summer (Henderson & Holmes, 1987; Tiews, 1970).

Crangon crangon undergoes seasonal migrations between shallow inshore and deeper offshore regions (Lloyd & Yonge, 1947; Tiews, 1970; Boddeke, 1975, 1976; Spaargaren, 1980; Henderson & Holmes, 1987, 1989; Bamber & Henderson, 1994). After settling in shallow waters, the juveniles move offshore during the winter. Males tend to remain in this area, whilst in spring, females brooding eggs move back into the shallower areas in order, it is believed, to feed in more productive areas (Tiews, 1970; Henderson & Holmes, 1989). The females move back offshore during mid-summer, enabling them to release planktonic larvae in deeper waters. This may be because offshore waters are less turbid, and have a higher planktonic standing stock for the larvae to feed upon (Bamber & Henderson, 1994). However, it also enables the females to mate for a second time with the offshore males, before moving back into shallower waters in late summer to brood their second batch of eggs. In late autumn, the inshore population of juveniles and the adult female population move offshore. Shrimps therefore experience large fluctuations in salinity and temperature, and this is particularly true for the juveniles and adult females. However, *C. crangon* is a euryhaline and eurythermal species. Some of the earliest experimental work connected with their osmoregulatory ability was conducted by Caudri (1937), who found that the salinity which resulted in optimal

survival of young shrimps kept at 4°C was at 34 ‰, whereas for those kept at 18.9°C, it was 20-30 ‰. These effects of temperature on the osmoregulatory ability of *C. crangon* were later confirmed by Broekema (1942) and Spaargaren (1971), the former of whom also found that one year old shrimps were better adapted to lower salinities than were two years old shrimps (optimum survival rates at salinities of 18-19 ‰ and 28-29 ‰ respectively at 22°C). Grimm (1965) and Spaargaren (1971) showed that over a salinity range of approximately 15 ‰ to 30 ‰, *C. crangon* maintained their internal osmotic concentration at a more or less constant level, whereas in *C. allmani*, which survives poorly at low salinities, the internal concentrations changed isosmotically with the external salinity. The ability of *C. crangon* to survive such large ranges in salinity is related to the low permeability of their outer surfaces (most ionic and water exchange being confined to the gill region), and their ability to regulate haemolymph and intracellular concentrations of ions and free amino acids (Grimm, 1965; Hagerman, 1971, 1973, 1978; Weber & van Marrewijk, 1972; Spaargaren, 1975; McLusky *et al.*, 1982). The combined effects of temperature and salinity on the osmoregulatory ability of *C. crangon* have been linked to their seasonal migration patterns (Broekema, 1942; Lloyd & Yonge, 1947; Spaargaren, 1971; Henderson & Holmes, 1987). Juveniles and adult females are better able than the males to withstand low salinities, and therefore the males are confined to deeper offshore waters during the summer. However, at the onset of winter, both temperature and salinity fall in shallow inshore waters, and this coincides with periods when the juveniles and females move offshore. Furthermore, the planktonic stages are not as well adapted to low salinities as the post-larval stages (Grimm, 1965), and this is an additional reason for berried females to move offshore at times when the larvae hatch from the eggs.

On a shorter time scale, *Crangon crangon* exhibits diel migration patterns. In tidal regions, shrimps move into intertidal areas at times of high tide, and move offshore again as the tide retreats (Hartsuyker, 1966; Al-Adhub & Naylor, 1975)). In some locations (e.g. the Wadden Sea), juvenile shrimps (< 25-30 mm total length) remain in intertidal pools at low tide, whilst larger shrimps congregate in sub-tidal channels (Janssen & Kuipers, 1980; Kuipers & Dapper, 1984). One advantage of this strategy is that it may offer some degree of population segregation, which reduces cannibalism and other predatory threats (Jansenn & Kuipers, 1980). The juveniles show better temperature tolerance than adults (van Donk & de Wilde, 1981), and during summer months, this allows them to occupy intertidal pools in which the water temperature may markedly exceed the sea temperature.

Activity rhythms of *Crangon crangon* involve behaviours which are associated with the tidal migrations. Shrimp behaviour patterns can be broken down into periods when they are buried within the substratum with only their eyes, antennules and antennae exposed (Pinn & Ansell, 1993), and periods of activity consisting of emergence and swimming (Al-Adhub & Naylor, 1975). During emergence, shrimps emerge onto the sediment surface, and may walk about or swim using movements of the pleopods. On a beach with a 6 m tidal range in the Isle of Man, Al-Adhub & Naylor (1975) showed that *C. crangon* emerged and dispersed over the lower half of the shore around the times of high tide, and retreated towards the low water mark and buried themselves at low tide. In the laboratory, emergence, and to a lesser degree swimming, was found to be under endogenous control, persisting with approximate tidal periodicity in constant conditions. However, light partially inhibited emergence, and a day/night cycle in the laboratory modulated the endogenous circadian rhythm into one of nocturnal periodicity. In locations where there are no tidal fluctuations, Hagerman (1970) showed that *C. crangon* is purely nocturnal, with peaks of activity at dawn and dusk, and light-dark changes acting as a Zeitgeber. In this regime, other factors were found to affect activity. Absence of food resulted in greater activity (but only at night), whilst the absence of a suitable substratum increased activity and resulted in a complete breakdown of the rhythm. Feeding behaviour is associated with periods of peak activity on the sediment surface, and occurs at dawn in the Wadden Sea (del Norte-Campos & Temming, 1994). On the west coast of Scotland, maximum activity of shrimps, as recorded by a subtidal camera under infra-red illumination, occurred at night time (Burrows *et al.*, 1994), and in the laboratory this coincided with periods of maximum feeding behaviour (Ansell & Gibson, 1993). Internal physiological processes such as oxygen consumption (van Donk & de Wilde, 1981) and haemolymph glucose levels (Poolsanguan & Uglow, 1974) may also exhibit rhythms which coincide with periods of activity.

Crangon crangon is ubiquitous, and often the dominant member of the larger mobile epifauna on northern European beaches (Salvat, 1962; Macer, 1967; Edwards & Steele, 1968; Smaldon, 1979; Phil & Rosenberg, 1982; Kuipers & Dapper, 1981; Evans & Tallmark, 1985; Jensen & Jensen, 1985; Phil, 1985; Le Mao, 1986; Gee, 1987; van de Veer & Bergman, 1987; Raffaelli *et al.* 1989; Gibson *et al.*, 1993). Although they are omnivorous, they generally prefer animal food (Lloyd & Yonge, 1947), and as they grow, their diet changes from smaller members of the meiofauna to larger members of the macrofauna (Jönsson *et al.* 1993). Pihl &

Rosenberg (1984) found that in the shallow waters of west Sweden small shrimps consumed mainly ostracods and harpacticoids, whilst larger ones consumed nereid polychaetes, amphipods (*Corophium volutator*), and recently settled bivalves (*Mya arenaria* and *Cardium edule*). Polychaete, amphipod and bivalve species are also typical diet items in other areas such as the Severn Estuary (Lloyd & Yonge, 1947), the east coast of Scotland (Raffaelli *et al.*, 1989), and the Dutch coast (Tiews, 1970). More recently, it has been shown that *C. crangon* is a major predator of juvenile flatfishes (van de Veer & Bergman, 1987; Ansell & Gibson, 1993; Modin & Pihl, 1994). Acting as an ambush predator, shrimps are able to catch and subdue small plaice (*Pleuronectes platessa*) with their chelipeds before consuming them (Gibson *et al.*, 1993).

Whilst *Crangon crangon* may pose a predatory threat to very small fish, the reverse is true in the case of larger fish, since *C. crangon* are eaten by a large variety of both commercially and non-commercially exploited fish species. Between 1954-1963, Tiews (1965) estimated that 10 fish species caught as by-catch in shrimp trawls off the German coast accounted for an annual consumption of 15,650 tonnes per year of *C. crangon* (equivalent to 145×10^9 shrimps). Extending this long-term data series, Tiews (1978) was later able to demonstrate a negative correlation between the predation pressure on *C. crangon* by 11 fish species and the commercial landing per unit effort the following year, indicating that predation pressure has a significant impact upon the shrimp population. Predators, in order of decreasing impact, were (i) armed bullhead (*Agonus cataphractus*), (ii) gobies (*Pomatoschistus* sp.), (iii) sea snail (*Liparis* sp.), (iv) whiting (*Merlangius merlangus*), (v) cod (*Gadus morhua*), (vi) dab (*Limanda limanda*), (vii) smelt (*Osmerus eperlanus*), (viii) short-spined sea scorpion (*Myoxocephalus scorpius*), (ix) five-bearded rockling (*Ciliata mustela*), (x) eel pout (*Zoarces viviparus*), (xi) butterfish (*Pholis gunellus*). Off the Belgian coast, gadoid species are the main predators of *C. crangon* (Redant, 1980). In some years in the Dutch Wadden Sea, exceptionally high recruitment of gadoid species can lead to predation which virtually eliminates juvenile shrimps in their nursery grounds. Records of such events exist from the 19th century, as well as for 1959 (due to whiting), 1970 (cod), 1983 (cod and whiting) and 1990 (whiting) (Berghahn, 1996). *C. crangon* also comprises the main component of the diet of the goby *Pomatoschistus minutus* (del Norte-Campos & Temming, 1994) and 0-group bib (*Trisopterus luscus*) (Hamerlynck & Hostens, 1993) at certain times of the year off the Netherlands coast, and the latter species also feed heavily on *C. crangon* in the Loire Estuary

in France (Robin & Marchand, 1986). In the case of bib (Hamerlynck & Hostens, 1993), the proportion of shrimps in the diet was found to increase at high tide, particularly when this occurred at night time, and this coincided with the shrimp's period of peak activity.

The large *Crangon crangon* population which occurs in the Bristol Channel is predated upon heavily by 0-group whiting during the winter. The whiting migration patterns in the region match those of *C. crangon*, and Henderson & Holmes (1989) hypothesise that this is because *C. crangon* is the only abundant prey species at certain times of the year. Other fish species which feed heavily upon *C. crangon* in this area include the flounder *Platichthys flesus* (Moore & Moore, 1976a) and the eel *Anguilla anguilla* (Moore & Moore, 1976b).

A vast literature exists on the diet of the cod (*Gadus morhua*) because of its commercial importance. The species is adapted for feeding on benthic-dwelling organisms (Brawn, 1969), although they may also feed pelagically (e.g. Nagabhushanam, 1965; DeBlois & Rose, 1995). Their diet is particularly broad, and varies between different regions, as well as among individuals collected from the same vicinity, and is determined to a large extent by the availability of certain prey items. In general, juvenile cod tend to feed predominantly on small epibenthic crustaceans, but as they grow, fish become more important in their diet. This can be attributed partially to the availability of prey of sufficient length (e.g. Rae, 1967; Daan, 1973; Langton, 1982), which increases in an approximately linear manner with cod length (Ursin, 1973; Dekker, 1983). In areas where *C. crangon* is abundant, 0 and I-group cod feed heavily upon them. This occurs particularly in the southern North Sea, which harbours large *C. crangon* and juvenile cod populations (Daan, 1973, Daan *et al.*, 1990). Around the coasts of Scotland, *C. crangon* is an important food item on the east coast, where shrimps are more abundant, but their prevalence declines in the north and on the west coast (Rae, 1967). Because of the importance which *C. crangon* may assume in the diet of juvenile cod, the relative ease with which they can be held in captivity, and their availability, this species has been used in the present study as a natural predator of *C. crangon*.

1.3 Defence mechanisms of *C. crangon* against predators

Since *Crangon crangon* (especially the smaller size classes) may suffer heavy predation, they have evolved a number of defence mechanism which enhance their probability of survival. Using the system of Edmunds (1974), these can be divided into primary defences, which reduce the chances of shrimps being detected by predators, and secondary defences,

which occur once the shrimp has detected the presence of a predator, and particularly once an attack has been initiated.

The diel activity rhythm of *Crangon crangon* is undoubtedly an important adaptation which reduces encounters with predators, since shrimps tend to restrict their activity on the sediment surface to periods of darkness. Although many fish predators are also active at night (e.g. juvenile cod - Hawkins *et al.*, 1974; Ansell & Gibson, 1993; Burrows *et al.*, 1994), they have to rely upon more time-consuming prey-location methods, involving tactile and olfactory cues, in order to find prey in the dark. Turbidity of the water has a similar effect, as demonstrated by Moore & Moore (1976a, 1976b). They found that flounder (*Platichthys flesus*) and sticklebacks (*Gasterosteus aculeatus*) collected from the Severn Estuary took longer to find prey (*Asellus aquaticus*) in turbid waters than in clear waters. The former prey species also feeds upon *C. crangon* in this region, where, contrary to findings in other areas, the shrimps are active during the day. This is due to the extremely high turbidity in the estuary which results in low light intensities on the seabed (Lloyd & Yonge, 1947; Henderson & Holmes, 1987).

When not active, *Crangon crangon* usually buries itself within the sediment, and this also reduces its availability to visual predators. Burrowing is achieved using a combination of pleopod beating (which creates a furrow in the sediment) followed by a series of body flexions (which drive the shrimp downwards into the substratum). At the end of this sequence, the shrimp covers the dorsal side of the body by sweeping sediment over itself with its long antennae. Complete burial occurs within 10 seconds, leaving only their antennae, eyes, and sometimes the antennules, exposed above the sediment surface (Pinn & Ansell, 1993). Tallmark & Evans (1986) found that when *C. crangon* were offered a choice between sand and mud substrata, they showed a preference for sand, and were more active when on mud, presumably in order to search for a more suitable substratum. This greater activity on mud resulted in higher predation rates by cod because they were able to locate shrimps more easily.

When *Crangon crangon* are active on the sediment surface, they make themselves less conspicuous by matching their colour to that of the substratum (Chassard-Bouchaud, 1965). This cryptic ability can be attributed to various chromatophore types located in the epidermis, and to a lesser extent, in the deeper tissues. Different chromatophore types are distinguished by the pigments they contain, and include melanophores (black/brown), leucophores (white), erythrophores (red) and xanthophores (yellow). Colour adaptation results from the dispersion

or concentration of pigment granules within the chromatophores, and is largely mediated by neurosecretory hormones (Rao, 1985).

The main secondary defence of *Crangon crangon* is its tail flip swimming response (Smith, 1993; Arnott *et al.*, 1994; Neil & Ansell, 1995). This avoidance reaction was described by Tallmark & Evans (1986) as taking the form of a 'series of zigzag leaps, and finally burrowing'; in the presence of cod 'attacks were very often unsuccessful'. The irregular and unpredictable nature of tail flip swimming in *C. crangon* has also been commented upon by Driver & Humphries (1988; p. 61).

The effectiveness with which *Crangon crangon* are able to avoid being caught by swimming crabs (*Macropipus holsatus*) was examined by Borremans & Redant (1983). They found that 'most attacks were unsuccessful because crabs were unable to seize the shrimp before it escaped with a rapid jump'. Moore & Moore (1976a) found that under clear water conditions, flounder (< 350 mm total length) were only able to catch *C. crangon* (> 15 mm) in 45 % of encounters due to the tail flip escape response, and that this fell towards zero in turbid conditions. They attributed the scarcity of *C. crangon* in the diet of flounder at certain times of the year, when other less elusive prey were present, to the escape ability of the shrimps. Moore & Moore (1976b) also concluded that small *C. crangon* were more prominent in the diet of various fishes because of the greater escape ability of larger shrimps. Therefore, it appears that the escape response of *C. crangon* is important in determining the relative proportion of this shrimp compared to other prey species in diet of fish, and the length of individuals that predators select.

1.4 Optimal foraging theory, and the effect of escape behaviour

The above predictions are in accordance with those of optimal foraging theory (OFT), a concept introduced by MacArthur & Pianka (1966) and Emlen (1966), which assumes that a predator will increase its fitness by foraging in a manner that maximises its net rate of energy gain. This energy-maximisation premise is the key assumption of OFT, and has been used extensively to explain searching behaviour, exploitation of food resources and selection of alternative food items in a wide range of animals. The theory behind these feeding aspects is mathematically the same (Stephens & Krebs, 1986; Hart, 1993), and has been derived by elaboration of the Holling Disc Equation. This was originally used by Holling (1959) to model the relationship between the number of prey items eaten by a predator during a foraging bout,

the density of the prey items, and the attack rate of the predator. It assumes that all prey are of equal profitability to the predator, whereas in reality, profitabilities between prey types differ according to different sizes and species. The model has therefore been extended to account for these differences, and in its simplest form is known as the Basic Prey Model (Stephens & Krebs, 1986). The two firmest predictions from the model are that a forager should always accept the most profitable food type, and that it should accept progressively less profitable types only when encounter rates with higher-ranking types fall below a critical level. The diet should expand and contract according to the quality and availability of alternative foods (Hughes, 1993). In accordance with the predation sequence outlined above (prey detection → attack → capture), the profitability of different prey items is affected (and modified) by (i) detection probability (modified by prey and predator activity, habitat overlap, refuge use and crypsis), (ii) attack probability (active predator choice), (iii) capture success (prey versus predator mobility), and (iv) consumption probability (post-capture defences). Prey profitability is a product of these parameters, such that:

$$\text{prey profitability} = (ec - (1 - c)x) / h$$

where e = the net energy gain if the prey is captured and consumed, c is the probability that an attack results in consumption, x is the energy cost if prey are attacked but not consumed, and h is the time taken to handle the prey (Sih, 1993).

Further complexity to the model is introduced by temporal shifts in the above parameters due to either external influences, such as light levels (e.g. Batty *et al.*, 1990) and the presence of higher predators (e.g. Metcalfe *et al.*, 1987), or changes in the internal state of the forager itself, such as the degree of satiation (e.g. Gill & Hart, 1994). More recent dynamic foraging models have been developed that account for changes in the motivation state of the predator (Hart & Gill, 1993).

1.5 Tail flip swimming in Crustaceans

Tail flip swimming, which has been identified as the main secondary defence of *Crangon crangon*, is a widespread escape mechanism within the Crustacea, occurring within the Mysidacea (Kaiser *et al.*, 1992a; Kaiser & Hughes, 1992; Neil & Ansell, 1995), Syncarida, Euphausiacea, and all decapod groups except the Brachyura and Paguroidea (Kils, 1982; Paul,

1990). The general form of the response in these species involves a rapid flexion of the abdomen, which by moving the expanded uropods (tail fan) through the water, propels the animal in a predominantly backward direction. After this power phase, the abdomen is re-extended, and a series of flexions and extensions may then follow, resulting in a swimming bout consisting of multiple tail flips (Neil & Ansell, 1995).

The neuronal control of tail flip behaviour has been studied extensively, particularly in the crayfish (e.g. Wine & Krasne, 1982; Krasne & Wine, 1984, 1988; Reichert, 1988). In many crustaceans, tail flips are initiated by giant interneurons (often called giant fibres), which, due to their large diameter, conduct neuronal signals rapidly and enable the animal to react with minimal latency (*c.* 6 ms) to a sudden attack (Reichert & Wine, 1983). Giant fibre mediation of escape responses occurs in many animal groups, but is not necessarily required for an escape to occur, and animals without giant interneurons are still capable of rapid escape responses. They occur in 9 phyla (Cnidaria, Platyhelminthes, Nemertina, Phoronida, Hemichordata, Chordata, Mollusca, Annelida and Arthropoda), although not all animals within these phyla possess giant fibres (Bullock, 1984). Within the Crustacea, certain groups, such as the Crangonidae, Palaemonidae, Nephropsidae and the Cambaridae possess two pairs of giant interneurons, whilst others possess just one pair (e.g. Upogebiidae), or no giant fibres at all (e.g. Galatheidae) (Paul, 1990). The two types of giant fibres are referred to as the medial giants (MGs) and the lateral giants (LGs) according to their position relative to one another in the dorsal portion of the ventral nerve cord. The occurrence of both MGs and LGs in *Crangon crangon* was demonstrated by Johnson (1924).

In the crayfish *Procambarus clarkii*, it has been shown that the MGs and LGs are selectively activated in response to sudden stimuli. The MGs are activated by visual stimuli and by mechanical stimulation to the cephalothorax and legs. They form output synapses onto the motor nerves which innervate the fast flexor muscles in all segment of the abdomen. These muscles, which together with the fast extensors occupy the majority of the abdomen, are adapted for brief bursts of rapid contraction, as characterised by their short sarcomere length (*c.* 3 μm) and anaerobic properties (Atwood, 1973). Activation of all 6 segments results in a flat swimming trajectory directed backwards which translates the animal away from the anterior stimulus source (Wine & Krasne, 1972). In the Norway lobster, *Nephrops norvegicus*, the posterior-most segments are activated prior to the anterior ones in the abdomen, minimising the vertical lift forces (Newland & Neil, 1990a).

The LGs are recruited in response to mechanical stimuli applied to the abdomen, and in *Procambarus clarkii* activate only the flexor muscles in the anterior three segments of the abdomen. This directs the tail flip in a predominantly vertical direction, as well as pitching it slightly forwards, away from the posteriorly-applied stimulus.

Crayfish giant fibres have come to be regarded as classical examples of 'command neurones', because by directly stimulating them, specific behavioural acts can be produced in a stereotyped manner. Therefore, they offer little flexibility, as indicated by the lack of lateral steering during LG tail flips when a stimulus is applied from the side of a crayfish (Reichert & Wine, 1983). The command neurone concept has been defined by Kupfermann & Weiss (1978) on the basis of neurones being 'necessary' and 'sufficient' for causing a particular behavioural action. However, more recent evidence suggests that peripheral nerve networks are also involved in producing 'normal' giant fibre mediated tail flips (Wine, 1984; Edwards & Mulloney, 1987; Krasne & Wine, 1988; Newland & Neil, 1990b).

After the first tail flip of an escape response, subsequent tail flips are generated by a neuronal network that does not involve the giant fibres, and hence these flips are called non-giant or swimming tail flips. When tail flips are initiated in response to stimuli which are not sudden and intense, the non-giants also mediate the first tail flip of an escape, rather than the giant fibres, and response latencies of these escapes are considerably longer (80-500 ms) than giant fibre mediated escapes (6 ms). Due to the greater latencies, non-giant tail flips are able to integrate information regarding the animal's surroundings, and incorporate directional steering into the escape response (Reichert & Wine, 1983).

The mechanics of the escape response in the crayfish *Orconectes virilis* has been studied by Webb (1979). He found that in animals with a length *c.* 8 cm, the flexion phase of LG tail flips lasted for 44 ms, followed by a re-extension phase of 173 ms. Subsequent (non-giant) tail flips in an escape had flexion and re-extension phases of 36 ms and 92 ms respectively. During flexion of the abdomen, thrust production was attributed almost entirely to the tail fan, producing forces of 0.92 N and 0.42 N during the lift-off (from the substratum) and swimming phases of the LG tail flip, and 0.29 N during subsequent tail flips. This resulted in maximum velocities (of the centre of mass, located within the cephalothorax) of between 0.8 and 0.9 m.s⁻¹. Force production during tail flips has also been also been studied in the caridean shrimp *Pandalus danae* by Daniel & Meyhöfer (1989), and this has revealed that, in addition to the force produced by the tail fan during flexion, an important 'squeeze force'

component is produced towards the end of flexion as the abdomen is pressed against the cephalothorax. This resembles the fling mechanism in hovering insects (Ellington, 1984) and the jetting reaction of squid (O'Dor, 1988), medusae and salps (Bone & Trueman, 1983; Daniel *et al.* 1992). In the palinurid lobster *Jasus lalandii*, the swimmerets contribute towards the efficiency of this squeeze force by channelling the water jetted out from between the abdomen and cephalothorax (Cattaert *et al.*, 1988).

Using a system of differential equations that rely on conservation of both linear and angular momentum, Daniel & Meyhöfer (1989) developed predictions for body movements, thrust forces and muscle stress associated with tail flip swimming in *Pandalus danae*. Escapes were modelled on a 'single-oar' model, in which movement is brought about by rowing of a single appendage (the abdomen). Body movements were analysed as the sum of two separate components: (i) rotational movement of the body about the shrimps centre of mass, caused by the moments of inertia created by the pivoting action of the abdomen about the centre of mass, and (ii) translational movement resulting in displacement of the centre of mass. From their theoretical calculations, it was possible to demonstrate that as the length of the abdomen relative to the rest of the body increases, the forces produced increase. However, above a certain limit rotational forces start to outweigh the translational forces causing a decline in escape performance. In addition to this, as shrimps increase in length, the differential scaling relationship between translational thrust, rotational thrust, and the cross sectional area of flexor muscle result in an optimal length which maximises performance for a given body dimension, which in the case of *P. danae*, is 60 mm.

In the majority of species which have been investigated, animals usually tail flip in an upright body position, although crayfish and the scyllarid lobster *Ibacus peronii* are also capable of performing complete somersaults (Wine & Krasne, 1972; Jacklyn & Ritz, 1986). In *Nephrops norvegicus*, deviations from the upright can be corrected, under the control of the statocyst, by a combination of rotating the abdomen about the abdominal-thoracic joint, and asymmetrical positioning of the uropods during flexion (Newland *et al.*, 1990b). Similar body movements can also be used to steer tail flips towards the left or right in response to asymmetrical stimuli (Newland *et al.*, 1992a)

Like crayfish and nephropid lobsters, scyllarid lobsters typically tail flip in an upright position, but they are able to produce roll manoeuvres in order to redirect their escape if an obstacle is encountered. These animals maintain height above the substratum during tail flip

swimming by using their large flattened antennal scales as ailerons. Rolls are introduced by elevating one scale with respect to the other, causing an imbalance in the amount of lift generated on the left and right sides of the body, and enabling tail flips to be re-directed to the side (Jacklyn & Ritz, 1986).

Considerably less work has been conducted on the tail flip behaviour of small crustaceans. However, preliminary observations of tail flip swimming in the mysid *Praunus flexuosus* have revealed substantial departures from the 'single-oar' tail flip mechanism described above (Neil & Ansell, 1995). Mysids lack the heavy armour and large chelipeds of lobsters, and therefore their centre of mass is situated more posteriorly, within the first abdominal segment. As a consequence, flexion results in a symmetrical 'jackknife' tail flip which allows the well-developed setose antennal scales ('head fan') to generate thrust additional to that produced by the tail fan. A further deviation in the escape behaviour of mysids is found in their body orientation during tail flips. When attacked by a predator, the whole body of the animal may be rotated towards the left or right during the first few milliseconds of an escape, causing the shrimp to tail flip laterally rather than posteriorly with respect to its pre-escape orientation (Kaiser *et al.*, 1992a). Asymmetrical spreading of the head and tail fan during this manoeuvre contributes towards the roll-inducing torque forces (Ansell & Neil, 1991; Neil & Ansell, 1995).

Some initial studies of tail flip swimming in *Crangon crangon* have been made by Smith (1993) and Berghahn *et al.* (1995). Using high speed video techniques, Smith (1993) measured changes in maximum swimming velocity in relation to temperature acclimation and acute temperature changes. Other experiments tested the reaction of shrimps to artificial fish predators. These revealed that shrimps do not react until a looming object has approached to within a few centimetres of it, and that reaction distances are reduced when shrimps are buried beneath the sediment, or when a transparent 'predator' is used in place of an opaque one. Berghahn *et al.* (1995) also investigated the role of visual and mechanical stimuli in eliciting escape responses in *C. crangon*, and found that both buried and emerged shrimps initiate an escape at a distance of 5-10 cm from an approaching trawl net. They concluded that visual stimuli and sudden water displacement pulses were the main stimuli triggering escapes, the former being of greater importance in clear water conditions. These preliminary results indicate that the tail flip escape response of *C. crangon* is an important mechanism enabling shrimps to evade both natural predators and fishing gear.

1.6 Optimal evasion strategies

Escape responses in animals have a number of components that contribute towards their success in evading predators, of which the relative kinematic performance and endurance of the predator and prey are perhaps the most intuitively obvious components. However, prey often have lower maximum velocities than their predators, and yet they are still able to successfully evade them during a pursuit. Unsuccessful predation is in fact very common; in a literature survey by Vermeij (1982) covering 60 predator species preying upon 100 prey species, only 19 % of the prey were captured with an efficiency of greater than 90 % once they had been detected.

Timing is an important aspect of an escape, because if the animal escapes too early the predator will be able to compensate for movement of the prey, whereas if it is too late the prey will be caught - there is therefore a brief period during the strike when the probability of evasion is maximised. The timing is determined largely by the response characteristics of the sensory systems involved, the conduction velocity of the neuronal pathway(s) which convey the nerve signals, and the threshold of the decision making circuits (which are themselves subject to the habituation state of the animal).

As well as timing and speed, the direction of an escape is crucial in removing the prey from the interception path of the predator. In many animals, the direction of an escape is influenced predominantly by the location of a refuge such as a burrow or crevice. The distance to, and nature of the refuge may vary widely between species and habitat, and this will further modify the escape trajectory. At one extreme, animals may have specific retreats from which they never completely emerge. Examples of this include various types of tube-dwelling polychaetes such as the sabellid *Branchiomma vesiculosum* (Krasne, 1965), and hermit crabs (Paguridae), which carry their shells with them (Barnes, 1987). An escape response in such animals consists of a sudden withdrawal into the refuge; it is therefore short-lived, and does not require elaborate directional or steering control.

In animals that stray further from their refuge, their escape response must be able to convey them accurately back to it in the event of an attack, whilst ensuring that they are not intercepted by the predator. For instance, fiddler crabs on intertidal mud flats retreat towards their burrows if they are threatened by a predator, but if displaced from their burrow, they instead run directly away from the predator (Nalbach, 1990b; Land & Layne, 1995). In other instances, the 'refuge' may be less well defined, as in the blue crab *Callinectes sapidus* and the

marine isopod *Idotea baltica*, both of which escape in an offshore direction towards deep water if threatened (Woodbury, 1986; Ugolini & Pezzani, 1993). In the case of *C. sapidus*, the escape is angled along a path which integrates both the offshore direction and the position of the predator.

At the other extreme, prey may have no specific refuge, and will therefore have to rely entirely upon their evasive ability to avoid being caught during a pursuit. Examples of this include gazelles fleeing from predators on the open plains of Africa (Walther, 1969) and pelagic fish escaping from large piscivorous predators (e.g. Blaxter & Batty, 1990). In these instances, once a pursuit has been initiated, the escape trajectory of the prey will be crucial in determining the outcome of the encounter. Weihs & Webb (1984) have calculated optimal evasion trajectories for animals, based on the assumption that the predator will abort its attack if the prey extends the duration of the pursuit. This maximises the energetic costs to the predator, making the prey too expensive (energetically) to be worth pursuing any further. Using a theoretical model, Weihs & Webb (1984) found that optimal escape trajectories lie within 21° of the heading directly away from the predator, regardless of their relative velocities. However, when the predator approaches within a distance where it can strike, a sudden turn by the prey is required to avoid capture. The success of this depends upon the timing of the turn with respect to the velocity and minimum turning radius of the predator and prey (Howland, 1974). Hence, the manoeuvrability of prey is important during the 'final end game' of a pursuit, and this may lead to the selection of body morphologies which enhance manoeuvrability. For instance, Srygley (1994) found that among 27 species of butterflies in Panama, there were three main anti-predation mechanisms: distastefulness (a form of aposematism), Batesian mimicry (looking like distasteful species) and evasive flight. In those species which used evasive flight, the position of centre of mass and the wing shape were better adapted for high velocities and manoeuvrability than in the other species.

In featureless habitats which offer no immediate refuge, animals may also use other mechanisms which influence the predator's pursuit success. Under these circumstances, many animals live in social groups (e.g. schooling fish and flocking birds), and this may confer a number of anti-predator advantages. In the case of a predatory attack, the combined escape pattern of the group may serve to confuse the predator, thereby reducing its ability to catch individuals (Landeau & Terborgh, 1986; Pitcher & Parrish, 1993).

At the individual level, a further confusing effect may be introduced by the incorporation of unpredictability in an escape response. Chance and Russell (1959) recognised that unpredictable behaviour of prey animals is an important aspect which increases their survival when attacked or threatened by predators, and introduced the term 'Protean Displays' to describe this unpredictability (after the mythical Proteus, who constantly changed his shape to confuse pursuers). Driver & Humphries (1988) define protean behaviour as:

'... that behaviour which is sufficiently unsystematic in appearance to prevent a reactor predicting in detail the position or actions of the actor'.

Many animals display unpredictability by escaping along a zigzag trajectory rather than a straight line, making it more difficult for a predator to pursue them. Other types of irregular escape trajectories also occur, such as those observed by Roeder (1962) in noctuid and geometrid moths. These moths react strongly to the ultrasonic sound of an approaching predatory bat, causing their flight path to change suddenly into an unpredictable descent pattern which may involve passive or power dives, loops, rolls, and one or more tight turns. This erratic escape behaviour counteracts the ability of bats to predict the interception path of objects moving through the air along a simple ballistic trajectory (Roeder & Treat, 1961).

Alternatively, animals may escape along relatively linear trajectories, but choose between one of several preferred directions in an unpredictable manner to prevent the predator from compensating for the escape (Domenici & Blake, 1993). This is likely to increase the time required by the predator to react to the prey's escape, which reduces the probability of a successful capture (Webb, 1984).

A variety of escape strategies may be employed by the same animal at different times of their development according to the strengths of their ability, as observed during larval ontogeny in the wood frog *Rana sylvatica* (Brown & Taylor, 1995). Escape swimming velocity increases significantly with larval length, up to the point where their hind legs begin to develop. At this stage, the additional drag produced by the legs causes a dramatic reduction in their escape swimming performance. Correspondingly, the smallest larvae and the metamorphosing larvae have poorer escape success from predators, and are subject to higher predation rates than the mid-larval stages (Wassersug & Sperry, 1977; Wilbur *et al.*, 1989; Richards & Bull, 1990; Semlitsch, 1990). As a possible means of off-setting their low escape

velocity, the early and late larval stages escape along trajectories which contain more turns, and sharper turns, than escapes by the mid-larval stages. Therefore, protean behaviour is increased when escape velocity is compromised (Brown & Taylor, 1995), and may be influenced by the neuronal circuitry involved in mediating the escape response (Boothby & Roberts, 1995).

Although it is recognised that the success of an animal's escape response depends upon a variety of factors, there are comparatively few studies which address the relationship between these different factors. Despite being widely accepted, aspects of protean behaviour are particularly lacking in rigorous quantitative studies (Driver & Humphries, 1988).

1.7 Aims of the study

The central theme of this study is the tail flip escape response of the brown shrimp *Crangon crangon* in the context of predator-prey interactions. This species, which is capable of performing a rapid tail flip escape response, is abundant in European shallow water marine communities, and is vulnerable to predation by a large number of fish species. Furthermore, *C. crangon* is fished commercially in many areas, and study of its escape response has potential implications for the design of selective fishing gear. The comparative lack of knowledge of tail flip behaviour in small decapods compared with larger ones such as crayfish and lobsters also makes investigation of this species timely.

High speed video analysis (200 f.s⁻¹) has been used to examine in detail the tail flip mechanism of *Crangon crangon*, and to compare this with the tail flip swimming behaviour of other decapod and mysid crustaceans. In addition, the kinematic properties of tail flips (mean velocity, maximum velocity, acceleration, and rate of abdomen flexion) have been measured in shrimps ranging in length from 11 to 69 mm in order to determine the effects of body size upon escape performance. The results of these high speed video observations are presented in **Chapter 2**.

The escape trajectories of shrimps in response to attacks by a natural predator (juvenile cod, *Gadus morhua*) and an artificial predator (a wooden rod) have also been recorded using conventional video (50 f.s⁻¹) techniques. These results have been analysed using circular statistical techniques in order to detect differences between escape trajectories produced by different directions of attack, and to quantify the degree of unpredictability (protean behaviour) which they display. Differences in escape trajectories can be explained, in part, by

physical constraints experienced by the shrimps, and emphasis is placed upon the effect of the shrimp's habitat in determining various escape strategies. These data are presented in **Chapter 3**, and are compared with the optimal evasion model of Weihs & Webb (1984) (described **section 1.6**), as well as with escape trajectories determined for a variety of other animals.

Further laboratory experiments have been conducted to examine the effectiveness with which *Crangon crangon* is able to use its tail flip escape response in avoiding predation by juvenile cod, and to determine the effect of relative body size upon this. Encounters between shrimps and cod of varying length ratios have been filmed under fluorescent lighting in artificial (no sediment substratum) and semi-natural (with a sediment substratum) habitat conditions. The cost (in terms of time) of pursuing shrimps of different lengths has been estimated and compared with the handling time required to consume shrimps of different lengths. Preliminary data are also presented on the effectiveness of the tail flip escape response of *C. crangon* in evading juvenile cod in the 'dark' (filmed using infra-red lighting) (**Chapter 4**). These laboratory data have been compared with results obtained from stomach content analysis of juvenile cod collected from Tralee Beach on the West coast of Scotland (**Chapter 5**). The aim of this field study was to determine the proportion of cod diet attributable to *C. crangon*, and to examine the *in situ* relationship between shrimp length and the length of cod which predate upon them.

The main findings from these separate areas of study are assimilated in **Chapter 6**, and ideas for further work arising from the results are suggested.

Chapter 2

High speed video analysis of tail flip swimming in *Crangon*

crangon

A considerable amount of research has been conducted on tail flip behaviour in crustaceans, and in particular, the neuronal control of tail flip behaviour in crayfish (see, for instance, Wine & Krasne, 1982). However, relatively little is known about the interspecific and intraspecific variability of tail flip swimming among the large number of crustacean species in which this behaviour occurs, despite its significance with respect to their survival. This study compares and contrasts the tail flip mechanism of the brown shrimp *Crangon crangon* with that of other crustaceans, and quantifies size-dependent changes in the kinematics of their tail flip swimming performance.

Disparities between tail flip behaviour of different species might be expected, considering the variability in body morphologies, body sizes and habitats which characterise divergent crustacean species. This is because, although tail flip behaviour is likely to have evolved in a manner which increases the probability of an animal's survival, traits which are beneficial under one set of circumstances may not necessarily provide a universally optimal strategy.

Indeed, investigations into the neural circuitry controlling tail flip behaviour in various species of crustaceans do reveal differences. For example, whilst many decapods such as *Crangon crangon*, *Palaemonetes sp.* (both Caridea) and *Nephrops norvegicus* (Astacidea) possess, like crayfish, a pair of medial giant (MG) and lateral giant (LG) interneurons used for initiating tail flip escapes (Johnson, 1924; Newland & Neil, 1990a), mud shrimps (Thalassinoidea) possess only MGs, whilst squat lobsters (Galatheidae) possess none (Paul, 1990). Further differences are evident at the behavioural level, as illustrated by the orientation mechanisms of different species whilst tail flipping. In relatively large crustaceans, tail flips are usually performed in an upright body position, and destabilising roll movements which upset this balance can be corrected by changing the attitude of various body appendages such as the uropods (e.g. *N. norvegicus*; Newland & Neil, 1990b), the swimmerets (e.g. palinurids lobsters; Cattaert *et al.*, 1988; Newland *et al.* 1992a), or the antennal scales (e.g. scyllarid lobsters; Jacklyn & Ritz, 1986). However, the mysids *Neomysis integer* and *Praunus flexuosus* differ since they execute a rapid lateral roll about their longitudinal axis when a tail flip response is initiated, and this results in a laterally directed escape with the shrimp swimming on its side (Kaiser *et al.*, 1992a; Neil & Ansell, 1995).

Intraspecific variability in tail flip behaviour and performance also occurs. For instance, juvenile lobsters (*Homarus americanus*) have a comparatively large abdomen and small claws, and respond to predators by tail flipping, whereas adults have a comparatively small abdomen and large claws, and respond to predators with defensive displays (Lang *et al.*, 1977). Similarly, different neuronal pathways may be used in initiating tail flips (MG, LG or non-giant), and may be used in different situations, not only as an escape response, but also when feeding (Wine & Krasne, 1972; Bellman & Krasne, 1983), or in intraspecific agnostic encounters (Edwards, 1995). The physiological state of the animal is also influential, as shown by changes in tail flip performance over the moult cycle of the lobster (Cromarty *et al.*, 1991), and a decrease in tail flip performance of *Crangon crangon* after experiencing a temperature shock (Smith, 1993).

Body length is also an important morphological feature which affects the kinematic performance of tail flips, because forces produced by tail flips scale differently to linear changes in animal length. Daniel & Meyhöfer (1989) have shown that, in the caridean shrimp *Pandalus danae*, linear increases in body dimensions result in nearly cubic increases in thrust. This occurs because the hydrodynamic forces scale in part with the area of the abdomen (*viz.* the drag forces created by moving the uropods through the water), and in part with the volume of the abdomen (*viz.* the acceleration reaction forces, or 'added mass' - see Batchelor, 1967). Therefore, one might expect kinematic performance to improve as shrimps become larger. However, two confounding factors become influential as body length increases. The first of these is the moment of inertia created by the pivoting action of the abdomen, which generates rotational thrust and pitches the animal forward. This increases as a quartic function of shrimp length, compared with the cubic increases in translational thrust (*i.e.* centre of mass displacement). Therefore, as shrimps become larger, their movements become increasingly dominated by rotational movements, and translational thrust is eventually compromised. Furthermore, whilst an increase in body length results in an almost cubic increase in thrust, the cross-sectional area of the flexor muscles in the abdomen increases with the square of linear dimensions. Therefore, since the propulsive stress cannot exceed the maximum contractile force of the flexor muscles, the physical capabilities of the muscles become limiting as body length increases. As a consequence of these interacting factors, Daniel & Meyhöfer (1989) have shown theoretically that, for an animal of given morphological dimensions, there is an optimal body length that maximises the kinematic performance of tail flips. For *P. danae*, in

which the abdomen grows isometrically with shrimp length, this length was calculated to be 6 cm.

These predictions have important ecological implications with regard to the probability of shrimps of different sizes being eaten by predators. *Crangon crangon* range in size from a few millimetres when they first settle from the plankton, to approximately 70-90 mm when fully grown (Tiews, 1970). Therefore, this study attempts to quantify the kinematic performance of *C. crangon* over the full size range of shrimps available (6-69 mm), and to determine the nature of the relationship between shrimp length and tail flip performance.

2.2

MATERIALS & METHODS

2.2.1 Animals

Male and female brown shrimps (*Crangon crangon*) were caught during July 1994 in a hand-held trawl net at a depth of less than 1 m in Dunstaffnage Bay on the west coast of Scotland, and transferred to holding tanks (100 x 50 x 30 cm), containing seawater maintained at approximately 13°C with 1-2 cm sand on the bottom. The shrimps were kept for approximately 2 weeks before being used in experiments, and were fed *ad lib.* every other day on chopped mussels and/or mysids. None of the experimental shrimps was in a berried condition (i.e. carrying eggs attached to its pleopods).

Shrimps were only used if they had hard exoskeletons and showed no obvious signs of poor health or damage. Twenty-five shrimps with total body lengths (tip of the rostrum to the posterior tip of the telson) of between 11 and 69 mm were used for experiments to determine the kinematic variability in their tail flip escape performance with size. In addition, a subset of experiments was conducted to determine the relative importance of the antennal scales and uropods in generating thrust during tail flip swimming. For these, 15 shrimps of approximately the same body length were divided into four groups: (i) a control group of intact shrimps (mean total length = 38.4 ± 5.1 mm, $n = 6$); (ii) shrimps (43.9 ± 4.9 mm, $n = 3$) from which the antennal scales removed at their attachment point with pair of surgical scissors; (iii) shrimps (43.0 ± 4.0 mm, $n = 3$) from which the uropods were removed; (iv) shrimps (43.1 ± 3.2 mm, $n = 3$) from which both the antennal scales and uropods removed (see Fig. 2.1). The surgery was performed one week before the experiments were conducted. Operated shrimps were kept

under the same conditions as unoperated shrimps, and survived without any discernible adverse effects for the duration of the experimental period.

2.2.2 Estimation of the centre of mass

The shrimp's centre of mass was determined by suspending frozen specimens between two opposed points formed by fine pins mounted on the tips of a pair of forceps. Shrimps were frozen (-10°C) with their abdomen fully extended (i.e. in the normal resting body posture), or with their abdomen fully flexed, in order to determine the shift in position of the centre of mass during the course of a tail flip. In each case, the position of the pins on the shrimp was adjusted until the animal could be placed in any pitch orientation, without rotating. The centre of mass was then assumed to lie on the axis between the pin attachment points.

When in a fully extended position, the centre of mass was found to be located within the most anterior segment of the abdomen (segment 1), and when in a fully flexed position, the centre of mass was level with the coxa of the 5th pereopod (**Fig. 2.2 a**). This shift in the position of the centre of mass between the fully extended and fully flexed postures is relatively minor. Therefore, a single point (point *d* in **Fig. 2.2 a**) on the postero-ventral portion of the shrimp's cephalothorax was used for digitising the estimated centre of mass when tail flipping. Differences in centre of mass arising from changes in shrimp body length were assumed to be negligible.

2.2.3 Experimental set-up

All experiments were conducted in an experimental arena (diameter = 1 m, sea water depth = 17 cm) in an air conditioned room at 13°C, and were recorded from directly above with a high speed video camera linked to a NAC HSV400 video recorder (**Fig. 2.3**). This provided a view of the horizontal position of the shrimp within the arena (camera view). In addition, a mirror was placed on the bottom of the arena at an angle of 45° to the camera to provide a view of the shrimp's vertical elevation above the substratum (mirror view). A 5 or 10 cm marker on the bottom of the arena enabled calibration of distance on the video films. A synchronised strobe was used for illumination, and the light was orientated along the axis of the camera lens by reflecting it in a half-silvered mirror angled in front of the camera lens. The base of the arena was covered with reflective material (3M Scotchlite), so that a sharp silhouette image of the shrimp was created when viewed from above. A silhouette image was

also obtained in the mirror view by placing an upright board covered in 3M Scotchlite at one end of the arena. All experiments were recorded at 200 frames per second on a high speed video recorder.

2.2.4 Experimental protocol

For each experiment, a shrimp was removed from its holding tank by pressing lightly down on its carapace, and then lifting it up by hand. This method tended to inhibit the tail flip escape response (a similar response has been noted in crayfish - see Krasne & Wine, 1975), and therefore enabled shrimps to be moved without inducing muscle fatigue. The shrimp was then placed on the bottom of the experimental arena, and covered for 10 minutes with an up-turned clear plastic container in which perforations had been made. During this period, the water was aerated with an air-stone. At the start of an experiment, the video recording equipment was turned on, and the plastic container and air-stone were removed. Tail flip escape responses were then induced, either by a rapid flick with a submerged finger, or by rapidly propelling a submerged rod towards the shrimp. No direct physical contact was made with the shrimp, and so the source of the stimulus comprised mainly visual and water-borne vibrational cues. Experiments on dead animals confirmed that no passive movement of the shrimp was created by water displacement arising from either of the stimuli. Each shrimp was made to perform between 1 and 5 multiple tail flip swimming bouts, during which no signs of physical exhaustion were visible.

An additional set of data on the mean tail flip swimming velocity of 38 shrimps of between 6 and 36 mm was obtained from Experiment 1 of **Chapter 4** in which shrimps were induced to escape by an approaching juvenile cod (*Gadus morhua*). These experiments were recorded using conventional video techniques (frame rate of 50 f.s⁻¹; see section 4.2.2.i for further details).

2.2.5 Analysis of video films

The video sequences were replayed frame by frame onto a monitor (JVC) linked to a digitising tablet (NAC). Reference points on the shrimp's body were digitised, and analysed using MOVIAS 3.00-4 (NAC, 1989) and Excel 5.0 (Microsoft, 1995) software. Only escapes in which the shrimp performed more than one tail flip during an escape swimming bout were analysed. The mirror view of the shrimp made it possible to identify multiple tail flip

swimming bouts in which the shrimp was swimming off the bottom of the arena, and parallel to the horizontal plane.

2.2.5.i Analysis of body angle and centre of mass parameters

Movement in the horizontal plane was analysed by digitising four points from the camera view of the shrimp (Fig. 2.2 b). These were: point 1 - the eyes; point 2 - the leading edge of the mid-flexion point of the abdomen; point 3 - the posterior tip of the 6th abdominal segment; and point 4 - the estimated centre of mass.

The body angle of the shrimp was defined as the angle subtended by points 1, 2 and 3. Changes in this angle between each frame (i.e. every 5 ms), were used to calculate the angular velocity and angular acceleration of the body angle.

Displacement of the shrimp was determined by measuring the distance travelled by the estimated centre of mass between one frame and the next. From this, the velocity and acceleration of the shrimp's centre of mass were calculated.

2.2.5.ii Measurement of the rotation angle in the shrimp's pitch plane

Rotation in the shrimp's pitch plane was measured by fitting a line to the trajectory of the centre of mass for each tail flip. The angle between successive trajectories was measured as the pitch angle (see Fig. 2.4). Positive angles were assigned to rotation in the rostral direction, and negative angles to rotation in the caudal direction.

2.2.5.iii Measurement of antennal scale and uropod extension and retraction rates

The shrimp's antennal scales and uropods were moved laterally during periods of the tail flip cycle. Their movements were analysed in a number escape sequences by digitising the most lateral point of the left and right antennal scales or uropods (as seen from the shrimp's dorsal or ventral aspect) and measuring the linear distance between the opposite points (Fig. 2.2 c).

2.2.5.iv Measurement of the velocity of the head and tail fan relative to the centre of mass

The velocities of the head and tail fan with respect to the shrimp's centre of mass were calculated from two escape sequences (total of 7 tail flips; shrimp total lengths = 33 mm and

40 mm). These were calculated by subtracting the x-y co-ordinates of the centre of mass (point 4) from the concurrent position of point 1 and point 3, and then calculating their displacement per frame. Mean velocities of point 1 and point 3 were calculated over the total duration of each flexion and each re-extension phase.

2.2.5.v Measurement of escape response latencies

Escape response latencies were determined in a few instances by measuring the time elapsed (i.e. number of frames) between the first detectable movement of the manually delivered stimulus, and the first detectable movement of the shrimp.

2.2.6 Statistical analysis of data

Statistical calculations were performed using Minitab 10Xtra (Minitab Inc., 1994) software unless stated otherwise.

Comparisons of rotation in the pitch plane between intact shrimps and operated shrimps were performed using a Kruskal-Wallis test, followed by a multiple comparison test (Zar, 1996).

Comparisons between the kinematic properties of the first and second tail flips of an escape swimming bout for individual shrimps were made using two-tailed paired t-tests. Regressions were fitted to size-dependent variations in the kinematic parameters. Where quadratic regressions have been fitted, these fitted the data better than either linear or log-linear fits. Differences between the mean velocity of intact and non-intact shrimps were tested using oneway ANOVA, followed by a Tukey multiple comparisons test.

2.3

RESULTS

2.3.1 Description of the tail flip swimming behaviour

Shrimps responded to a stimulus with either a single tail flip, or multiple tail flips. The minimum latency between the initiation of a stimulus and the first detectable movement of the shrimp was in the order of 10 ms (2 frames), although longer latencies were also observed. During multiple tail flip swimming bouts, the abdomen underwent a series of flexions and re-extensions (Fig. 2.5). The duration of a single tail flip (1 flexion + re-extension cycle) was typically between 30 and 130 ms, with the flexion phase lasting for approximately 15-40 ms

and the re-extension phase lasting for approximately 15-70 ms (depending upon the length of the shrimp). During the flexion phase of the tail flip, both the antennal scales and the uropods were expanded to form propulsive surfaces (the head fan and tail fan surfaces respectively). These were retracted during the re-extension phase of the abdomen.

During the body flexion phase of the tail flip (see 0-40 ms of **Fig. 2.6**), flexion occurred predominantly in the more anterior portion of the abdomen, and virtually no movement was observed at the joint between the 6th abdominal segment and the telson. Therefore, tail flips were relatively symmetrical about the flexion mid-point (located approximately at abdominal segments 2-3). Flexion of the abdomen resulted in the tail fan being brought near to, or into contact with, the shrimp's cephalothorax.

During the re-extension phase of the tail flip (see 40-110 ms of **Fig. 2.6**), the abdomen was not fully re-extended, but achieved a maximum body angle of between 75° and 165° . The anterior abdominal segments were extended prior to the posterior segments. The joint between segment 6 and the telson was held in a flexed position during most of the re-extension phase, thereby reducing drag. Movement about this joint was probably brought about (at least in part) by passive forces exerted by the incident flow of water. Full extension of the telson was not achieved until flexion had been initiated in the rest of the abdomen (see 100-110 ms of **Fig. 2.6**).

The shrimp's centre of mass was accelerated during the flexion phase of tail flips, and decelerated during the re-extension phase, causing the shrimp's velocity to increase to a maximum of between 0.6 and $2.3 \text{ m}\cdot\text{s}^{-1}$ at the end of flexion (depending upon the shrimp length), and decrease to a minimum of between 0.05 and $0.6 \text{ m}\cdot\text{s}^{-1}$ at the end of re-extension (**Fig. 2.7**). This resulted in a displacement of between 1.1 and 12.7 cm per tail flip.

2.3.2 Movements of the head and tail fan during tail flips

During the flexion phase of each tail flip, the antennal scales and uropods were expanded to form a head and tail fan respectively (see 140-170 ms of **Fig. 2.8**). Full expansion of the tail fan occurred within 5-10 ms of the start of flexion, and within 10-15 ms for the head fan (**Fig. 2.9 a**). However, each fan was maximally spread for the duration of only a single frame during the flexion phase of a tail flip; towards the end of the flexion phase, both fans were gradually retracted again. It was not always possible to measure the width of the fans when in a flexed position due to them being obscured by the silhouette image of the

cephalothorax. During re-extension of the abdomen, the width of the tail fan (as seen from the dorsal aspect of the telson) was only 15-20 % of its maximum width, compared to the head fan, which closed to 40-60 % of its maximum width. The difference between these values is due to the fact that shrimps not only retract the tail fan, but also fold the uropods ventrally beneath the telson during body extension (so that the ventral surfaces of the uropods meet), thereby minimising drag during the re-extension phase. Reduction in the width of the head fan occurred primarily as a result of retracting the antennal scales into a closed position, rather than folding them ventrally.

In measurements taken from 2 shrimps (total lengths = 33 mm and 40 mm), the mean velocity of the head fan with respect to the centre of mass during flexion was 0.39 m.s^{-1} compared with 0.79 m.s^{-1} for the tail fan (Fig. 2.9 b). Therefore, the velocity of the head fan was 52 % that of the tail fan.

2.3.3 Orientation of shrimps whilst tail flipping

2.3.3.i Movements in the shrimp's roll plane

2.3.3.i.a Roll movements during the first tail flip of an escape response

In the majority of escape responses observed, the first tail flip of a swimming bout was accompanied by a lateral roll of the shrimp's body about its antero-posterior axis, so that the shrimp escaped either to its left or right side (Fig. 2.8 & 2.10). Therefore, subsequent tail flips took place with the shrimp swimming on its side. This rotation was evident on the first frame in which movement was detected (i.e. within 5 ms of the onset of movement). A large roll angle resulted in the shrimp travelling horizontally during the first tail flip and subsequent tail flips of an escape response.

However, in a few responses, no roll occurred, and the first tail flip of an escape response was performed with the shrimp orientated in an upright position. Tail flips of this type were directed along a predominantly vertical trajectory, regardless of whether the stimulus was applied rostrally or caudally. Vertical tail flips usually occurred in response to more intense stimuli.

If the flexion phase of the first tail flip was vertically elevated, a body roll was nevertheless usually executed during the extension phase, thereby rolling the shrimp onto its side before the second tail flip (Fig. 2.11). Body rolls of this type were often accompanied by pleopod movements during the re-extension phase.

2.3.3.i.b Roll movements during subsequent tail flips of the escape response

If the first tail flip incorporated body roll (either during the flexion phase or re-extension phase) subsequent tail flips occurred with the shrimp swimming on its side, and its trajectory was directed predominantly in the horizontal plane. However, rather than maintaining constant elevation above the substrate of the arena, subsequent tail flips often involved a small degree of roll which directed the shrimp downwards. Therefore, shrimps frequently made contact with the substrate of the arena during escapes, and rarely exceeded elevations of greater than 10 cm above it.

2.3.3.ii Movements in the shrimp's pitch plane

2.3.3.ii.a Pitch movements during the first tail flip of an escape response

In a few cases, the first tail flip of an escape response incorporated little or no body roll during either the flexion or re-extension phase. Instead, the shrimp rotated rostrally in the pitch plane as it re-extended its abdomen, and the second tail flip resulted in the shrimp pitching further rostrally (i.e. performing a partial forward somersault). This had the effect of reorientating the direction of travel in the horizontal plane, but instead of the shrimp swimming on its side, subsequent tail flips occurred with the shrimp's head lower-most and its tail upper-most.

2.3.3.ii.b Pitch movements during subsequent tail flips of the escape response

Rotation in the pitch plane was important in bringing about directional changes between one tail flip and the next. When shrimps were swimming on their side (as occurred most frequently), this enabled them to steer in the horizontal plane. If large steering manoeuvres were performed, they usually occurred within the first one or two tail flips of an escape response. Shrimps were able to perform larger changes of direction between one tail flip and the next when steering rostrally (up to approximately 70° - 80°) than when steering caudally (10° - 15°).

During the re-extension phase of a tail flip immediately preceding a large rotational pitch in the rostral direction, a single beat of the pleopods was often observed. (This action can be seen in **Fig. 2.10**).

2.3.3.ii.c Effects of removing the head and/or the tail fan upon steering in the pitch plane

During the 3rd and subsequent tail flips (i.e. after the largest steering manoeuvres had been executed), intact shrimps swam along a relatively straight trajectory in the horizontal plane (mean rotation in the pitch plane = $+7.2^\circ$, s.d. = 7.7°). Removal of the head fan alone caused shrimps to swim along a curved trajectory, rotating rostrally with a mean pitch angle of $+40.7^\circ$ (s.d. = 13.7°). Removal of the tail fan alone resulted in shrimps rotating in the opposite direction, pitching caudally with a mean angle of -25.2° (s.d. = 20.3°). If both the head and tail fan were removed, then an intermediate mean pitch angle of -1.2° (s.d. = 29.1°) occurred. All of the experimental groups differed significantly from one another (Kruskal-Wallis test, $p < 0.001$, followed by multiple comparison tests in which $p < 0.01$ for intact shrimps *versus* no head and no tail fan, and 0.001 for all other comparisons) (Fig. 2.12).

2.3.3.iii Movement in the shrimp's yaw plane

Movement of the shrimp in the yaw plane were not examined in detail. However, rotation in the yaw plane does occur, adding to the complexity of the tail flip orientation. This was especially evident during the re-extension phase of tail flips. In many of the escapes, when shrimps were swimming on their side, yaw rotation resulted in the shrimp's body being at an angle (rather than parallel) to the horizontal, with the tail fan being elevated a greater distance above the substrate of the arena than the head fan.

2.3.4 Effect of shrimp length on the duration of tail flips

For each escape response, there was no significant difference between the total duration (i.e. flexion + re-extension phase) of the first and second tail flip of an the escape swimming bout (paired t-test, $n = 20$, $p = 0.14$), but the duration of the tail flip increased as a positive linear function of shrimp length (see Table 2.1 and Fig. 2.13 a). Tail flips of the smallest shrimps (11 mm) typically had a duration of between 30-50 ms, compared to 95-110 ms for the largest shrimps (68 mm).

The flexion phase of tail flip 1 had a significantly greater duration than that of tail flip 2 (paired t-test, $n = 25$, $p = 0.019$), probably in part because the body started from a fully extended position at the beginning of tail flip 1, compared to the partially extended position in

subsequent tail flips. However, the re-extension phase of the second tail flip had a significantly shorter duration than that of the first tail flip (paired t-test, $n = 20$, $p = 0.019$).

For both the first and second tail flips, the duration of both the flexion and extension phases increased as a positive function of shrimp length (Fig. 2.13 b-c) (see Table 2.1 for regressions). The ratio (flexion time):(total tail flip time) had mean values of 0.47 (s.d. = 0.10) and 0.39 (s.d. = 0.08) for tail flip 1 and 2 respectively.

2.3.5 Effect of shrimp length on body angle measurements

2.3.5.i Body angle

Consecutive flexion and re-extension movements of the abdomen during a tail flip swimming bout resulted in cyclic changes in the body angle (Fig. 2.14 a). Tail flips usually resulted in full flexion of the abdomen so that the tail fan came into close or direct contact with the cephalothorax. There was no significant difference between the minimum body angles at the end of the first and second tail flips (paired t-test, $n = 25$, $p = 0.08$), and therefore the data were pooled. Regression analysis on the pooled data shows that there was no significant change in minimum body angle with shrimp length (t-test on slope of line, $n = 25$, $p = 0.12$). The mean minimum body angle at the end of each tail flip was 25.0° (standard deviation = 4.9° , $n = 62$) (Fig. 2.14 b).

The maximum body angle at the end of the re-extension phase of a tail flip was more variable (75° - 165°) than the minimum body angle at the end of the flexion phase. There was no significant difference between the maximum body angles at the end of tail flip 1 and tail flip 2 (paired t-test, $n = 22$, $p = 0.14$). The maximum body angle of the pooled data increased significantly with shrimp length (t-test on slope of regression, $n = 22$, $p < 0.001$), but the degree of variability attributable to change in shrimp length was low (r^2 of regression = 0.12) (Fig. 2.14 b).

2.3.5.ii Mean and maximum angular velocities of the body angle

Fig. 2.15 shows the mean and maximum angular velocities attained during the flexion and re-extension phases of tail flip 1 and 2 of an escape swimming bout. Negative values represent flexion of the abdomen, whilst positive values represent re-extension.

The rate of change of body angle (degrees per second) was greater during the flexion phase than during the re-extension phase (paired t-tests; $n = 27$, $p < 0.001$ for tail flip, and $n =$

22, $p < 0.001$ for tail flip 2). During the flexion phase of the first tail flip, the body angle decreased with a mean angular velocity of between -6316 deg.s^{-1} and -7800 deg.s^{-1} in small (11 mm) shrimps (maximum angular velocities attained were between $-10400 \text{ deg.s}^{-1}$ and $-12660 \text{ deg.s}^{-1}$), compared to mean angular velocities of between -3218° and -4434° for large (> 60 mm) shrimps (maximum angular velocities were between -6120 deg.s^{-1} and -7800 deg.s^{-1}). Both the mean and the maximum flexion rates of tail flip 1 decreased in a linear manner with increasing shrimp length (see Table 2.1 for regressions). This was also true for the flexion phase of tail flip 2, but for individual shrimps the mean and maximum flexion rates were greater during tail flip 1 than during tail flip 2 (paired t-tests; $n = 25$, $p < 0.001$ in both instances). Therefore, separate regression lines were fitted to the data from flexion 1 and flexion 2.

The rate of re-extension also declined in a linear manner as shrimps became larger. There was no significant difference between re-extension angular velocities of tail flip 1 and 2 (paired t-tests; $n = 22$, $p = 0.07$ and $p = 0.12$ for mean and maximum angular velocities respectively). Therefore, regression lines were fitted to pooled data from both tail flips (Table 2.1). Mean angular velocities during re-extension decreased from between 2867 deg.s^{-1} and 4163 deg.s^{-1} in small shrimps (maximum values were between 4080 deg.s^{-1} and 9100 deg.s^{-1}) to between 1209 deg.s^{-1} and 2188 deg.s^{-1} in large shrimps (maximum values were between 3000 deg.s^{-1} and 5000 deg.s^{-1}).

2.3.5.iii Maximum angular acceleration of the body angle during the flexion phase

There was no significant difference between the maximum angular acceleration of the body attained during the flexion phase of the first and second tail flips (paired t-test, $n = 25$, $p = 0.63$). Maximum angular acceleration values were greater in small shrimps than large shrimps, and decreased in a linear manner with shrimp length (Table 2.1). For 10-20 mm shrimps, angular acceleration was between -114000 and $-248000 \text{ deg.s}^{-2}$, whilst for 60-70 mm shrimps, values were between -56000 and $-88000 \text{ deg.s}^{-2}$ (Fig. 2.16).

2.3.6 Effect of shrimp length upon centre of mass displacement

2.3.6.i Distance travelled by the centre of mass per tail flip

The distances travelled by the centre of mass during the first and second tail flip of a swimming bout were not significantly different from one another (paired t-test, $n = 22$, $p =$

0.14), and values for subsequent tail flips were also similar (Fig. 2.17). Displacement per tail flip increased as a positive function of shrimp length from 10-30 mm for small (11 mm) shrimps to 80-120 mm for large (> 55 mm) shrimps. The relationship between shrimp length and distance travelled per tail flip was best described by a quadratic function (see Table 2.2 and Fig. 2.17 a). Over the size range of shrimps used in the experiments (11-69 mm), the fitted regression line predicts that the shrimp length with the maximum displacement per tail flip is 69 mm.

In terms of body length equivalents, values for displacement per tail flip lay between 0.6-0.28 bl.

2.3.6.ii Mean velocity of the centre of mass during multiple tail flips

The mean velocities measured from high speed video recordings agree very closely with the mean velocities of shrimps of the same size range measured from conventional video recordings (50 f.s⁻¹) made during cod predation experiments, and therefore these data have been pooled.

The lowest mean velocity measured was 0.26 m.s⁻¹ by an 8 mm shrimp, and the highest was 1.42 m.s⁻¹ by a 46 mm shrimp. The largest shrimps (> 60 mm) had lower mean velocities than those of animals between 45-55 mm. A quadratic function fits the data better than does either a linear or log-linear regression. From the quadratic function (Table 2.2), it was calculated that the shrimp length resulting in the maximum mean velocity is 52 mm (with a mean velocity of 1.07 m.s⁻¹) (see Fig. 2.18 a).

Mean velocity, measured in terms of body lengths per second (bl.s⁻¹), decreased as a linear function of shrimp length (Fig. 2.18 b). The highest measured value was 50.5 bl.s⁻¹ for a shrimp with a length of 8 mm, and the lowest was 11.7 bl.s⁻¹ for a shrimp with a length of 69 mm.

2.3.6.iii Effect of removing the head and/or tail fan on the mean velocity

The mean velocity of the centre of mass differed significantly between the intact shrimps, and those of a similar length in which the head and/or tail fan had been removed (oneway ANOVA, $p < 0.001$) (Fig. 2.19). The intact shrimps had a mean tail flip velocity of 0.95 m.s⁻¹ (s.d. = 0.19). Removal of the head fan alone resulted in a significant decline in mean velocity (mean = 0.61 m.s⁻¹, s.d. = 0.07; Tukey's comparison with intact shrimps, $p <$

0.05). Removal of the tail fan alone resulted in an even greater decline in the mean velocity (mean = 0.40 m.s^{-1} , s.d. = 0.06; $p < 0.001$), and this was similar to the effect of removing both the head and tail fans (mean = 0.38 m.s^{-1} , s.d. = 0.04; $p < 0.001$).

2.3.6.iv Maximum velocity of centre of mass during the flexion phase of the tail flip

There was no significant difference between the maximum velocity achieved by the centre of mass during the first and second tail flips of each escape (paired t-test, $n = 25$, $p = 0.58$). Subsequent tail flips which were analysed (up to the 4th of an escape swimming bout) were also very similar to the first and second tail flips in this measure. Data were therefore pooled from tail flips 1-4 of an escape swimming bout.

The lowest maximum velocity for a single tail flip was 0.59 m.s^{-1} by a shrimp of 20 mm, and the highest was 2.31 m.s^{-1} by a shrimp of 57 mm. A quadratic function fitted to the data (see Table 2.2) predicts that the shrimp length with the highest maximum velocity is 58 mm (Fig. 2.20 a).

Expressed as body lengths per second, the highest maximum velocity was 76 bl.s^{-1} by an 11 mm shrimp, whilst the lowest was 17 bl.s^{-1} by a shrimp of 60 mm. (Fig. 2.20 b).

2.3.6.v Maximum acceleration of centre of mass during the flexion phase of the tail flip

The maximum acceleration attained during the first tail flip of an escape response was significantly greater than the maximum acceleration attained during the second tail flip (paired t-test, $n = 25$, $p = 0.05$). Therefore, a regression analysis has been conducted on data from only the first tail flips of escape swimming bouts, since this is likely to be the most important stage during a predatory strike.

The lowest acceleration measured during the first tail flip was 64 m.s^{-2} by an 11 mm shrimp, and the highest was 244 m.s^{-2} by a 63 mm shrimp. A quadratic function fitted to the data (Table 2.2) predicts that the shrimp length with the highest maximum acceleration is 52 mm (Fig. 2.21 a).

The highest maximum acceleration, measured in terms of body lengths per second, was 8150 bl.s^{-2} by a 12 mm shrimp, and the lowest was 1620 bl.s^{-2} by a 59 mm shrimp (Fig. 2.21 b).

2.4

DISCUSSION

2.4.1 Neural pathways involved in initiating escape responses

Although the imprecise nature of the stimulus made it inappropriate to perform a rigorous investigation of the escape response latencies, values of between 5 and 10 ms (i.e. 1-2 frames from the onset of the stimulus to the first detectable movement by the shrimp) were observed for a number of responses. Values in the literature for crayfish giant fibre latencies are less than 10 ms, compared to greater than 100 ms for non-giant mediated tail flips (Wine & Krasne 1972). This suggests that at least a proportion of escapes were initiated by giant fibre interneurons. Giant fibre mediated actions typically occur in a highly stereotyped manner (Reichert, 1988). In *Crangon crangon*, short latency responses occurred in both vertically directed tail flips (i.e. with no body roll during flexion 1), as well as horizontally directed tail flips (i.e. incorporating body roll during flexion 1). This contrasts with the behaviour of crayfish, which, when presented with an asymmetrical mechanical stimulus, produce an initial giant fibre mediated flexion which results in no lateral displacement of the animal (Reichert & Wine, 1983), in part, because the giant neural fibres stimulate both ipsi- and contralateral sides of the abdominal musculature (Roberts *et al.*, 1982).

However, Newland & Neil (1990b) have shown that, in the Norway lobster *Nephrops norvegicus*, activation of the giant fibres can lead to lateral steering forces during the first flexion of an escape. Furthermore, high speed video observations of the mysid *Praunus flexuosus* show that they are able to produce asymmetrical movements of their antennal scales and uropods within 5 ms of the stimulation, and this results in lateral steering forces which direct the first tail flip sideways (Neil & Ansell, 1995; Ansell & Neil, 1991). These latter cases are more analogous to the escape of *Crangon crangon*, which displays short latency steering responses. In the investigation of Reichert & Wine (1983) though, the crayfish were not able to see the approaching stimulus, and therefore would have received minimal information on the stimulus directionality prior to its arrival (although the crayfish would have been able to detect water-borne vibrations). In the escapes performed by *C. crangon* and *P. flexuosus*, the shrimps were able to see the position of the stimulus several seconds prior to its arrival. Similarly, in the experiments on *N. norvegicus* where giant fibre mediated tail flips incorporated steering forces, the animal was tilted onto its side before the stimulus was

applied. This may have allowed them to 'pre-set' their escape direction before the sudden application of the stimulus initiated an escape response.

2.4.2 Movements of the abdominal segments during tail flips

During body flexion in *Crangon crangon*, very little flexion occurred at the joint between the 5th and 6th abdominal segment, or between the 6th abdominal segment and the telson. Therefore, movements of the cephalothorax and of the abdomen were relatively symmetrical about the midpoint of flexion, and this 'symmetrical' tail flip mechanism was common to all first, as well as subsequent tail flips of an escape swimming bout, regardless of the stimulus direction. This flexion pattern is similar to that of the first tail flip in LG mediated escape responses in crayfish (Wine & Krasne, 1972; Webb, 1979) and *Nephrops norvegicus* (Newland & Neil, 1990a), which, in both cases, produce vertically elevated escape trajectories. In crayfish, this occurs because the 4th, 5th and 6th abdominal segments lack direct neuronal pathways linking them to the LGs (Larimer *et al.*, 1971; Mittenthal & Wine, 1973), and also because a parallel set of neurones feed-forward and inhibit the excitation of the fast flexor (Dumont & Wine, 1987; Takahata & Wine, 1987). In *N. norvegicus*, the posterior flexor muscles are activated, but their recruitment occurs with a delay of approximately 50 ms after the initiation of flexion in the anterior abdominal segments.

A comparison of flexion mechanisms in various crustaceans is illustrated in Fig. 2.22. *Crangon crangon* is unusual, since it produces a symmetrical tail flip (directed vertically when there is no body roll) in response to both rostral and caudal stimuli, whereas this only occurs in response to caudal stimuli in other animals. Also, although initial LG tail flips in many animals are symmetrical and vertically directed, subsequent tail flips of an escape typically involve flexion along the full length of the abdomen, so that the tail fan curls underneath the animal, and moves primarily in an anterior direction. This pattern does not occur in *C. crangon*, in which the symmetrical tail flip mechanism persists during subsequent tail flips of a swimming bout.

One effect of this symmetrical tail flip mechanism is that it moves the cephalothorax, as well as the abdomen, about the point of flexion. In *Crangon crangon*, this has the advantage of moving the expanded head fan as well as the tail fan through the water, thereby enabling both surfaces to generate thrust. Another potential advantage of a symmetrical tail flip is that it probably increases the squeeze force produced at the end of the flexion phase, because more

water is trapped between the abdomen and cephalothorax. Squeeze force contributes a significant proportion of the thrust generated by tail flips in shrimps (Daniel & Meyhöfer, 1989), and this may be a method of maximising the velocity of tail flip swimming. Confirmation of this hypothesis would be aided by an extension of the model created by Daniel & Meyhöfer (1989) to predict the various thrust components of the tail flip.

2.4.3 Use of the antennal scales and uropods for generating thrust

Webb (1979) has shown that drag-based thrust during tail flips in the crayfish *Orconectes virilis* is produced almost entirely by the uropods and telson. This is because, being further from the point of flexion, they have a greater velocity (relative to that of the animal's centre of mass), than any of the other abdominal segments, and also present a larger surface area. The symmetrical tail flip mechanism of *Crangon crangon* results not only in movement of the tail fan relative to the shrimp's centre of mass, but also in movement of the head fan. This enables both surfaces to generate drag-based thrust. However, the relative velocity of the head fan was only 54% that of the tail fan during the flexion phase of tail flips, and therefore one would expect the tail fan to generate a greater proportion of the thrust. This was confirmed by removing the uropods, which resulted in a 58 % decline in the mean velocity, whereas removal of the head fan alone resulted in only a 35 % decline in the mean velocity (Fig. 2.19).

It is perhaps surprising that removal of both the head and tail fan together resulted in a reduction in the mean velocity by 60 %, which is not significantly different from that occurring when the tail fan alone was removed. This occurs because removal of the tail fan reduces the total surface area of the posterior flexing region of the shrimp by > 40% (the antennal scales contribute a much smaller proportion of the surface area to the cephalothorax flexing region). Therefore, with the tail fan alone removed, the remaining part of the abdomen offers very little resistance, and flexion results in rapid movement of the abdomen through the water, with very little movement (or thrust) produced by the head region.

The rotational components of the thrust generated by the head and tail fans have been demonstrated by measuring the pitch angle between one tail flip and the next (Fig. 2.12). Removal of the head fan caused the shrimp to pitch rostrally, producing a curved trajectory, whilst removal of the tail fan caused them to pitch in a caudal direction. This demonstrates

that the rotational forces generated by one fan serve to balance the rotational forces generated by the opposing fan, thereby enabling the shrimp to tail flip along a straight trajectory.

2.4.4 Orientation of the shrimp's body whilst tail flipping: the influence of anatomy and habitat

In the majority of tail flips analysed, *Crangon crangon* performed a roll about its longitudinal axis during the first flexion of an escape response, and thereafter, swam on its side. In those cases where the first flexion involved no body roll, the shrimp escaped with an initial vertical trajectory, but then usually rolled onto its side during the re-extension phase, and continued to swim in this orientation thereafter. Therefore, there is a strong tendency for *C. crangon* to swim on their side. This contrasts with the typical tail flip behaviour of crayfish (e.g. Wine & Krasne, 1972; Webb; 1979), nephropid lobsters (e.g. Newland & Neil, 1990a), palinurid lobsters (Jacklyn & Ritz, 1986; Newland *et al.* 1992a), galatheoid lobsters (Sillar & Heitler, 1985; Wilson & Paul, 1987) and scyllarid lobsters (e.g. Jacklyn & Ritz, 1986; Spanier *et al.*, 1991). These animals generally tail flip in an upright position, and have dynamic self-righting mechanisms which maintain this orientation during an escape response (Newland & Neil, 1990b; Newland *et al.* 1992a).

However, a similar behaviour to *Crangon crangon* has been reported for tail flip swimming in the mysids *Praunus flexuosus* and *Neomysis integer* (Ansell & Neil, 1991; Kaiser *et al.*, 1992a; Neil & Ansell, 1995) which are also capable of rolling onto their side during an escape response, producing laterally directed trajectories. *C. crangon*, *P. flexuosus* and *N. integer* have four features in common which may be linked to their behaviour of tail flipping on their side: (i) they are relatively small (usually < 70 mm total length), (ii) they possess antennal scales which expand during the flexion phase of a tail flip to form a head fan, (iii) they have a relatively symmetrical tail flip mechanism which enables both the head fan and tail fan to generate thrust, and (iv) they live in open habitats (on, or just above the sediment), rather than within permanent burrows or crevices.

The relatively small size of these shrimps is probably an important characteristic which enables them to swim on their side, because the relative mass of the exoskeleton is less in small crustaceans than it is in large ones. As a consequence of this, larger crustaceans have to generate a greater proportion of lift when tail flipping, which is facilitated by being in an upright position because the rotational forces generated during abdominal flexion (and which

create lift) are orientated in the vertical plane. In the comparatively large and heavily calcified scyllarid lobsters *Ibacus peronii* and *Thenus orientalis*, roll manoeuvres can in fact be performed during an escape in order to steer the animal around an obstacle. Nevertheless, they seem to swim preferentially in an upright body position, and in these species, this is required in order to maintain height above the substratum because their large antennal scales generate lift by acting in a similar manner to aircraft ailerons (Jacklyn & Ritz, 1986).

The possession of a head fan and a symmetrical tail flip mechanism are intrinsically linked factors, since the symmetrical tail flip enables the head fan to generate thrust. However, symmetrical tail flips result in vertical escape trajectories, as demonstrated by *Crangon crangon* when they do not perform a roll during the first flexion of an escape, and by LG tail flips in crayfish (Wine & Krasne, 1972) and *Nephrops norvegicus* (Newland & Neil, 1990a). Vertical trajectories, in the case of *C. crangon*, translate the shrimp up into the water column, and this possibly makes them more vulnerable to predation, since it removes them from the refuge provided by the sediment (see section 3.4.6). By rolling onto their side, *C. crangon* are able to employ a symmetrical tail flip mechanism (which maximises their velocity), whilst at the same time, escaping in the horizontal plane (which keeps them close to the substratum). A further advantage offered by this initial roll is that there may be unpredictability in whether this will occur to one side or the other - a factor that may assist shrimps in evading approaching predators (see section 3.4.7).

The tail flip mechanism of *Crangon crangon* is only compatible with an existence in relatively open habitats. Crustaceans living in a burrow or crevice employ a tail flip mechanism which produces a backward trajectory with little vertical elevation, since this enables them to retreat into their refuge.

2.4.5 Steering of tail flips

2.4.5.i Steering in the shrimp's roll plane

In first flexions that incorporated body roll, the roll movement started within the first 5 ms of the tail flip. It is not intuitively obvious how these rotational forces were brought about. Neil & Ansell (1995) noted that when *Praunus flexuosus* rolled on to its side during the first tail flip of an escape response, its antennal scales and uropods were expanded asymmetrically at the beginning of the tail flip, and acted as rotors which contributed towards the forces bringing about the body roll. Occasionally, asymmetrical spreading of the antennal scales or

uropods was observed in *Crangon crangon*, but this did not occur in all escapes, and was not necessary in order for body roll to occur. Furthermore, in shrimps in which both the antennal scales and uropods had been removed, roll still occurred during the initial flexion phase. Therefore, the rotor mechanism used by mysid shrimps appears to be of little importance in *C. crangon*.

Instead, it seems probable that roll during the first flexion is brought about primarily by asymmetrical muscle activity within the abdomen. Newland & Neil (1990b) have shown that, during tail flip swimming in *Nephrops norvegicus*, dynamic righting reactions in the animal's roll plane are brought about primarily by rotation of the abdomen relative to the cephalothorax about a specialised joint. *Crangon crangon* possess oblique fast muscles in this joint which enable rotation of the abdomen to occur in a similar manner (personal observations), although, in this case, the rotation might serve to tilt the shrimp from the upright rather than counteracting destabilising movements in the roll plane. No information exists on the co-ordination of muscle contraction within the abdomen of *C. crangon*, and investigations into this aspect are needed in order to fully understand their roll behaviour.

Another possible contributor to roll is suggested by the observation that, in the palinurid lobster *Jasus lalandii*, asymmetrical movements of the swimmerets can cause movements in the animal's roll plane during tail flips (Cattaert *et al.*, 1988). In the video sequences of *Crangon crangon*, it was not possible to see the pleopods during the first flexion of an escape because they were obscured by the abdomen. However, when shrimps performed a vertical flexion, and then rolled onto their side during the re-extension phase of the first tail flip, a pleopod beating motion was visible. Therefore, it is possible that the pleopods assist in bringing about body roll, at least under some circumstances.

In scyllarid lobsters, roll manoeuvres are controlled during the glide phase of the tail flip (i.e. at the end of the flexion phase) by asymmetrically raising or lowering their large flattened antennal scales (Jacklyn & Ritz, 1986). It was not possible to determine whether this occurs in *Crangon crangon*.

2.4.5.ii Steering in the shrimp's pitch plane

When the first flexion of an escape did not incorporate body roll, the shrimp always escaped vertically off the bottom with little or no posteriorly directed movement (with respect to the shrimp's pre-escape orientation), regardless of whether the stimulus was applied

rostrally or caudally. In the several hundred escapes which have been filmed of *Crangon crangon*, an escape response which propelled the shrimp directly backwards during the first tail flip was never observed, despite the fact that *C. crangon* possess 2 pairs of giant axons (MGs and LGs; Johnson, 1924). This contrasts with the initial escape trajectories of crayfish (Wine & Krasne, 1972) and *Nephrops norvegicus*, in which an LG tail flip (in response to a caudal stimulus) produces a vertical tail flip, whilst an MG tail flip (rostral stimulus) produces a tail flip which is directed backwards, with little vertical elevation. Therefore, a fundamental difference between the MG tail flip of *C. crangon* and the latter species exists. One reason, with regard to habitat, why this difference may occur in *C. crangon* is that they usually shelter from predators by burying telson-first into the sediment (Pinn & Ansell, 1993), and an escape directly backwards from this position may therefore be hampered.

When *Crangon crangon* do perform a body roll during their first tail flip, and then swim on their side, control of rotation in the shrimp's pitch plane brings about horizontally directed steering. Shrimps were able to steer at a greater angle rostrally (70-80°) than caudally (10-15°), probably in part because of the greater proportion of thrust which the tail fan is able to generate compared with the head fan.

During the largest steering manoeuvres in the rostral direction (which, when they occurred, were executed between the first and second tail flip of an escape), a backward beat of the pleopods was often observed during the first re-extension phase (Fig. 2.10). This prevented the cephalothorax from pivoting about the centre of mass as the abdomen re-extended (i.e. the cephalothorax did not move relative to the centre of mass), so that the subsequent tail flip was directed along a new trajectory.

However, large pitching manoeuvres also occurred without the assistance of pleopod activity. It is possible that the temporal sequence of muscle activation in segments of the abdomen may have contributed to these pitching movements (see Newland & Neil, 1990a). Additionally, in some cases, the head fan was not fully retracted during the re-extension phase of a rostrally directed pitch movement, and this may have created additional drag which affected the shrimp's orientation in the pitch direction. At present, the steering mechanism of the tail flips remains poorly understood, and requires further investigation.

2.4.6 Kinematic variability with shrimp length

Daniel & Meyhöfer (1989) have calculated that, for a shrimp of given dimensions, there is a unique body length which will maximise kinematic performance of tail flipping. This arises because of the complex relationships between the translational thrust, rotational thrust, and cross-sectional area of abdominal muscle, which scale differently from one another as the length of the shrimp increases. The tail flip swimming performance of *Crangon crangon* supports this supposition. The strongest evidence for this comes from the analysis of the mean velocity data, which are less prone to error than the maximum velocity and maximum acceleration data (see Harper & Blake, 1989). A quadratic regression equation produced a better fit to the mean velocity data than did either a linear regression, or a log-linear regression. The latter two regression fits would indicate that the mean velocity continues to increase as shrimp length increases, whilst the quadratic regression predicts that mean velocity starts to decrease in the largest shrimps. A quadratic regression was also the best fit for the maximum velocity and maximum acceleration data.

The fitted quadratic regression equations (Table 2.2) predict that the lengths of shrimps that can produce the greatest mean velocity, maximum velocity, and maximum acceleration are 52 mm, 58 mm and 52 mm respectively. The first value is slightly less than that of 60 mm which was calculated by Daniel & Meyhöfer (1989) to maximise the mean velocity of the shrimp *Pandalus danae*.

2.4.7 Comparison of escape kinematics of *Crangon crangon* with other animals

Smith (1993) investigated maximum tail flip swimming speeds in *Crangon crangon* using the same recording equipment as in this study (with the exception that a frame rate of 400 f.s⁻¹ was used). The mean values of the kinematic parameters which she determined for shrimps with a mean length of 51 mm (range = 39-55 mm) were: duration of tail flip = 211.5 ms; displacement per tail flip = 63.3 mm; mean velocity during a single tail flip = 0.58; maximum velocity attained = 1.07 m.s⁻¹; maximum acceleration = 48.31 m.s⁻²; maximum angular velocity of body angle during flexion = -6310 deg.s⁻¹. If these values are compared with the predictions made from the regression equations in Table 2.1 and Table 2.2 for a shrimp of 51 mm, the shrimps in Smith's investigation performed less well than in the present investigation. One possible reason for this is that her experiments were conducted at 10°C, compared with 13°C here. However, in Smith's investigation, shrimps acclimated to 15°C still

performed less well than shrimps in this investigation. Some discrepancies may have arisen from differences in the experimental protocol (e.g. Smith analysed escape responses consisting of just a single tail flip rather than multiple tail flip swimming bouts, and analysed vertical rather than horizontal tail flips).

Table 2.3 shows a list of maximum burst swimming velocities reported for a number of crustacean and fish species. It is difficult to make comparisons between species because of the different temperatures under which experiments were performed, and the different frame rates of the recording equipment used. Nevertheless, among the crustaceans, the range of maximum tail flip swimming velocities is comparatively low considering the range of body lengths. Daniel & Meyhöfer (1989) suggest that tail flip swimming in large crustaceans should be less effective than in small ones, partly because of the disproportionate increase in rotational forces as body length increases. However, large species such as *Scyllarides latus* and *Nephrops norvegicus* are still able to achieve relatively high tail flip velocities. One factor which is probably important with this regard is the tail flip mechanism of the larger crustaceans (Fig. 2.22) in which the abdomen only re-extends by a small amount during each tail flip, and then flexes along its full length causing the tail fan to curl under the body. These actions reduce the moments of inertia created by the tail flip. Differences in muscle anatomy may also be important.

The tail flip velocity of *Crangon crangon* is relatively high compared to the other crustacean species listed in Table 2.3, although not as high as the maximum velocity of 2.8 m.s⁻¹ reported for *Pandalus danae* (length = 70 mm). The velocities of the mysids *Praunus flexuosus* and *Neomysis integer* were similar to *C. crangon* of the same size in the studies of Neil & Ansell (1995), and Rademacher & Kils (1996), but the result for *N. integer* reported by Kaiser *et al.* (1992a) suggests that they may in fact be able to achieve greater velocities than *C. crangon*.

Juvenile plaice (*Pleuronectes americanus*, length = 10 mm) are considerably slower than *Crangon crangon* of an equivalent length, but the five fish species investigated by Webb (1986) and Domenici & Blake (1991) (*Pimephales promelas*, *Micropterus salmoides*, *Lepomis macrochirus*, *Esox sp.* and *Pterophyllum eimekei*) have maximum velocities which, although slightly lower, are more comparable, with their *C. crangon* length equivalents. However, when the velocities of *C. crangon* of length 10-20 mm are compared with those of fish with lengths in the range of their potential predators (10-20 mm shrimps are preyed upon by 100 mm

juvenile cod - see section 4.3.2.v), they are more discrepant. Cod of 100 mm, and other fish of this approximate length, are able to achieve maximum velocities greater than those achieved by the shrimps of the range upon which they feed. It follows that, in a straight-line predator-prey 'race', *C. crangon* would be expected to lose. As a consequence of this, the ability of shrimps to outmanoeuvre predators during an encounter (see Howland, 1974; Webb, 1976; Weihs & Webb, 1984) will be an essential factor in their survival.

Table 2.1 Statistical analysis of parameters derived from body angle measurements during tail flip escapes by *Crangon crangon*

L = shrimp length (mm).

 t_x = duration (ms) of tail flip x in a tail flip swimming bout. ω_x = angular velocity (deg.s^{-1}) of tail flip x in a tail flip swimming bout.

Significance of all regressions tested by ANOVA.

	Tail flip 1	Tail flip 2
Duration of whole tail flip (ms)	$t = 27.0 + 1.11(L)$ $p < 0.001$ $r^2 = 0.57$ [Data from tail flip 1 & 2 combined (not significantly different from one another, paired t-test, $n = 20$, $p = 0.14$)].	
Duration of flexion phase (ms)	$t_{\text{flex 1}} = 16.9 + 0.34(L)$ $p < 0.001$ $r^2 = 0.56$	$t_{\text{flex 2}} = 12.5 + 0.40(L)$ $p < 0.001$ $r^2 = 0.53$
Duration of extension phase (ms)	$t_{\text{ext 1}} = 6.23 + 0.82(L)$ $p < 0.001$ $r^2 = 0.49$	$t_{\text{ext 2}} = 22.6 + 0.56(L)$ $p = 0.010$ $r^2 = 0.27$
Minimum body angle at the end of flexion (deg)	Mean for all tail flips = 25.0° Standard deviation = 4.9° [paired t-test on tail flip 1 & 2, $n = 25$, $p = 0.08$]	
Maximum body angle at the end of re-extension (deg)	$\text{Max angle} = 113 + 0.413(L)$ $p = 0.004$ $r^2 = 0.12$ [Data combined from tail flips 1-4]	
Mean angular velocity during flexion (deg.s^{-1})	$\omega_1 = -7777 + 70.9(L)$ $p < 0.001$ $r^2 = 0.61$	$\omega_2 = -4639 + 29.0(L)$ $p = 0.002$ $r^2 = 0.34$
Mean angular velocity during re-extension (deg.s^{-1})	$\omega_1 = 3889 - 31.6(L)$ $p < 0.001$ $r^2 = 0.39$ [Data combined from tail flip 1 and 2 (not significantly different; paired t-test, $n = 22$, $p = 0.07$)].	
Maximum angular velocity during flexion (deg.s^{-1})	$\omega_1 = -12336 + 93.1(L)$ (ANOVA; $p < 0.001$) $r^2 = 0.52$	$\omega_2 = -8929 + 70.9(L)$ (ANOVA; $p = 0.001$) $r^2 = 0.35$
Maximum angular velocity during re-extension (deg.s^{-1})	$\omega = 7106 - 55.8(L)$ $p = 0.009$ $r^2 = 0.32$ [Data from tail flip 1 & 2 combined (not significantly different from one another, paired t-test, $n = 22$, $p = 0.12$)].	
Maximum angular acceleration during flexion 1 and 2 (deg.s^{-2})	$\text{Angular acceleration} = -228573 + 2486(L)$ $p < 0.001$ $r^2 = 0.57$ [Data from flexion 1 and 2 combined (not significantly different from one another; paired t-test, $n = 25$, $p = 0.63$)].	

Table 2.2 Statistical analysis of parameters derived from centre of mass displacement during tail flip escapes by *Crangon crangon*

a_{\max} = maximum acceleration attained during tail flip 1 of a swimming bout.

d = distance travelled (mm).

L = shrimp length (mm).

v_{\max} = maximum velocity ($\text{m}\cdot\text{s}^{-1}$) attained during a tail flip.

v_{mean} = mean velocity for all tail flips filmed of an escape swimming bout.

Significance of all regressions tested by ANOVA.

	Tail flip 1	Tail flip 2
Distance travelled per tail flip (mm)	$d = -14.6 + 2.88(L) - 0.019(L^2)$ $p < 0.001$ $r^2 = 0.60$ [Data from tail flip 1-4 combined (1 & 2 not significantly different from one another, two-tailed paired t-test, $n = 22$, $p = 0.14$)].	
Mean velocity for all tail flips combined ($\text{m}\cdot\text{s}^{-1}$)	$v_{\text{mean}} (\text{m}\cdot\text{s}^{-1}) = -0.0079 + 0.0415(L) - 0.000401(L^2)$ $p < 0.001$ $r^2 = 0.77$ [Data combined from cod predation and high speed video experiments]	
Maximum velocity ($\text{m}\cdot\text{s}^{-1}$)	$v_{\max} (\text{m}\cdot\text{s}^{-1}) = 0.082 + 0.0596(L) - 0.000511(L^2)$ $p < 0.001$ $r^2 = 0.58$ [data combined from tail flips 1-4]	
Maximum acceleration during tail flip 1 of a tail flip swimming bout ($\text{m}\cdot\text{s}^{-2}$)	$a_{\max} (\text{m}\cdot\text{s}^{-2}) = 25.7 + 5.25(L) - 0.0502(L^2)$ $p = 0.009$ $r^2 = 0.29$	-----

Table 2.3 Maximum burst swimming speeds of various crustacean and fish species

Common name	Species	Body length (mm)	Mean velocity (m.s ⁻¹)	Mean max. velocity (body lengths s ⁻¹)	Temp (°C)	Frame rate (f.s ⁻¹)	Reference
CRUSTACEANS							
Slipper lobster	<i>Scyllarides latus</i>	320	0.9	3	13-25	25	Spanier <i>et al.</i> (1991)
Norway lobster	<i>Nephrops norvegicus</i>	110	0.6	5	13-15	64	Newland 1985
Crayfish	<i>Orconectes virilis</i>	83	0.9	11	15	250	Webb (1979)
Dock shrimp	<i>Pandalus danae</i>	70	2.8	41	12	200-500	Daniel & Meyhöfer (1989)
Lobster	<i>Homarus americanus</i>	60	0.7	12	19-20	15	Cromarty <i>et al.</i> (1991)
Krill	<i>Euphausia superba</i>	58	1.0	17	1	55	Kils (1982)
Brown shrimp	<i>Crangon crangon</i>	50	1.1	22	10	400	Smith (1993)
		10-20	0.8	77	13	200	This study
		50-60	1.8	40	13	200	This study
Mysid	<i>Praunus flexuosus</i>	25	0.9	34	10	400	Neil & Ansell (1995)
Mysid	<i>Neomysis integer</i>	9.5	0.8	80	(not known)		Rademacher & Kils (1996)
		10	1.2	123	15	50	Kaiser <i>et al.</i> (1992a)
		16	1.7	104	15	50	Kaiser <i>et al.</i> (1992a)
FISH							
Cod	<i>Gadus morhua</i>	100	1.3	13	13	50	Arnott (Chapter 4)
		100	1.7	17	14	predicted	Wardle (1975)
		300	3.3	11	14	predicted	Wardle (1975)
Haddock	<i>Melanogrammus aeglefinus</i>	100	2.6	26	12	50	Wardle (1975)
Rainbow trout	<i>Salmo gairdneri</i>	100	2.0	20	15	64	Webb (1976)
		390	2.2	6	15	64	Webb (1976)
Knifefish	<i>Xenomystus nigri</i>	113	1.5	13	25	400	Kasapi <i>et al.</i> (1992)
Angelfish	<i>Pterophyllum eimekei</i>	73	1.0	13	25	400	Domenici & Blake (1991)
Fathead minnow	<i>Pimephales promelas</i>	58	0.7	11	15	60	Webb (1986)
Largemouth bass	<i>Micropterus salmoides</i>	51	0.9	18	15	60	Webb (1986)
		64	1.1	17	15	60	Webb (1986)
Bluegill	<i>Lepomis macrochirus</i>	65	1.1	17	15	60	Webb (1986)
Tiger musky	<i>Esox sp.</i>	100	0.8	9	(not known)		Rademacher & Kils (1996)
Stickleback	<i>Spinachia spinachia</i>	100	0.8	9	14	30	Williams & Brown (1992)
Plaice	<i>Pleuronectes americanus</i>	10	0.1	12			

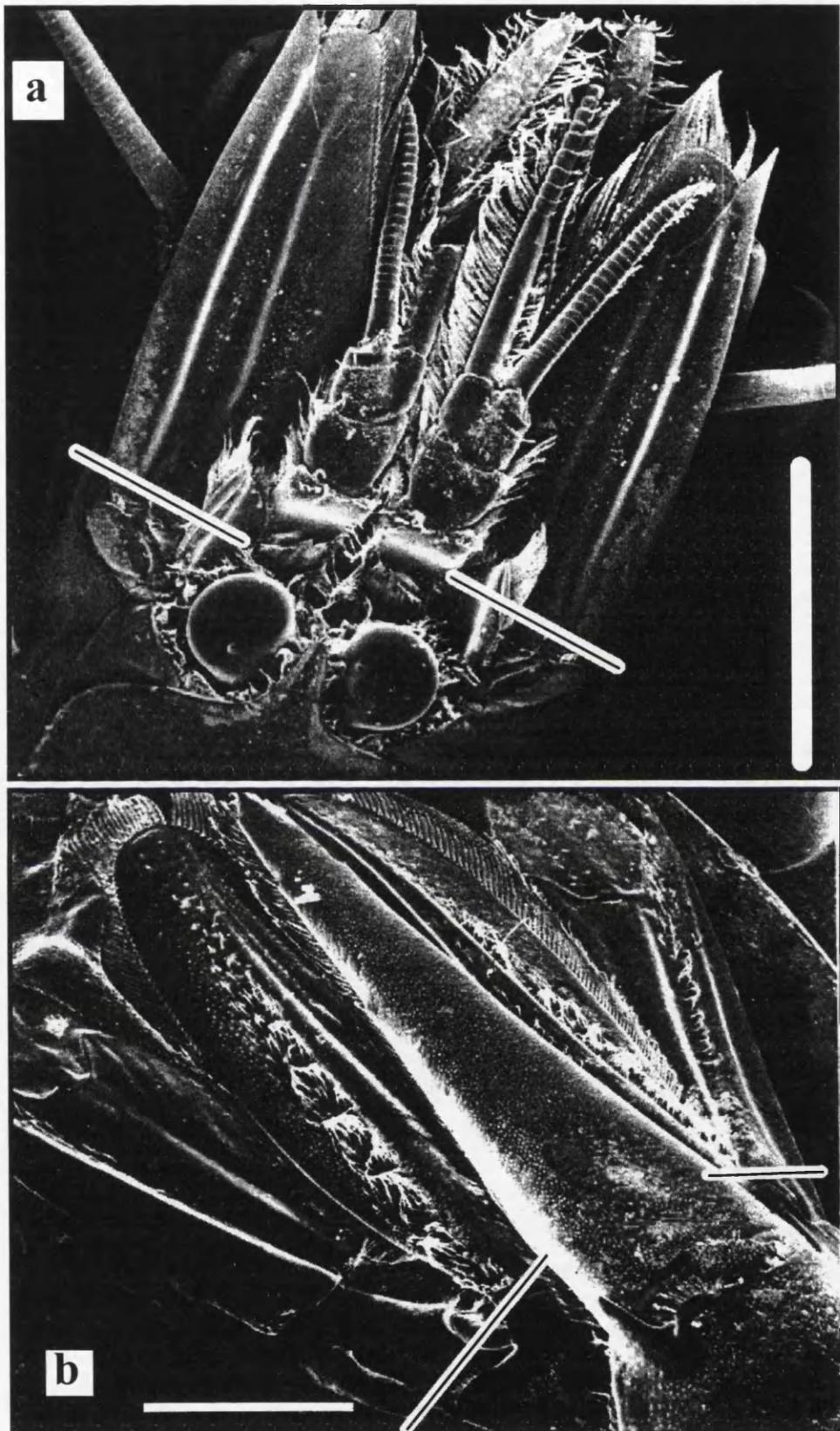


Fig. 2.1 Scanning electron micrographs of the head fan and tail fan of *Crangon crangon* (taken from Heinisch & Wiese, 1987)

Scanning electron micrographs of *Crangon crangon*, taken from Heinisch & Wiese (1987). (a) Dorsal view of the head region showing the large flattened antennal scales which form the head fan, and (b) dorsal view of the telson and uropods, which form the tail fan. White scale bars: (a) 5 mm, (b) 3 mm. Black within white lines represent lines along which amputations were made.

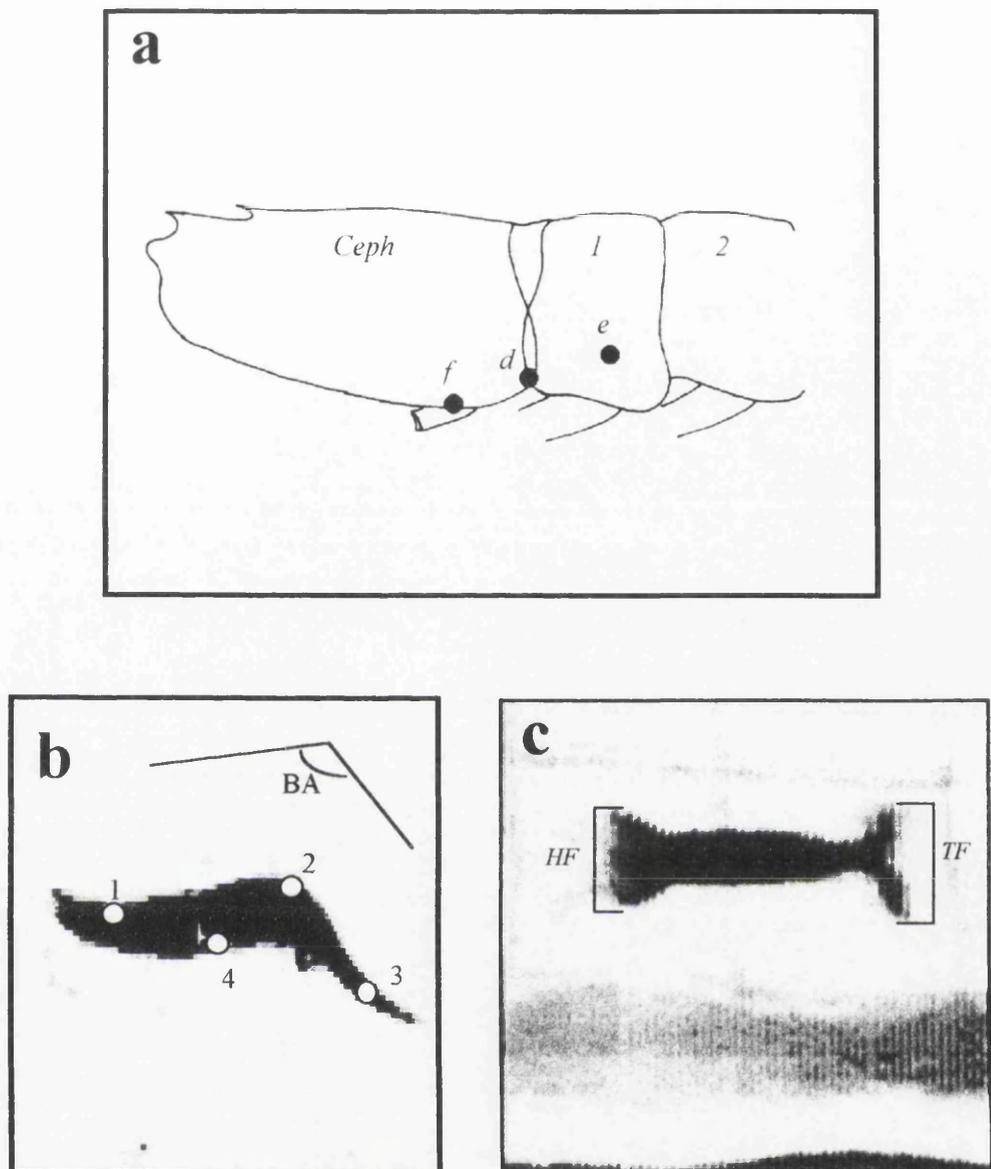


Fig. 2.2 Diagram showing the centre of mass of *Crangon crangon*, and the points on the shrimp's body that were digitised during video analysis

(a) Lateral view of *C. crangon* showing the cephalothorax (*Ceph*) and first 2 abdominal segments (*1* and *2*). The centre of mass is located in the first abdominal segment when the shrimp's abdomen is in an extended position (*e*), and level with the coxa of pereopod 5 when in a fully flexed position (*f*). An intermediate point (*d*) was digitised during video analysis as an estimate of the position of the centre of mass.

(b) Example of a video image showing the camera view of a shrimp during a tail flip, and points 1-4 which were digitised from the shrimp's lateral aspect. Point 1: the shrimp's eyes. Point 2: the leading edge of the mid-flexion point of the abdomen. Point 3: the posterior tip of the 6th abdominal segment. Point 4: the estimated centre of mass, as shown in (a). The body angle of the shrimp (*BA*) was measured as the angle subtended by points 1, 2 and 3.

(c) Example of a video image showing the mirror view of a shrimp during a tail flip, and the points from the shrimp's dorsal (or ventral) aspect that were used to determine the width of the head fan (*HF*) and tail fan (*TF*).

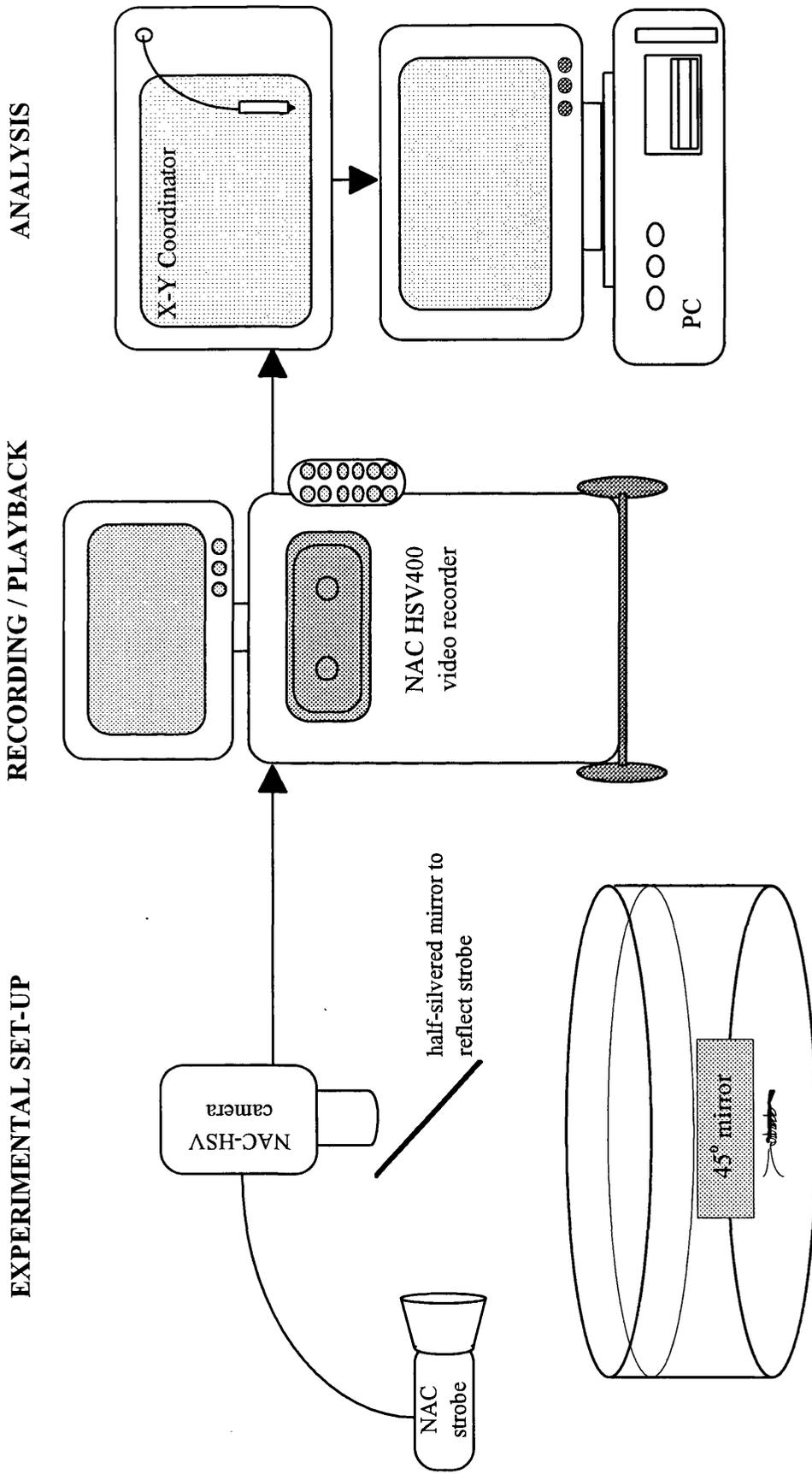


Fig. 2.3 Experimental set-up for high speed video analysis of tail flip swimming

Experimental set-up for video filming and analysis of tail flip swimming. Diameter of experimental arena = 1 m, water depth = 17 cm.

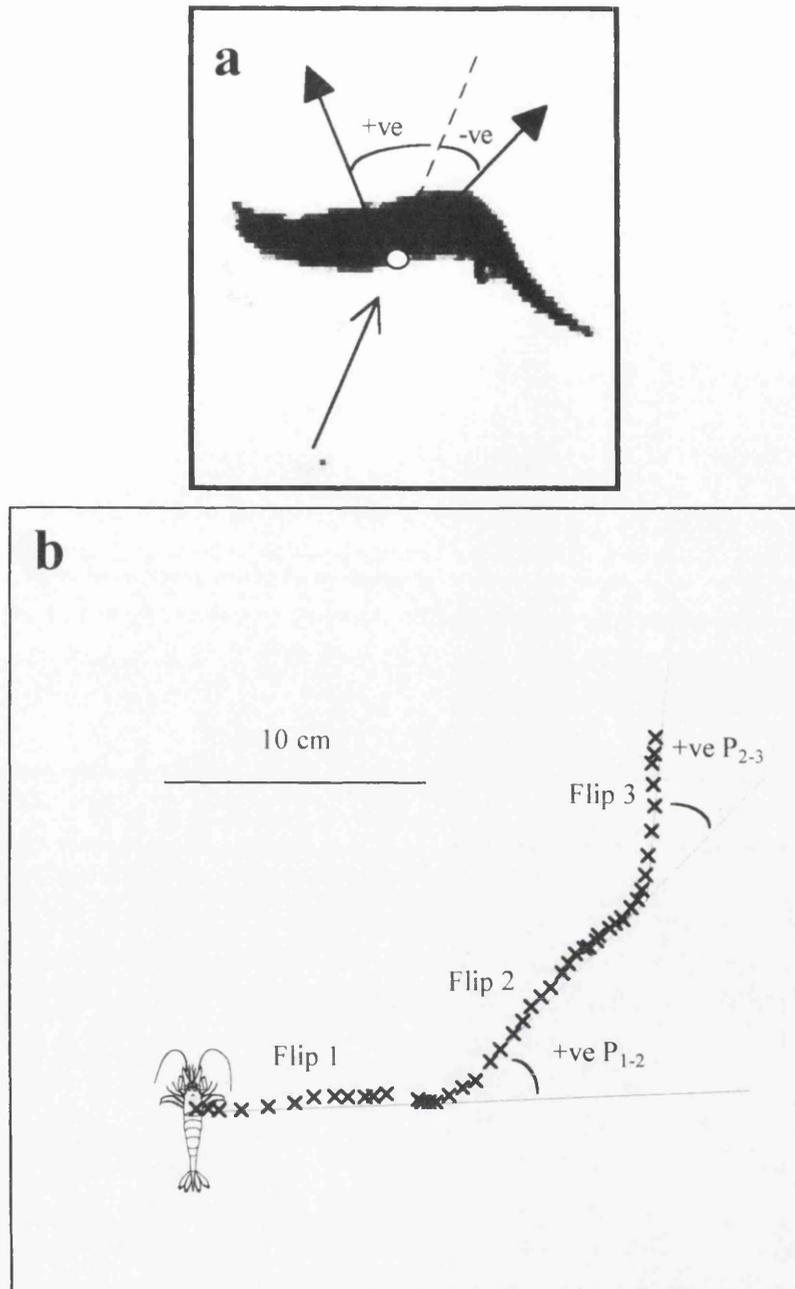


Fig. 2.4 Method of measuring the pitch angle between two successive tail flips

Method of measuring the pitch angle between two successive tail flips. **(a)** High speed video image showing the lateral aspect of a shrimp at the end of body re-extension of the first tail flip of an escape, and immediately before flexion of the second tail flip. The open headed arrow represents the line fitted to the trajectory of the centre of mass (circle) during the first tail flip, and the dashed line is an extrapolation of it. The solid headed arrows represent the line fitted to two potential trajectories of the centre of mass during the second tail flip, showing positive pitch (+ve) and negative pitch (-ve). **(b)** Example showing positive pitch during the first 3 tail flips of an escape by a 59 mm shrimp, as seen looking vertically downwards (camera view). Crosses represent the position of the shrimp's centre of mass every frame (5 ms). The solid lines were fitted through the trajectory of the centre of mass for each tail flip, and the pitch angle between tail flips 1 and 2 (+ve P_{1-2}) and tail flips 2 and 3 (+ve P_{2-3}) were measured as the angle between successive tail flip trajectories. Insert of shrimp indicates its pre-escape position; scale bar = 10 cm.

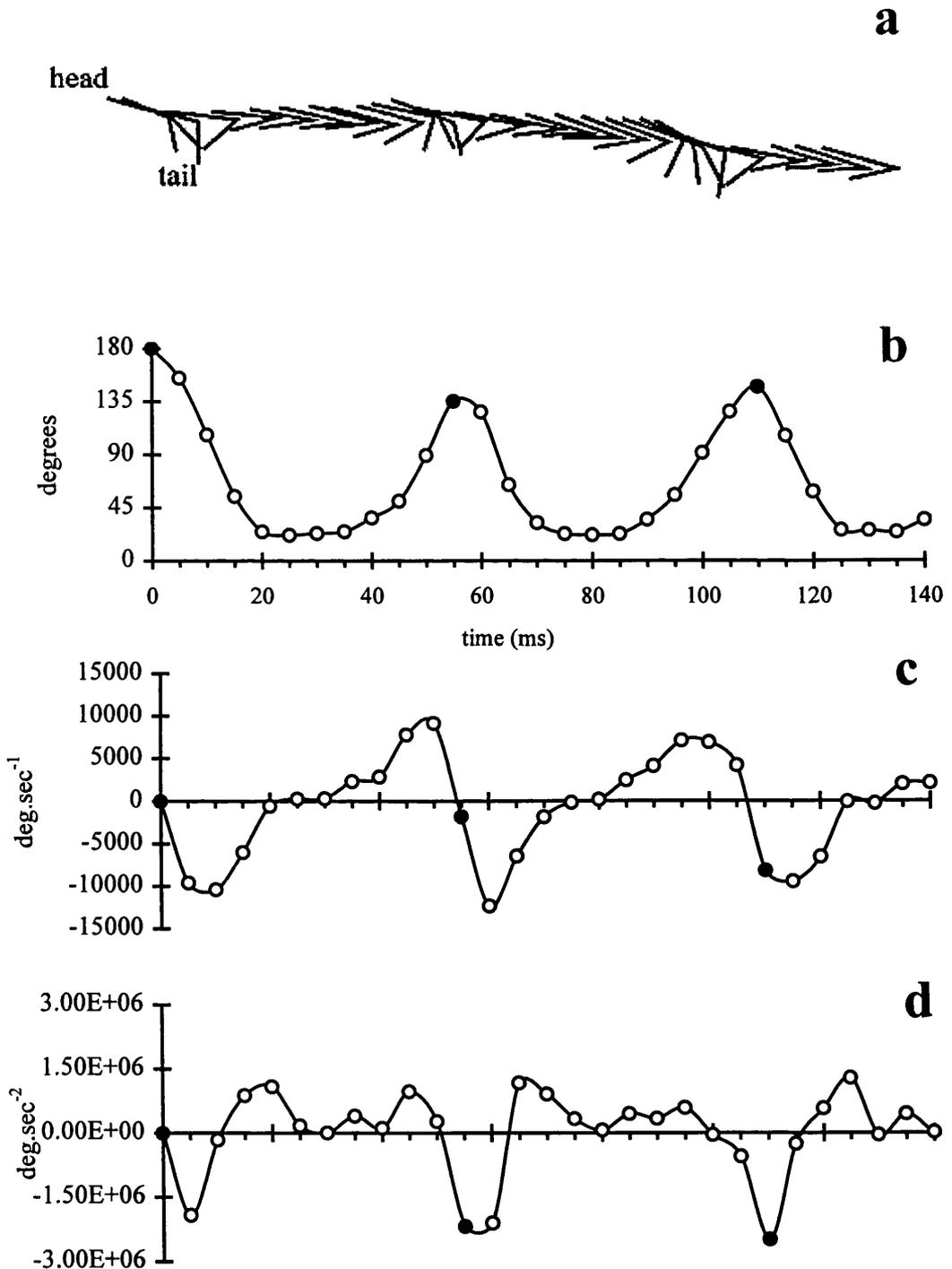


Fig. 2.5 Changes in body angle parameters during tail flips

Changes in body angle parameters during the first 3 tail flips of an escape by an 11 mm shrimp. (a) Stick diagram of shrimp whilst tail flipping. Interval between successive images = 5 ms (b) Changes in body angle against time. (c) Angular velocity of body angle. (d) Angular acceleration of body angle. Filled circles indicate the beginning of the flexion phase of each tail flip.

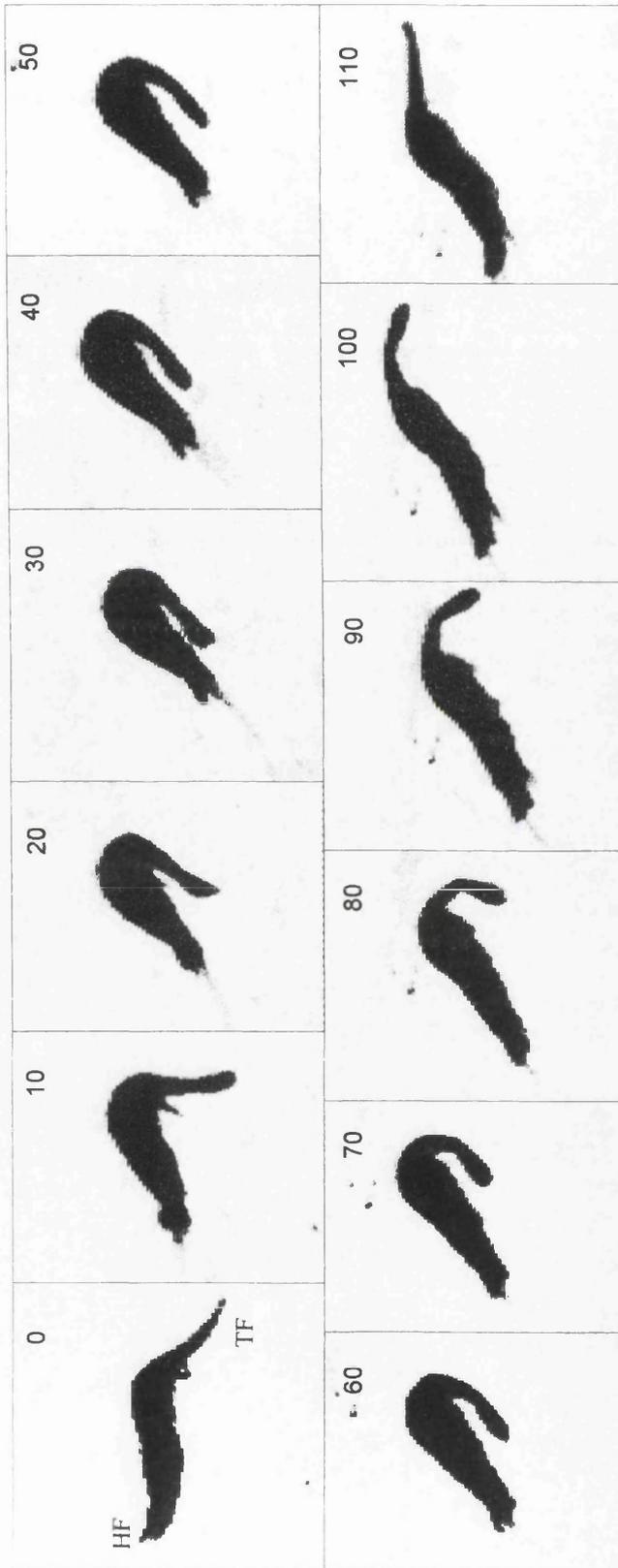


Fig. 2.6 High speed video images showing the flexion and re-extension phases of a tail flip

High speed video images showing the flexion and re-extension phases of the second tail flip of an escape swimming bout by *Crangon crangon* (every second video frame is shown; the numbers refer to the time elapsed in milliseconds). The shrimp is viewed from its lateral aspect, with the head fan (HF) on the left and the tail fan (TF) on the right. 0-40 ms = the flexion phase, 40-110 ms = the re-extension phase.

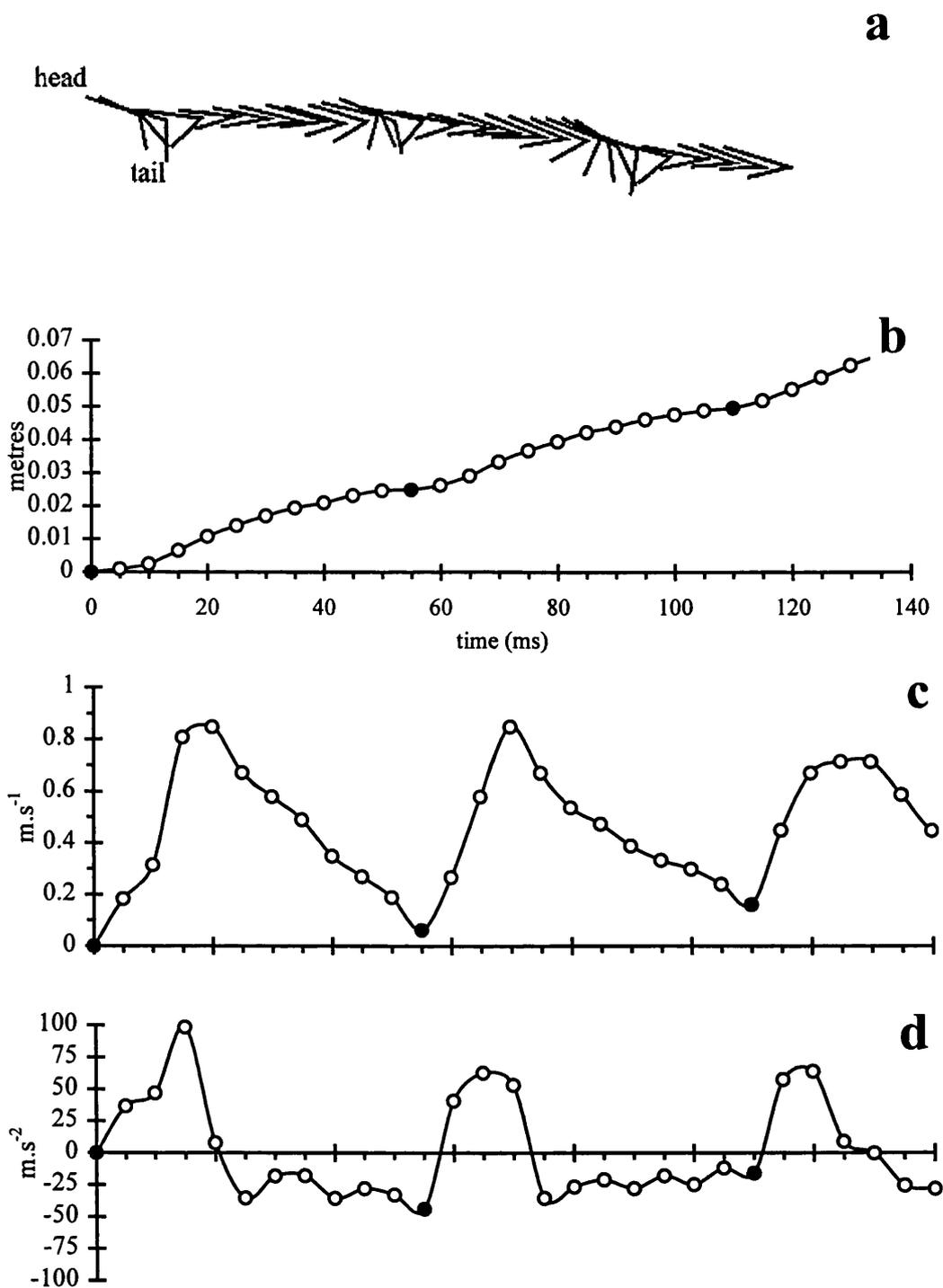


Fig. 2.7 Changes in kinematics parameters during tail flips

Changes in kinematic parameters of the shrimp's centre of mass during the first 3 tail flips of an escape by an 11 mm shrimp. (a) Stick diagram of shrimp whilst tail flipping. Interval between successive images = 5 ms. (b) Cumulative distance of the centre of mass. (c) Velocity of centre of mass. (d) Acceleration of centre of mass. Filled circles indicate the beginning of the flexion phase of each tail flip.

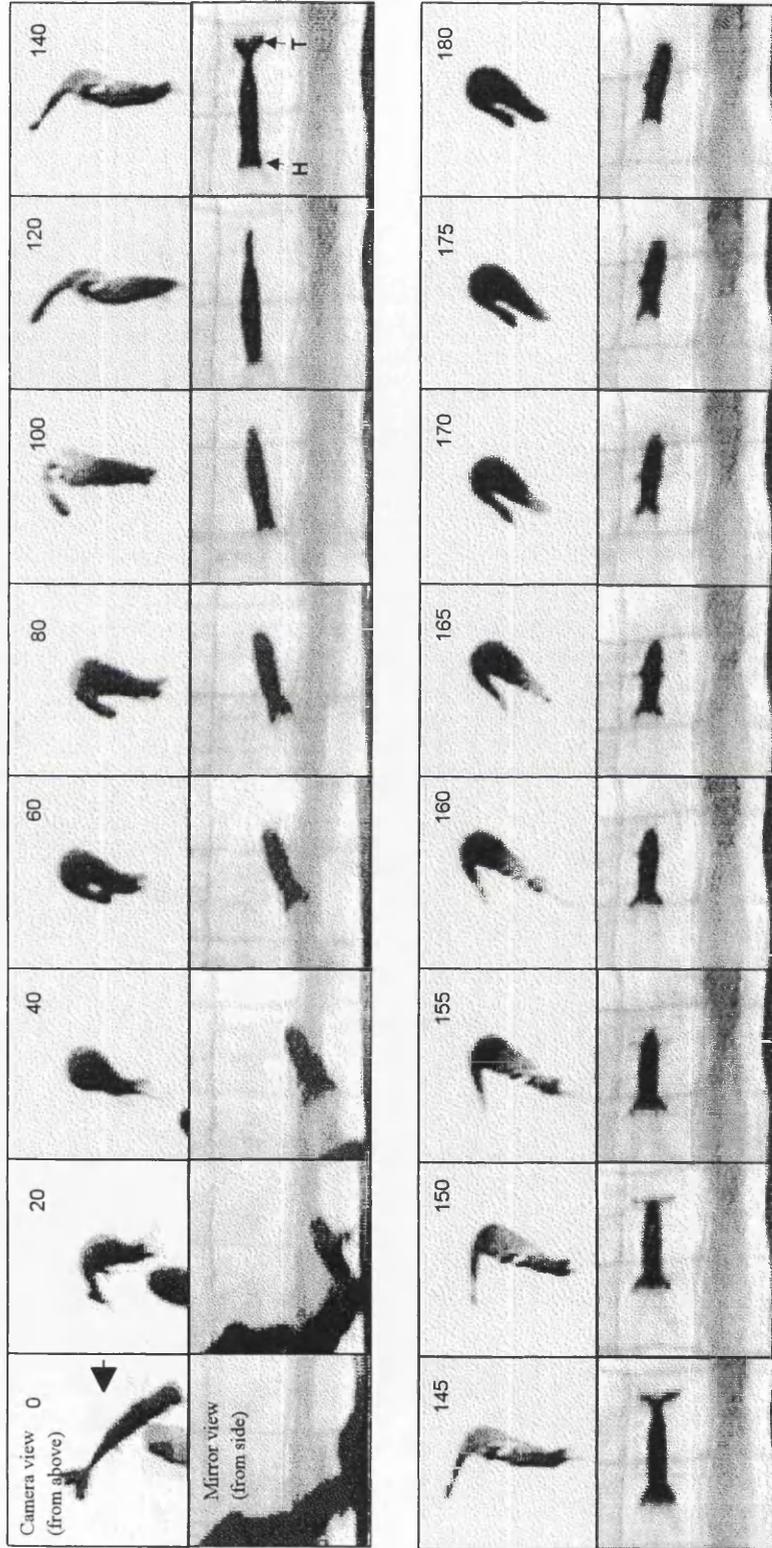


Fig. 2.8 High speed video sequence showing expansion and retraction of the head fan during tail flips

High speed video images of the first two tail flips of an escape swimming bout by *Crangon crangon*. Numbers refer to time (ms) elapsed since the first pair of images. Top images in each row: camera view of the shrimp, looking vertically downwards. Bottom images in each row: simultaneous view of the shrimp looking horizontally (from direction of arrow) in a mirror placed at 45° to the camera. Within the first 20 ms the shrimp started to rotate onto its side, causing it to swim horizontally. Expansion of the head (H) and tail (T) fan can be seen at the beginning of the second tail flip (140 ms), followed by retraction prior to the end of the flexion phase (180 ms). (*N.B.* time between each image changes from every 20 ms [every 4th video frame] to 5 ms [every frame] at the beginning of the second tail flip to show detail of head and tail fan movement).

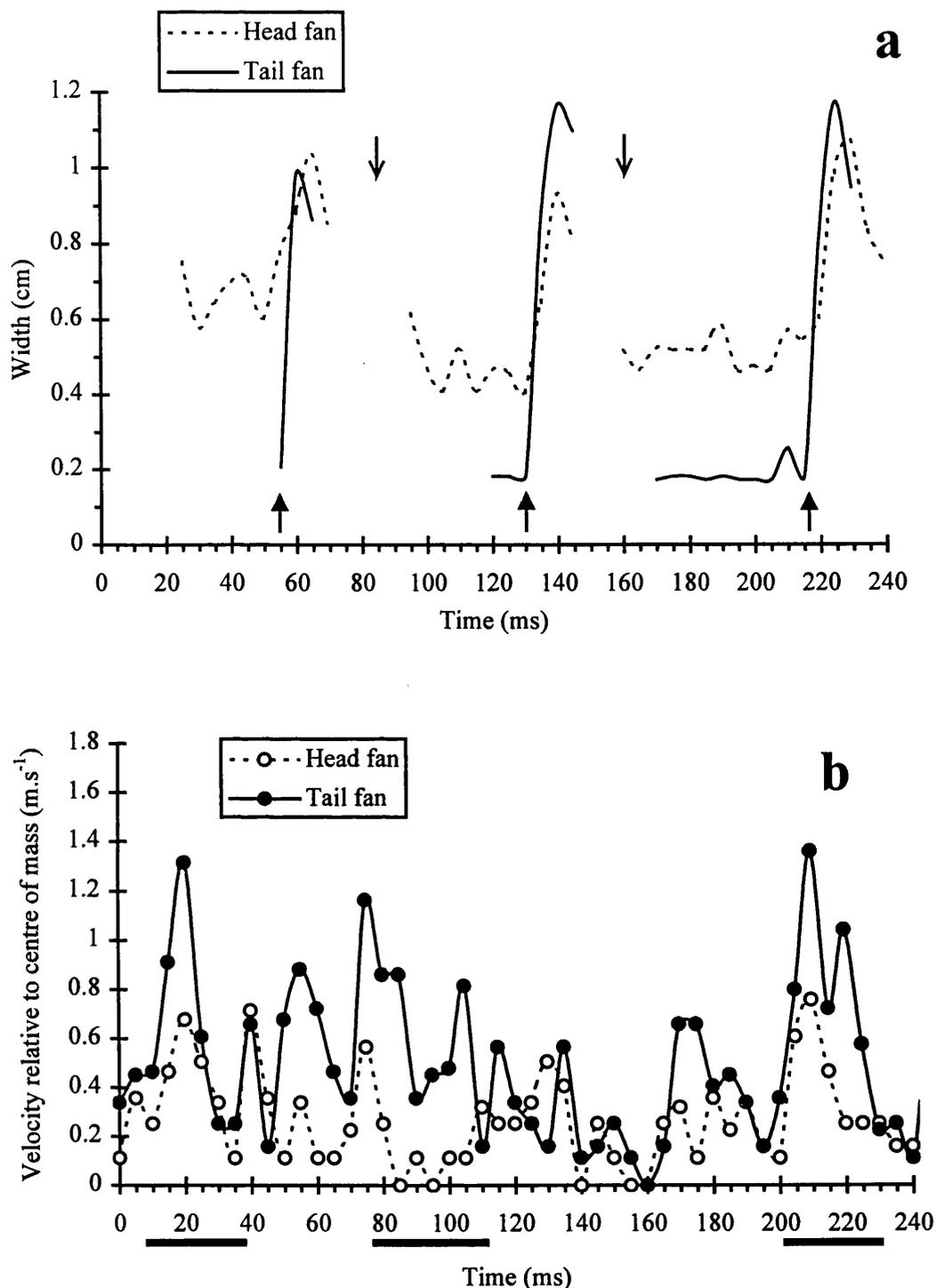


Fig. 2.9 Movements of head fan and tail fan in *Crangon crangon* during tail flips

(a) Width of head fan and tail fan (dorsal aspect) during the second, third and fourth tail flip of an escape swimming bout by a 31 mm shrimp. The start of each flexion phase is marked by solid arrow head, and each re-extension phase by an open arrow head. Some measurements have been omitted due to obscuring of the fan(s) by the cephalothorax or abdomen. (b) Velocity of the head and tail fan with respect to the shrimp's centre of mass during a multiple tail flip swimming bout by a 33 mm shrimp [*n.b.* not from the same sequence as in (a)]. Bars below the x-axis indicate the flexion phase of each tail flip.

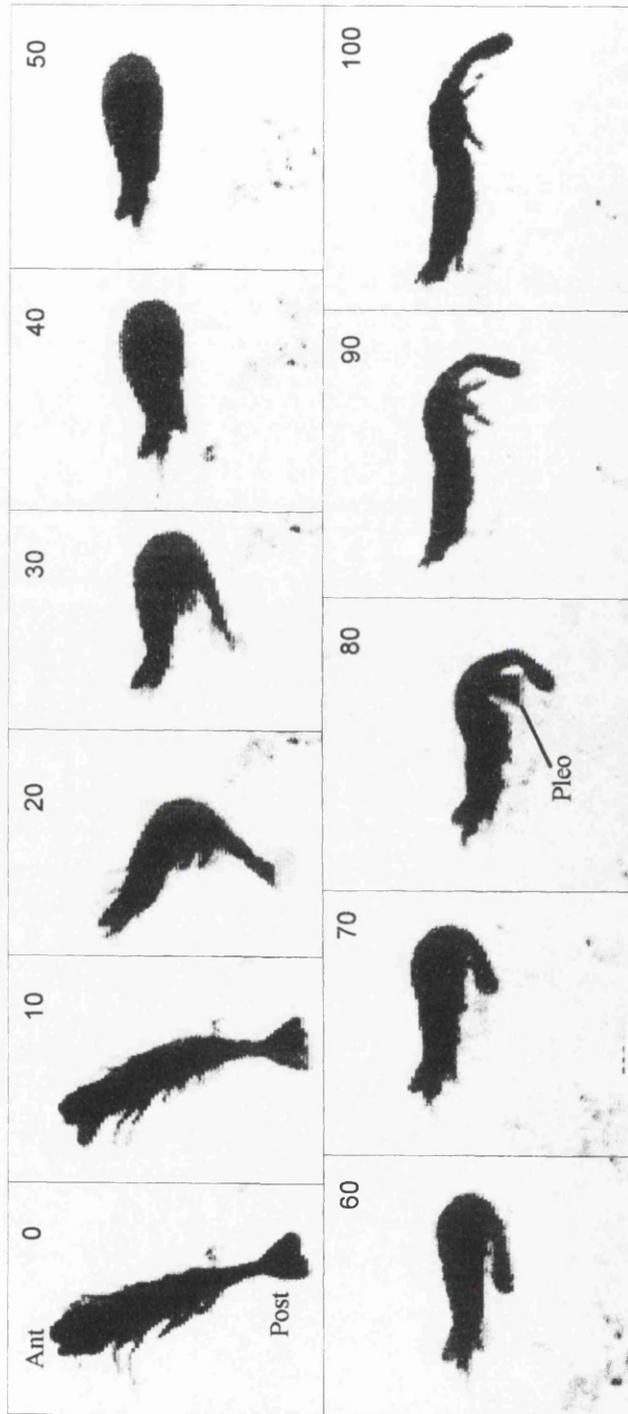


Fig. 2.10 High speed video images showing a laterally directed first tail flip during an escape response by *Crangon crangon*

High speed video images showing a laterally directed first tail flip during an escape response by *C. crangon* (every second video frame is shown; the numbers refer to the time elapsed in milliseconds). The shrimp is viewed from directly above the experimental arena (camera view), which at time 0, shows the dorsal aspect of the shrimp whilst it is stationary on the substratum (Ant = shrimp's anterior, Post = shrimp's posterior). By 20 ms, the shrimp has rotated onto its side, and is viewed from its lateral aspect for the rest of the sequence. During the latter stages of the re-extension phase (80–100 ms), movement of the pleopods (Pleo) can be seen, but this was not observed in all recordings of first tail flips, or during subsequent tail flips (compare with **Figs. 2.6 & 2.8**).

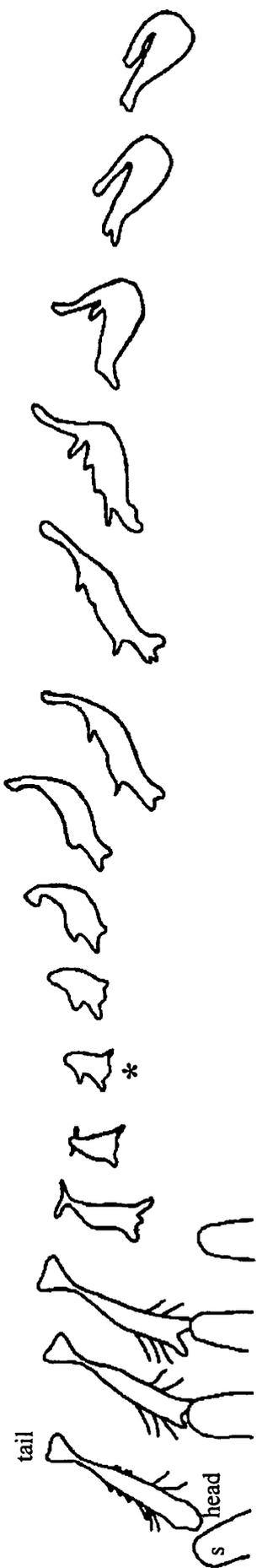


Fig. 2.11 Tracing from a high speed video recording of a vertically directed 1st tail flip

Camera view (looking vertically downwards) of an escape by *Crangon crangon* (total length = 44 mm) in response to a rostrally applied stimulus (s). The first tail flip is directed vertically, but the shrimp rolls onto its side during the re-extension phase (start of re-extension marked by *) so that the second flexion is directed horizontally, with the shrimp swimming on its side. Time between each image = 10 ms (i.e. every second frame). For clarity, each image has been displaced to the right of the previous one, and therefore displacement from the left to the right of the page is not representative of true distances.

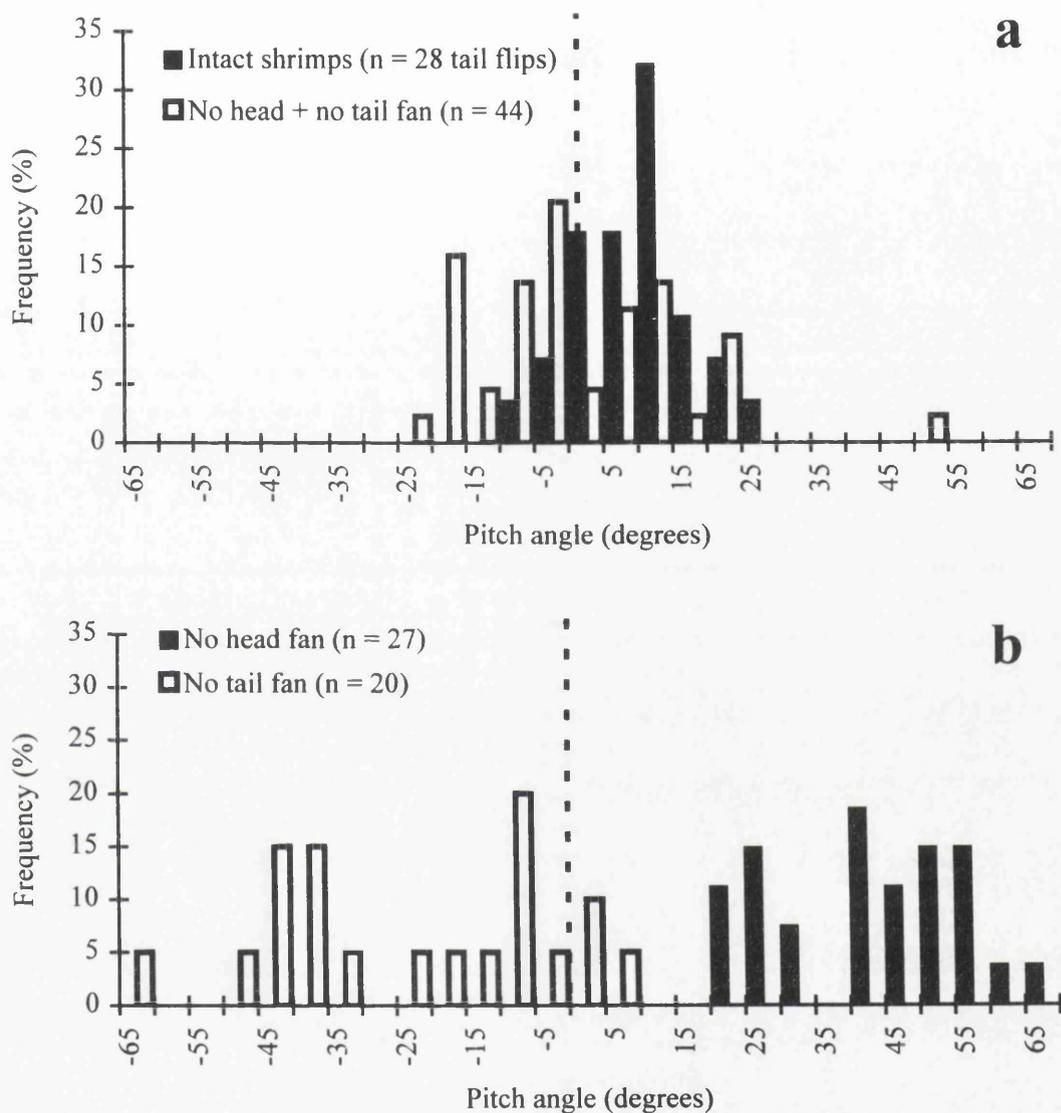


Fig. 2.12 Pitch angles of tail flips for intact *Crangon crangon*, and *C. crangon* with the head fan and/or tail fan removed

Rotation in the pitch plane between successive tail flips for (a) intact shrimps, and shrimps in which both the head fan and tail fan were removed, and (b) shrimps with no head fan, and shrimps with no tail fan. Dashed line represents zero pitch (i.e. no change of direction). All experimental groups were significantly different from one another (Kruskal-Wallis, $p < 0.001$, followed by multiple comparison tests).

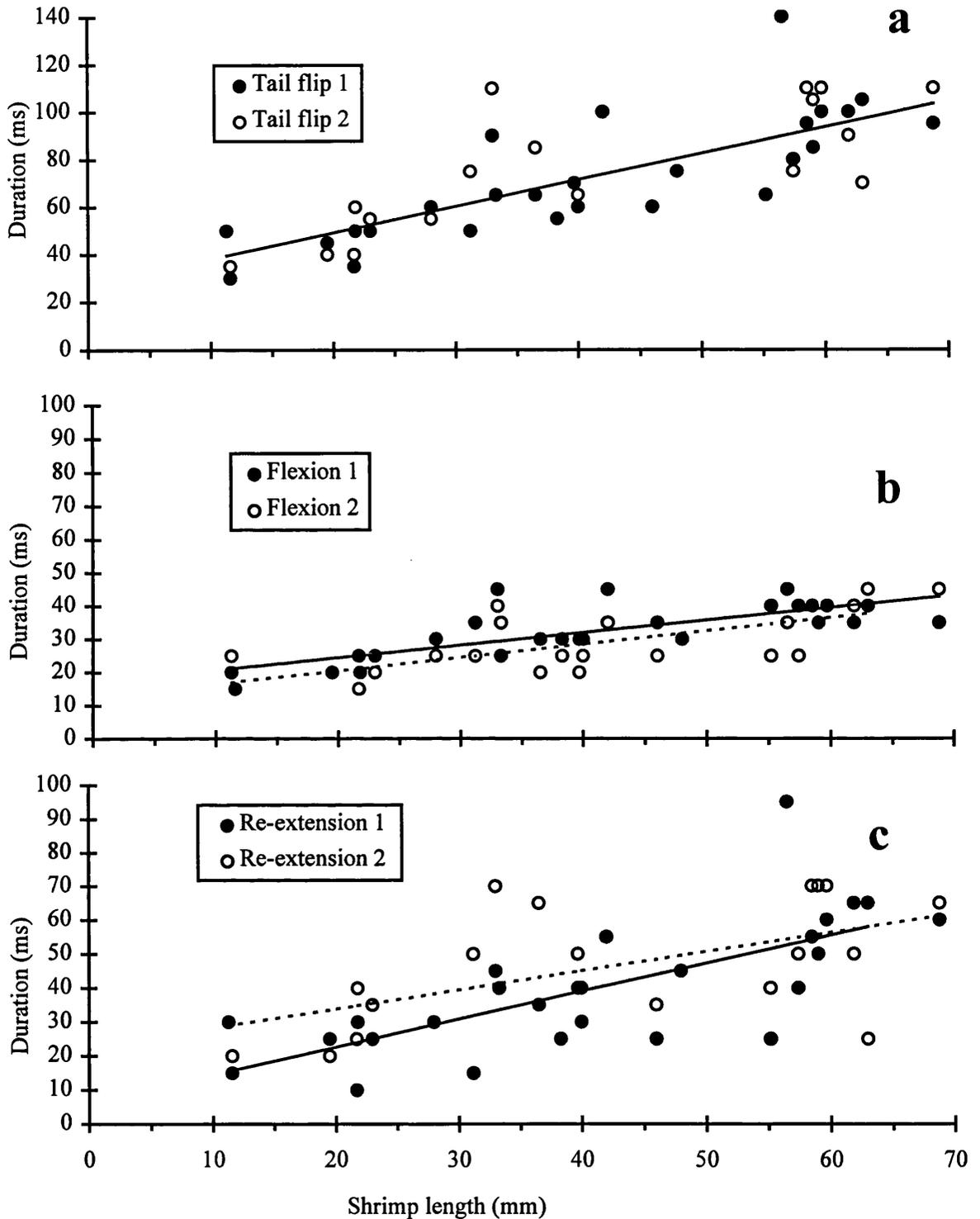


Fig. 2.13 Duration of tail flip phases against total length of *Crangon crangon*

Duration of tail flip phases against shrimp length for the first and second tail flips of an escape swimming bout. (a) Total tail flip duration (flexion + re-extension phase), with regression line fitted to pooled data. (b) Duration of flexion phases, with separately fitted regression lines. (c) Duration of re-extension phase, with separately fitted regression lines. In (b) and (c), solid line = flexion/re-extension 1; dash line = flexion/re-extension 2. Where separate regression lines have been fitted, they do not differ in slope or elevation, although the paired data differ significantly from one another (paired t-tests, $n = 25$, $p = 0.019$ and $n = 20$, $p = 0.025$ for flexion and re-extension respectively).

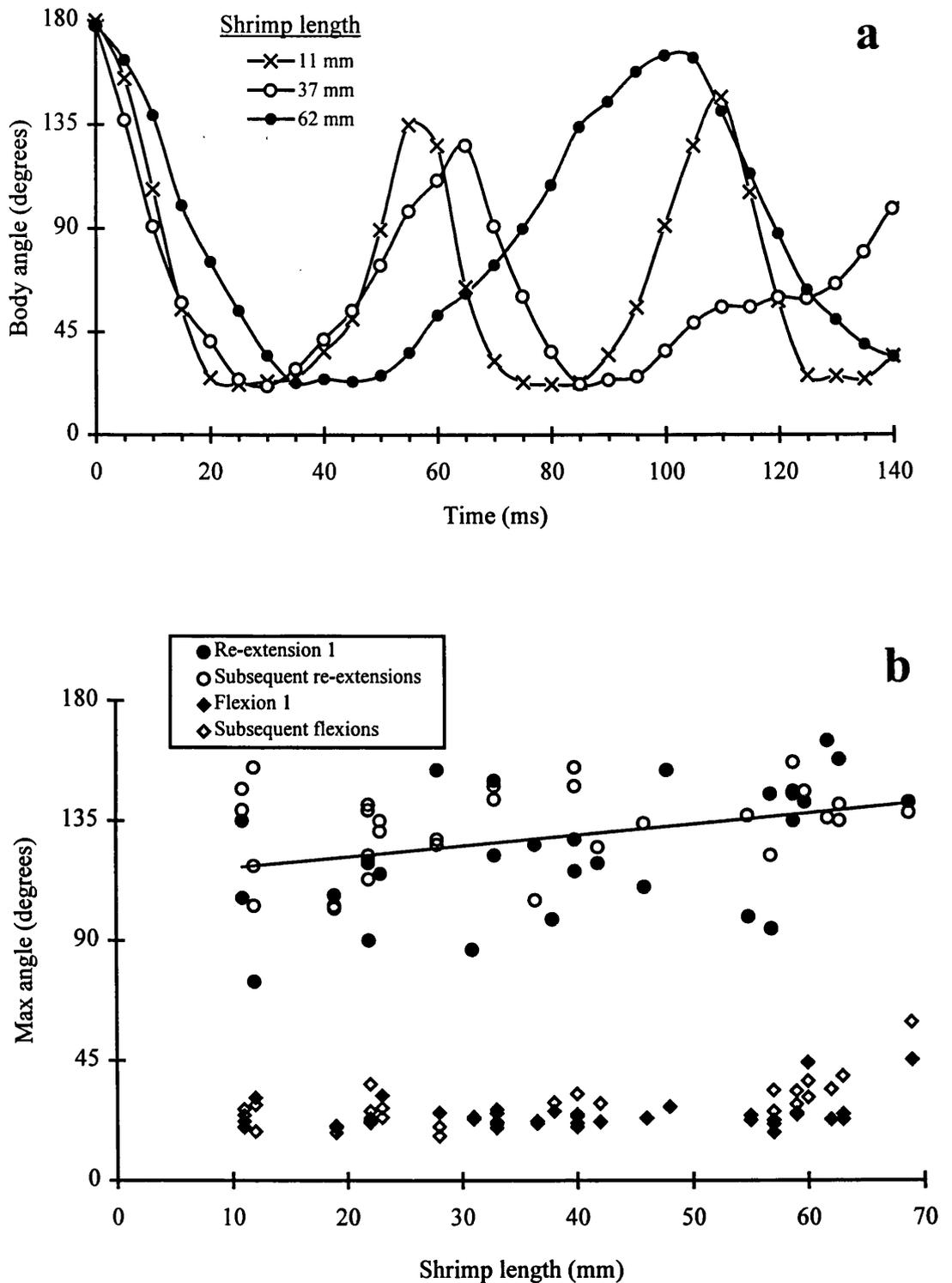


Fig. 2.14 Body angles (about the point of flexion) of *Crangon crangon* whilst tail flipping

(a) Typical examples of changes in body angle during tail flip swimming by *C. crangon* of 3 lengths. (b) Minimum and maximum body angles attained at the end of flexion and re-extension phases respectively of tail flip 1, and of subsequent tail flips (up to 2nd, 3rd or 4th). The minimum body angle attained at the end of flexion does not vary with shrimp length (mean = 25.0°), whereas the maximum body angle attained at the end of re-extension does marginally (regression ANOVA, $p = 0.004$, $r^2 = 0.12$).

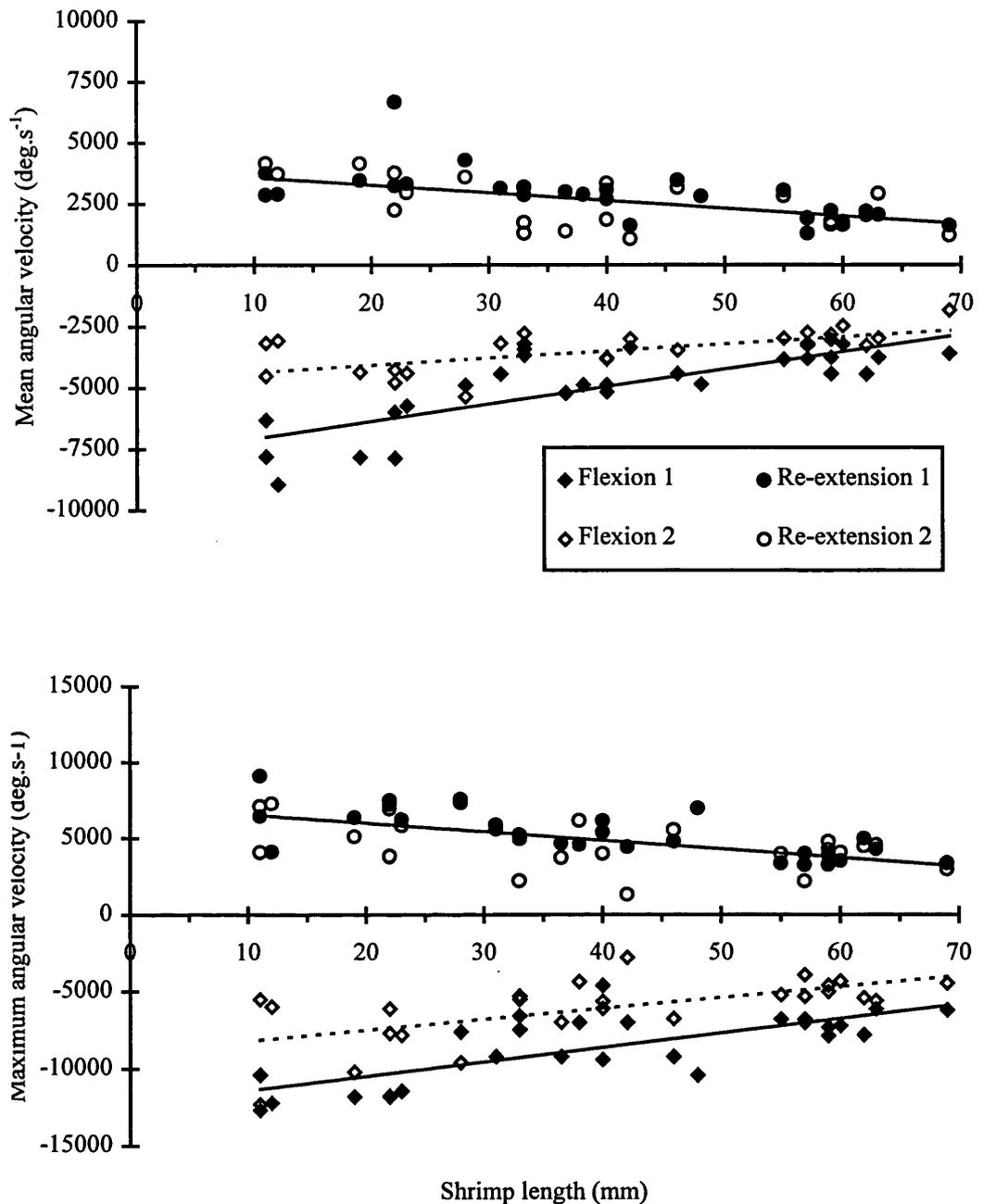


Fig. 2.15 Angular velocity of body angle during tail flips by *Crangon crangon*

(a) Mean angular velocities (deg.s⁻¹) during the flexion (negative values) and re-extension phases (positive values) of the first 2 tail flips in each escape swimming bout. For individual shrimps, the mean rate of flexion was significantly greater in tail flip 1 than tail flip 2 (paired t-test, $n = 25$, $p < 0.001$), whilst mean extension rates were not significantly different between tail flip 1 and 2 (paired t-test, $n = 22$, $p = 0.07$). (b) Maximum angular velocities attained during flexion and re-extension phases of tail flips 1 and 2. For individual shrimps, the maximum flexion rate during tail flip 1 was significantly greater than during tail flip 2 (paired t-test, $p < 0.001$), whilst maximum extension rates were not significantly different between tail flip 1 and 2 (paired t-test, $p = 0.12$). Fitted regression lines: lower solid line on each graph represents flexion 1; dashed line represents flexion 2; upper solid line on each graph represents pooled re-extension rates from tail flip 1 and 2. Legend applies to both (a) and (b).

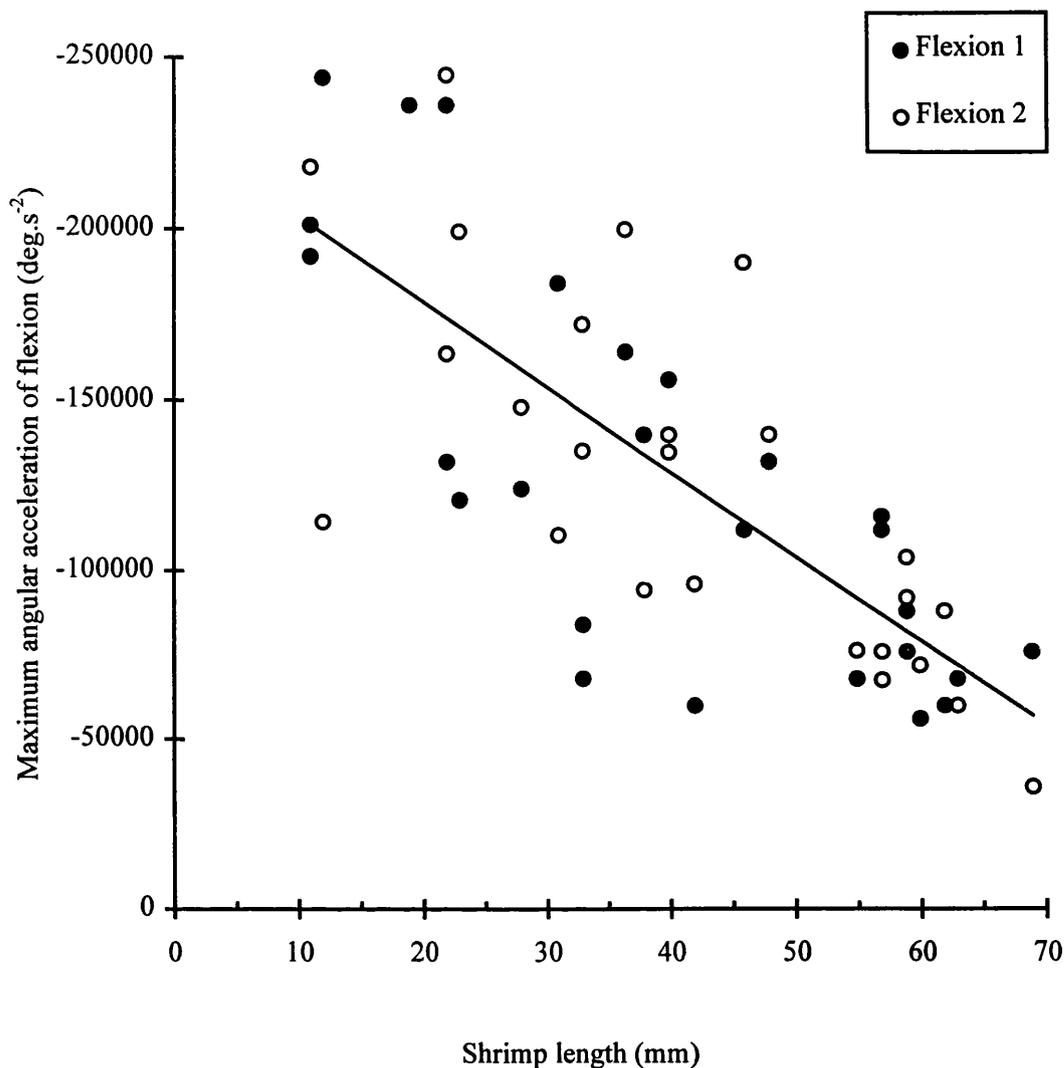


Fig. 2.16 Maximum angular acceleration of the body angle during the flexion phase of tail flips in *Crangon crangon* of different lengths

Effect of shrimp length upon maximum angular acceleration attained during the flexion phases of the first and second tail flips of an escape response. There was no significant difference between the values attained during flexion 1 and flexion 2 (paired t-test, $p = 0.63$). The linear regression is fitted to the pooled data ($r^2 = 0.57$).

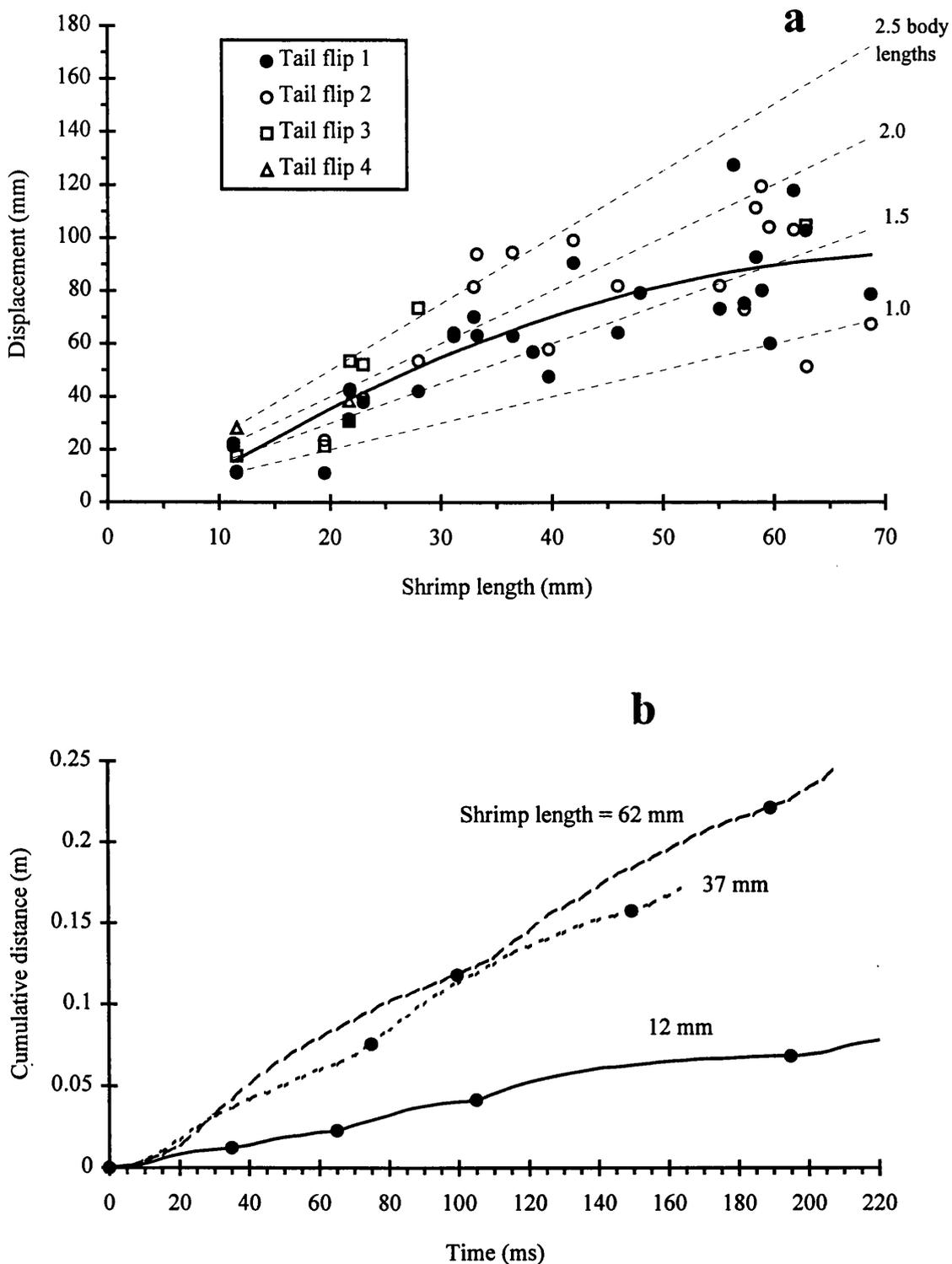


Fig. 2.17 Displacement of the centre of mass of *Crangon crangon* during tail flip escapes

(a) Horizontal displacement of the shrimp's centre of mass during individual tail flips (up to the 4th) of an escape response. The quadratic function is fitted to the pooled data (ANOVA, $n = 59$, $p < 0.001$, $r^2 = 0.60$). Dashed lines provide a comparative scale for the conversion of displacements into body length equivalents. **(b)** Typical examples, for shrimps of 3 lengths (12 mm, 37 mm and 62 mm), showing the cumulative displacement of the shrimp's centre of mass during the first 160-220 ms of an escape. Filled circles in (b) indicated the start of each flexion phase.

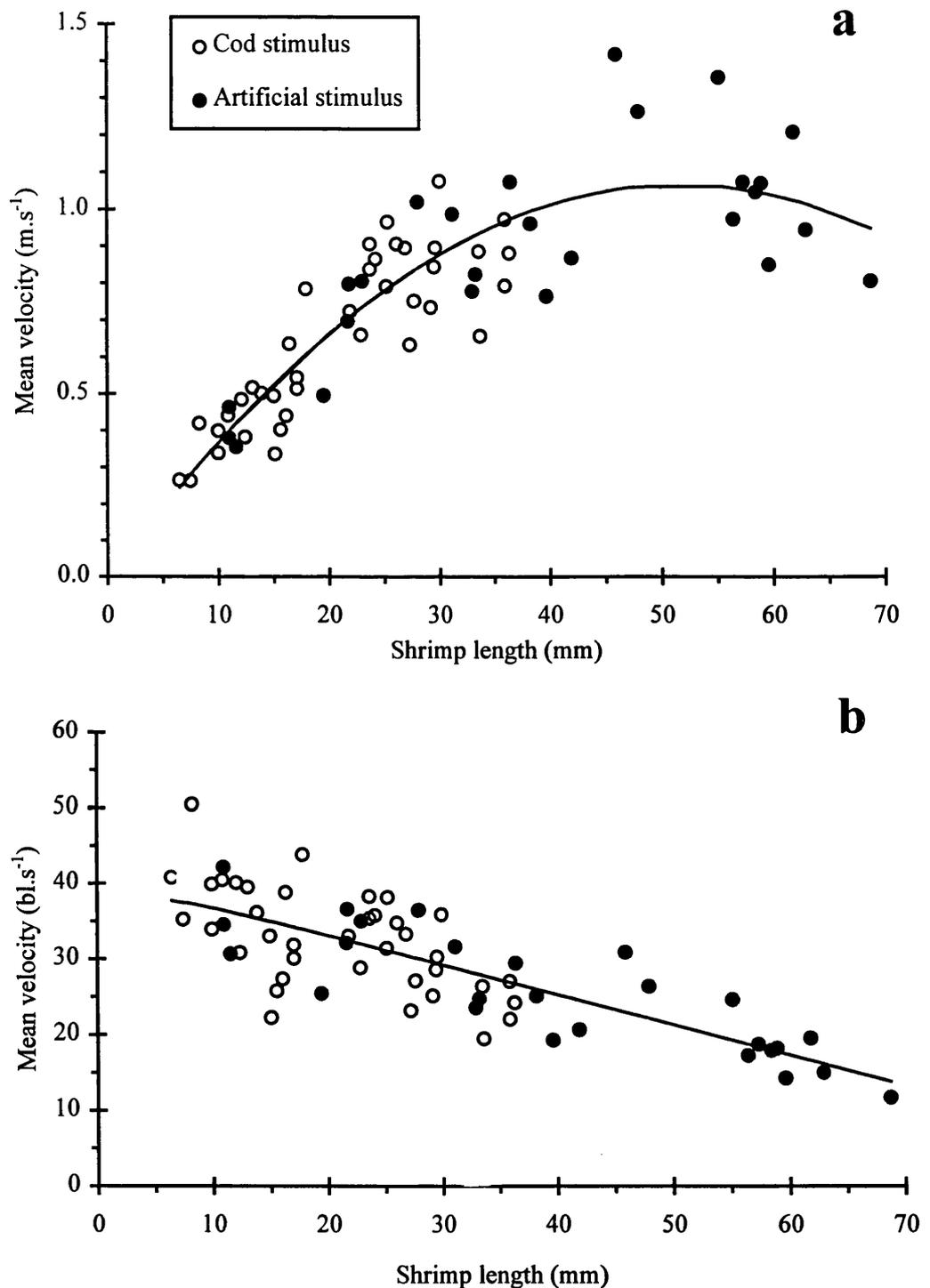


Fig. 2.18 Relationship between shrimp length and mean tail flip swimming velocity

Relationship between the length of *Crangon crangon* and the mean tail flip swimming velocity in response to attacks by a cod stimulus (recorded using conventional video) or an artificial stimulus (recorded using high speed video). (a) Mean velocity, measured in m.s⁻¹, with fitted quadratic function ($r^2 = 0.77$). The shrimp length with the greatest mean velocity, predicted from the fitted line, is 52 mm. (b) Mean velocity, measured in body lengths per second. The fitted curve is derived from the quadratic function used in (a). The figure legend applies to both (a) and (b).

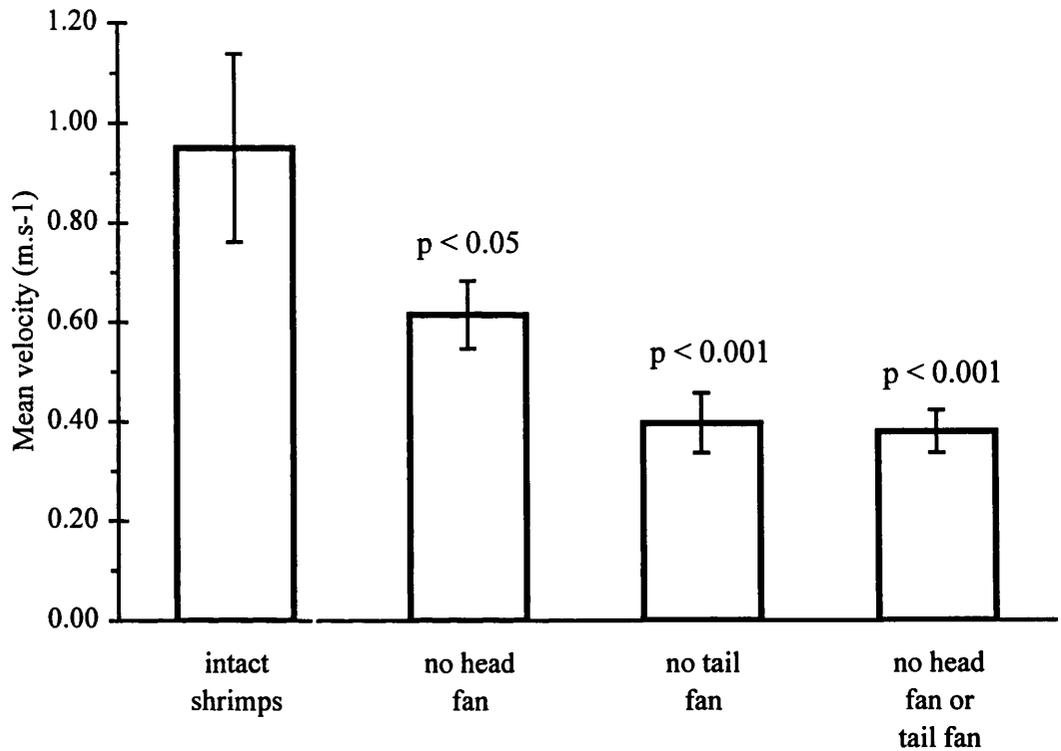


Fig. 2.19 Mean tail flip swimming velocity of intact *Crangon crangon*, and *C. crangon* with no head fan and/or no tail fan

Mean tail flip swimming velocities (+/- standard deviation) of intact *C. crangon* (n = 6 shrimps), and of *C. crangon* with no head fan (n = 3), no tail fan (n = 3), or neither fan (n = 3). Experimental groups were significantly different from one another (ANOVA, p < 0.001). p values on graph are derived from Tukey pairwise comparisons with the intact shrimps.

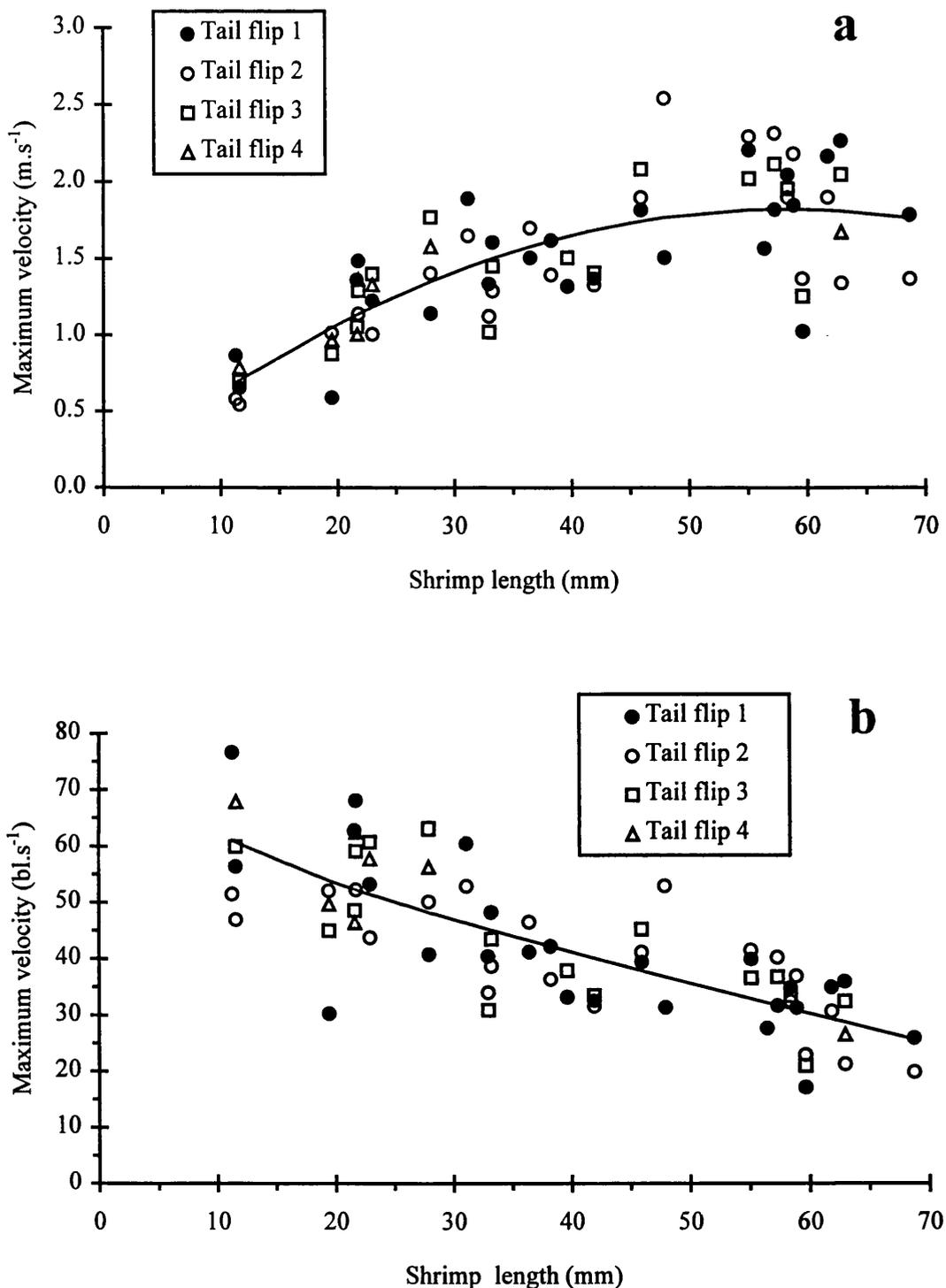


Fig. 2.20 Relationship between shrimp length and maximum tail flip velocity

Relationship between shrimp length and the maximum velocity attained during tail flips 1-4 of an escape swimming bout. (a) Maximum velocity (m.s^{-1}), with fitted quadratic function for the pooled data ($r^2 = 0.58$). The shrimp length with the greatest maximum velocity, predicted from the fitted line, is 58 mm (b) Maximum velocity in body lengths per second. The fitted line is derived from the quadratic regression curve in (a).

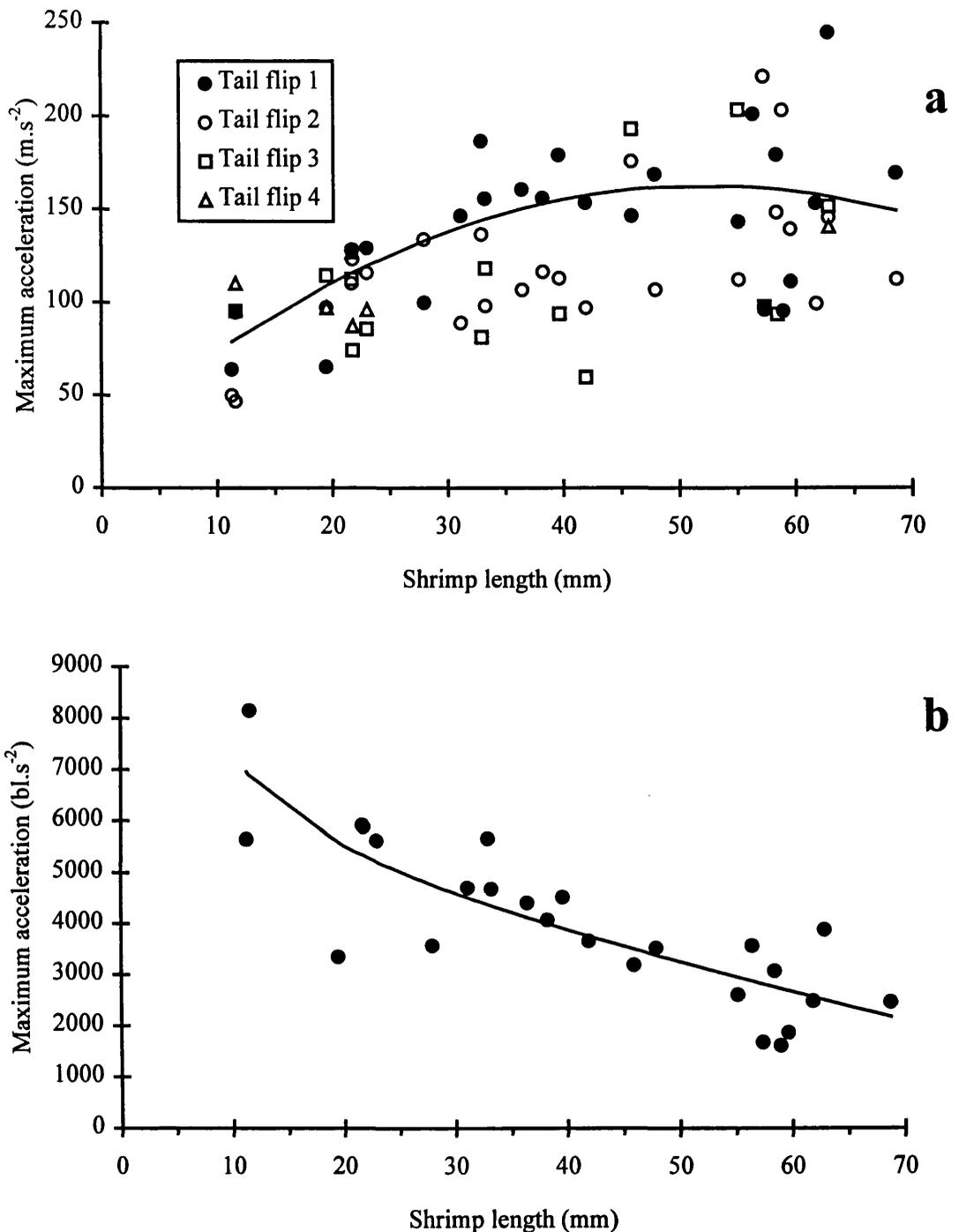


Fig. 2.21 Relationship between shrimp length and maximum tail flip acceleration

Relationship between shrimp length and the maximum acceleration attained during tail flips. (a) Acceleration (m.s^{-2}) of tail flips 1-4 of an escape swimming bout. Acceleration during tail flip 1 was significantly greater than during tail flip 2 (paired t-test, $p = 0.05$). The regression line is derived from a quadratic function, and is fitted only to the data for tail flip 1 ($r^2 = 0.29$). The shrimp length with the greatest maximum acceleration during tail flip 1, predicted from the fitted line, is 52 mm. (b) Acceleration in body lengths per second for tail flip 1 of an escape swimming bout. The fitted line is derived from the quadratic regression curve in (a).

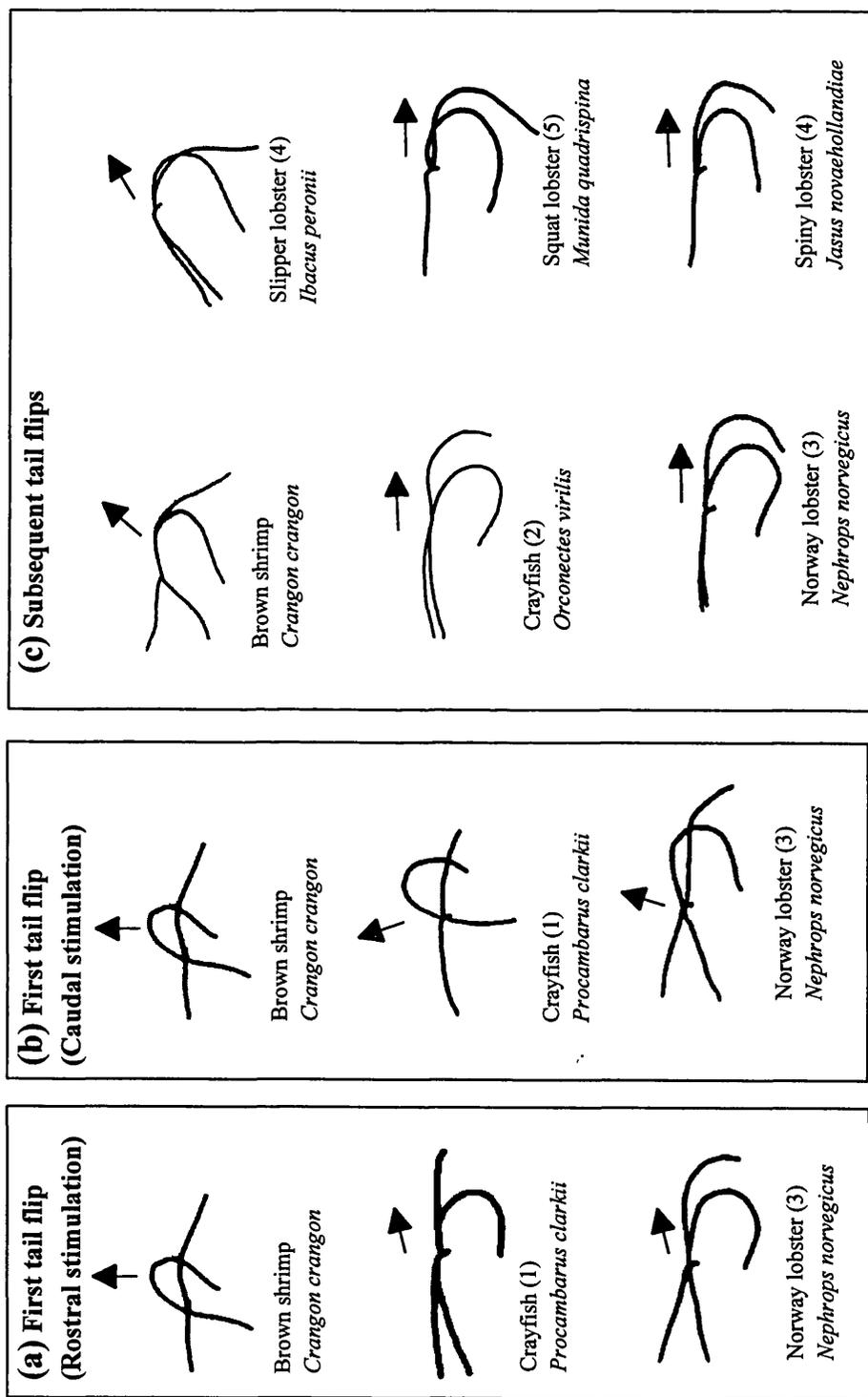


Fig. 2.22 Comparison of tail flip mechanisms in different types of decapod crustaceans

Comparison of typical tail flip mechanisms in different types of crustaceans during (a) the first tail flip of an escape in response to a rostral stimulus, (b) the first tail flip of an escape in response to a caudal stimulus, and (c) during subsequent tail flips. Figures show superimposed tracings of the dorsal surface of the animal's body (viewed sagittally) at the beginning of the flexion phase, and at the end of the flexion phase. The tips of the cephalothorax (to the left) and abdomen (to the right) which are upper-most in each figure represent the positions at the beginning of flexion. In each figure, the thoraco-abdominal joint has been superimposed on the same locus. All animals are swimming in an upright body posture, except in (c), in which *C. crangon* is swimming on its side. Arrows indicate the approximate direction of travel. Note in particular that, in *C. crangon*, both the cephalothorax and abdomen are moved through the water in all types of tail flips, thereby enabling both the head fan and the tail fan to generate thrust. Also, the first tail flip of *C. crangon* in response to a rostral stimulus is similar to the first tail flip in response to a caudal stimulus (both of these examples are for short latency, vertically directed flexions rather than laterally directed flexions). Sources of data: (1) Krasne & Wine, 1972; (2) Webb, 1979; (3) Newland, 1985; (4) Jacklyn & Ritz, 1986; (5) Wilson & Paul, 1987.

Chapter 3

Escape trajectories of *Crangon crangon* from natural and artificial predators

3.1

INTRODUCTION

The escape response of *Crangon crangon* from an attack by a predator has the objective of minimising the probability of the shrimp being caught. The initial stage of the escape ensures that the shrimp evades the predator's first strike; subsequent stages then minimise the probability of the predator pursuing the shrimp, and of capturing it on successive strikes. This is achieved, in part, by the high acceleration and velocity of tail flip swimming (sections 2.3.6). However, the ability to escape rapidly is, in itself, not sufficient to ensure evasion from a predatory attack; precise timing and orientation with respect to the predator are also essential for an escape to be successful (see sections 1.5 & 1.6).

After evading the initial predatory strike, further stages of the escape (to minimise the probability of the predator pursuing the animal, and of capturing it on subsequent strikes) may be achieved by a variety of means. A common strategy for prey is to retreat into a refuge, such as a crevice or burrow, where the predator can no longer reach it (section 1.6). However, when no immediate refuge is available, the prey may employ a different strategy. Weihs & Webb (1984) investigated the theoretical implications of this situation, and suggested that the optimal evasion trajectories for the prey are those which cause an attack to be aborted by extending the duration of an interaction (thereby maximising the energetic costs to the predator). Their evasion model predicts optimal trajectories which always lie within 21° of the heading directly away from the predator, regardless of their relative velocity. This prediction is only true until the predator approaches to a distance where it is close enough to launch another strike. The final 'end game' requires the prey to perform sudden turning manoeuvres, and the outcome of the encounter depends upon the timing of turn(s), the relative velocity of each animal, and the reaction time of the predator to the prey's movements (Howland, 1974; Webb, 1976). The outcome will also depend upon situation-specific factors such as the mouth size and suction power created by the feeding strike of a fish predator.

The predictions from the evasion model of Weihs & Webb (1984) are, to a certain extent, supported by empirical data derived from natural predator-prey encounters. Prey usually escape away from the direction of attack: e.g. cockroaches escaping from the strike of a toad's tongue (Camhi & Tom, 1978; Comer & Dowd, 1987); fathead minnows escaping from pike (Webb & Skadsen, 1980; Webb, 1982); crayfish (Reichert & Wine, 1983) and Norway lobsters (Newland & Chapman, 1989) escaping from mechanical and visual stimuli;

and soldier crabs escaping from approaching objects (when they have no available burrow to escape into) (Nalbach, 1990a).

A possible confounding factor in escaping along a trajectory precisely on a heading away from the predator is that this may inhibit the prey's ability to track the position of the predator. For instance, such a trajectory may exclude the predator from the prey's visual field, and so a compromise may occur in which the prey escapes at an angle so as to keep the predator just within its view. This mechanism has been postulated for the escape response of the blood sucking bug *Triatoma infestans* (Lazzari & Varjú, 1990), for gadoid fish escaping from trawl nets (Wardle, 1993), and also explains one of the two preferred escape trajectories of the angelfish *Pterophyllum eimekei* (Domenici & Blake, 1993).

The rate at which the prey is able to perform a turn away from a predator may also prevent it from escaping directly away. If the predator attacks from an angle which requires the prey to perform a very large, and therefore time-consuming turn, the time spent in executing the turn may increase the prey's vulnerability to the predator. Consequently, the final escape may be a compromise between the optimal trajectory and the maximum time available for turning.

Escape trajectories which deviate from the optimal evasion trajectories predicted by Weihs & Webb (1984) may also be expected in situations where the main premise of the model (that the optimum strategy is for the prey to prolong the encounter) represents only one of several possible solutions to reducing the probability of a chase and subsequent strikes occurring. Prolonging the encounter is likely to be most effective in situations where the predator becomes exhausted more rapidly than the prey during a chase (e.g. a cheetah chasing a gazelle; Walther, 1969). In the opposite case, where the prey becomes exhausted more rapidly than the predator (a situation which may be true for *Crangon crangon*) this strategy will be less beneficial, although it will still have the effect of increasing the energetic cost to the predator. However, it will also maximise the energetic costs to the prey, which may make it more vulnerable to a subsequent predatory attack by other predators, especially if the latter are in a rested physiological state.

Another confounding factor to this strategy is that many predator species have the ability to learn. Therefore, if they encounter the same type of prey on a regular basis, or if all types of prey employ the same escape tactic, they may learn to predict escape trajectories. The predator will then be able to compensate its strike and chase behaviour in advance of the prey performing an evasive manoeuvre. This effectively reduces the response latency of the

predator, which increases the probability of prey capture (Webb, 1984). Therefore, although a particular optimal escape trajectory may offer the maximum probability of evasion if predators are always in a naïve state, this may not be the case of experienced predators. Unpredictability is one strategy which the prey may incorporate into its repertoire to counteract the effect of predator learning (Chance & Russell, 1959; Driver & Humphries, 1988; section 1.6).

Although, in general, animals tend to escape in a direction away from a predator (in agreement with the model of Weihs & Webb, 1984), closer examination suggests that variability in escape trajectories may be quite common. For instance, Domenici & Blake (1993) have shown that angelfish (*P. eimekei*), cockroaches (*Periplaneta americana*) and soldier crabs (*Mictyris longicarpus*) have two or more preferred escape trajectories from predators. Consequently, the escape trajectory of a prey from a predator may be a compromise between a variety of factors, especially when there is no immediate refuge for it to retreat into.

The natural habitat of *Crangon crangon* is open, sandy/muddy substrates, and therefore, refuge from predators on or within the sediment is equally available in all horizontal escape directions. In this investigation, the escape trajectories of *C. crangon* when attacked from a variety of directions have been analysed during the first tail flip, and subsequent tail flips, of multiple tail flip escape responses in order to determine the 'strategies' which shrimps employ to evade feeding strikes by predators, and to investigate how these strategies are influenced by the anatomical limitations of the shrimp's escape performance. The results are compared with escape trajectories of other animals, and allow a comparison to be made with the optimal evasion trajectories predicted by the model of Weihs & Webb (1984).

3.2

MATERIALS & METHODS

3.2.1 Animals

Brown shrimps (*Crangon crangon*) were caught in a hand-held trawl net at a depth of less than 1 m in Dunstaffnage Bay on the west coast of Scotland, and transferred to holding tanks (100 x 50 x 30 cm) with 1-2 cm sand on the bottom. The shrimps were fed *ad lib.* every other day on chopped mussels and/or frozen mysids collected from Dunstaffnage Bay.

Juvenile cod (*Gadus morhua*) were caught at night time in the same location with a beach seine net, and immediately transferred to circular holding tanks (100 cm diameter, 70 cm water depth). The cod were fed daily, either on frozen mysids, or a mixture of live mysids and *Crangon crangon*. Both holding tanks had a constantly renewing sea water supply

maintained at approximately 13°C and aerated with an air stone. Animals were kept for at least 2 weeks before being used for experiments, and for a maximum of 2 months.

3.2.2 Experimental Protocol

3.2.2.i Escapes trajectories from juvenile cod

A series of experiments was conducted in an air conditioned room (13°C) to determine the escape trajectories of *Crangon crangon* from approaching predatory cod. An experimental arena (30 cm diameter, 20 cm water depth) with a white base was illuminated from a distance of ~3 m with shaded fluorescent lighting, and filmed (50 f.s⁻¹) from directly above with conventional video equipment (Vista NCD 360 TV camera, IMP Electronics V9000 time inserter, Panasonic AG-6024 VHS recorder; see Fig. 3.1 a). Before each experiment, a single shrimp (10-40 mm rostrum-telson length) and a single cod (61-105 mm total length) were placed in the arena and kept separate from one another for 15 minutes by covering the shrimp with an upturned perforated container. Aeration was provided at this stage with an air stone. At the start of the experiment, the air stone was removed, and the container was lifted remotely with an attached string from behind a screen in order not to startle the animals (in particular, the more excitable cod). Experiments proceeded for 1 hour, or until the shrimp was eaten by the cod. A total of 30 escapes responses were analysed.

3.2.2.ii Escapes trajectories from artificial stimuli

A further series of experiments was performed using an artificial stimulus rather than cod to provoke escapes by *Crangon crangon*. Temperature, illumination and filming procedures were the same as in the cod experiments. Experiments were conducted in a 1 m diameter holding tank filled with sea water to a depth of 40 cm. A white base plate (75 cm diameter) was placed inside the tank and supported 15 cm off the bottom by a cylindrical stand. The base plate was therefore covered with water to a depth of 25 cm, and had a gap of ~12.5 cm between its edge and the side of the main holding tank (Fig. 3.1 b). For each experiment, an individual shrimp (25-40 mm rostrum-telson) was placed on the base plate, and covered with an upturned container to allow the shrimp to settle. After 15 minutes, this was removed by hand, and the shrimp was startled by rapidly accelerating a hand-held wooden rod (2 cm diameter) towards it. The mean velocity of the rod during an approach was between 1 and 2.5 m.s⁻¹. Before each strike, the tip of the rod was held under the surface of the water, about 20 cm away from the shrimp, at an elevation of between approximately 30° - 45°. Trials

in which the rod made direct contact with the shrimp or the base plate, or in which the approaching stimulus was not in direct line with the shrimp's body, were rejected. Attacks were applied in a random order from various angles which were grouped into five approximate directional categories with respect to the shrimp's longitudinal axis (head on = 0° , 45° , 90° , 135° , and tail on = 180° ; $n = 12, 17, 16, 18$ and 13 respectively). At the end of a tail flip swimming bout, the shrimps either landed back on the base plate, or swam off it and sank down to the bottom of the holding tank. In the former instance, the shrimp was stimulated again after 1-2 minutes until another tail flip swimming bout occurred. In the latter case, the experiment was terminated, and another shrimp was used. A total of 30 shrimps were used, with each performing between 1 and 4 tail flip swimming bouts.

3.2.2.iii Experiments on blinded shrimps

10 shrimps were semi-blinded by painting multiple layers of black oil paint over one eye (left or right eye allocated randomly). These shrimps were then kept in aquaria (fed every other day) for between 1 and 2 weeks before being used for experiments. Shrimps which underwent a moult during this period shed their paint layer, and were therefore rejected and replaced with new shrimps.

The same experimental apparatus and procedures were used as for the artificial stimulus experiments. Shrimps were attacked with the artificial stimulus from an angle of approximately 0° , and the frequency of escapes to ipsilateral and contralateral sides of the blinded eye were recorded.

Some shrimps were also fully blinded by painting over both eyes. These shrimps were attacked from various angles with the artificial stimulus rod in order to determine whether tail flip escape responses could be evoked in the absence of visual stimulation.

3.2.2.iv Application of an asymmetrical pre-stimulus before attacks

20 trials were conducted in which shrimps were exposed to a laterally applied 'pre-stimulus' before being attacked by the artificial stimulus rod from 0° . The pre-stimulus was applied by bringing the stimulus rod slowly towards the shrimp from its left or right side until the shrimp started to lean towards the contralateral side (Fig. 3.2). The rod was then slowly withdrawn (during which time the shrimp remained leaning towards its left or right side), and an attack from 0° was applied. The frequency of escapes to the ipsilateral and contralateral side of the pre-stimulus was recorded.

3.2.3 Analysis of escape trajectories

Escapes consisting of multiple tail flips were analysed from the video recordings. Escapes which started less than 5 cm from the side of the arena were not used. In the case of the cod experiments, escape trajectories were plotted from a TV monitor (JVC) onto an acetate sheet by recording the position of the shrimp's centre of mass (see section 2.2.2) on each frame (i.e. every 20 ms). The points were subsequently digitised on an XY plotter and then downloaded into a personal computer (PC). In the artificial stimulus experiments, video frames were captured on a PC monitor, and XY co-ordinates were digitised from these frames using a program written in Visual Basic (Dr. M.T. Burrows).

Correction was made for spherical aberration arising from recording and playback error by digitising the diameter of the circular base plate across the x and y axes, and using the length ratio between one and the other as a correction factor. Distances were calibrated against a 10 cm marker placed on the base plate of each respective experimental arena. Escapes were plotted either until the shrimp hit the side wall of the arena (cod experiments), swam off the edge of the base plate (artificial stimulus experiments), or resettled on the base plate (both sets of experiments).

Data from all escapes in response to the cod, and escapes in response to laterally applied attacks (45°, 90°, and 135°) by the artificial stimulus were reflected, where necessary, so that they are expressed as if attacks were from the right of the shrimp.

3.2.4 Reaction distances

The frame immediately prior to the one in which movement of the shrimp was first detected was designated frame zero. For each escape, the position of the snout of the cod, or the tip of the artificial stimulus, was digitised from frame zero. The distance from this point to the position of the shrimp's centre of mass on the same frame was measured as the reaction distance.

3.2.5 Convention used for escape angles and directions

Escape angles were either measured with respect to the orientation of the shrimp's body immediately before it escaped (head = 0°, tail = 180°), or with respect to the attack angle. Angles measured in a clockwise direction between 0° and 180° were assigned with positive values, and those in an anti-clockwise direction between 0° and 180° were assigned negative values. When comparisons are made between the absolute values of negative and

positive angles, the mathematical convention of moduli is used (e.g. $|90^\circ|$ describes both the angles $+90^\circ$ and -90°).

For attacks from the right of the shrimp, responses in which the shrimp escaped to its left side are termed contralateral escapes, and those to its right side are termed ipsilateral escapes.

3.2.6 Measurement of the attack angle

In the cod experiments, it was sometimes impossible to determine a narrowly-defined attack angle because turning manoeuvres performed by the cod resulted in a wide angle being presented to the shrimp. Therefore, cod escape trajectories were separated into two categories; those in response to cod approaching from the (normalised) right anterior quadrant, and those in response to approaches from the (normalised) right posterior quadrant.

For the artificial stimulus experiments, the attack angle was measured as the angle between the longitudinal axis of the shrimp (head = 0°) and the attack axis of the stimulus rod (Fig. 3.3 a). The five attack categories used (for shrimps with full vision) had mean vectors (\pm circular standard deviation) of $+2.7^\circ$ (± 2.3), $+47.6^\circ$ (± 5.4), $+90.3^\circ$ (± 6.0), $+138.9^\circ$ ($\pm 7.2^\circ$) and $+176.0^\circ$ ($\pm 3.9^\circ$) respectively (Fig. 3.4).

3.2.7 Measurement of escape angles

3.2.7.i Initial $\mathcal{E}_{\text{body}}$ angle (initial escape angle with respect to the shrimp's body orientation)

The initial (first tail flip) escape angle with respect to the shrimp's body orientation (initial $\mathcal{E}_{\text{body}}$ angle) was determined by fitting a line from the shrimp's centre of mass on frame 0 (when stationary) through its position on frames 2 and 3 (i.e. after escaping, on average, for 30 and 50 ms respectively, or within the first flexion/re-extension phase of the first tail flip - see section 2.3.4). The angle between this line and the orientation of the shrimp on frame 0 (head = 0°) was measured as the initial $\mathcal{E}_{\text{body}}$ angle (Fig 3.3 a).

3.2.7.ii Initial $\mathcal{E}_{\text{attack}}$ angle (initial escape angle with respect to the attack angle)

The initial (first tail flip) escape angle with respect to the attack angle (initial $\mathcal{E}_{\text{attack}}$) was determined in the same manner as the initial $\mathcal{E}_{\text{body}}$ angle, with the exception that angles were measured with respect to the attack angle of the stimulus rod on frame 0 (Fig. 3.3 b). Initial toward responses were defined as those in which the initial $\mathcal{E}_{\text{attack}}$ angle was

less than $|90^\circ|$, and **initial away responses** as those in which the initial $\mathcal{E}_{\text{attack}}$ angle was greater than $|90^\circ|$.

3.2.7.iii Final $\mathcal{E}_{\text{attack}}$ (final escape angle with respect to the attack angle)

After the first one or two tail flips of an escape swimming sequence, the shrimp escaped along an approximately linear path. A line was fitted to this final escape trajectory, and the final escape angle with respect to the attack angle (**final $\mathcal{E}_{\text{attack}}$**) was measured as the angle subtended between the fitted line and the attack angle of the rod on frame 0 (**Fig. 3.3 c**). **Final toward responses** were defined as those in which final $\mathcal{E}_{\text{attack}}$ angle $< |90^\circ|$, and **final away responses** as those in which final $\mathcal{E}_{\text{attack}}$ angle $> |90^\circ|$.

3.2.8 Graphical representation of escape angle frequencies

Escape angle frequencies have been represented using radial plots in which the distance from the origin is proportional to the frequency of escapes in the specified direction (10 degree bins). Where pooled data from more than one attack angle category have been plotted, equal weighting has been applied (to allow for the different number of escapes between categories) by pooling the percentage frequencies for each category. Data points for attacks from the left have been reflected so that they are depicted as if from the shrimp's right, except in **Fig. 3.13 b**. This figure presents the same data as that shown in **Fig. 3.13 a**, but data in response to attacks from the side of the shrimp (45° - 135°) have been represented twice (original data as well as reflected data) to depict escape paths in response to attacks from all directions.

3.2.9 Statistical analysis

Reaction distances were tested for normality (Ryan-Joiner test), and compared using oneway analysis of variance. Following this test, oneway multicomparisons between the reaction distances of different attack categories were performed using Tukey's pairwise comparison test (Zar, 1984; calculations performed using 'Mintab 10.51 Xtra', Minitab Inc., 1995).

The frequencies of escapes to the left and right of the shrimp were tested for randomness using a χ^2 test.

Escape angles were analysed using circular statistics (Batschelet, 1981). The circular distribution of escape angle frequencies were tested for randomness using Rayleigh's test of uniformity. Watson's F test was used for comparing the escape angles of different attack

categories. The circular statistical parameters calculated for pooled final $\mathcal{E}_{\text{attack}}$ from all the artificial stimulus attack categories (Table 3.3, column 7) were used for fitting a circular normal (von Mises) distribution to the data. The significance of the fitted curve against the pooled percentage frequency distribution of final $\mathcal{E}_{\text{attack}}$ was tested using a χ^2 test.

'Oriana for Windows' PC-based software (Kovach, 1994) was used for calculating Rayleigh's test of uniformity, Watson's F test, and circular parameters of all attack and escape angles (Tables 3.1, 3.2 and 3.3).

3.3

RESULTS

3.3.1 General description of the tail flip escape responses

Shrimps responded to approaching cod by escaping with either a single tail-flip, or a series of multiple tail-flips. This occurred either as the cod swam directly towards the shrimp (range of mean approach velocities were between 0.1-1.0 m.s⁻¹), or when an actual feeding strike occurred. During a feeding strike, the cod accelerated towards the shrimp and attempted to capture it with a rapid expansion of its buccal apparatus. Escaping shrimps did not appear to modify their trajectories as they approached the side wall of the arena, and frequently swam straight into it. Escapes in response to the artificial stimulus were similar to those in response to cod.

The first tail-flip of an escape swimming sequence was preceded by a roll of the shrimp's body about its antero-posterior axis so that the subsequent tail-flips occurred with the shrimp swimming on its side, and predominantly in the horizontal plane (see section 2.3.3.i.a). Escapes were therefore initially directed to the side of the shrimp, and during subsequent tail flips shrimps were able to steer in the horizontal plane by controlling the degree of pitch whilst tail flipping (see section 2.3.3.ii).

3.3.2 Reaction distances

Cod usually directed their attack towards the cephalothorax of the shrimp. The mean reaction distance (\pm s.d.) between the shrimp's estimated centre of mass and the leading edge of the cod on frame 0 (shrimp stationary) was similar for attacks from the postero-lateral quadrant (2.5 cm, \pm 0.89, n = 10) and attacks from the antero-lateral quadrant (2.2 cm, \pm 0.94, n = 20).

The reaction distances in response to the artificial stimulus were 5.4 cm (± 1.87 , $n = 12$), 4.7 cm (± 1.61 , $n = 17$), 6.6 cm (± 1.81 , $n = 16$), 6.3 cm (± 1.69 , $n = 18$) and 5.3 cm (± 1.57 , $n = 13$) for attack angles progressing from 0° to 180° respectively.

There were significant differences between the reaction distances of different attack categories ($p < 0.001$, oneway ANOVA). All artificial stimulus attack categories resulted in significantly greater reaction distances than cod attacks ($p < 0.001$ in all Tukey's pairwise comparisons, except cod postero-lateral quadrant attacks *versus* 45° attacks, were $p < 0.01$). The reaction distance in response to 90° attacks was also significantly greater than in response to 45° attacks ($p < 0.01$, Tukey's pairwise comparisons). No other significant differences were found.

Direct contact between the cod and the shrimp's body did not occur in any of the escapes analysed. However, it was not possible to determine whether contact with the antennae occurred.

3.3.3 Differences between escapes to contralateral and ipsilateral sides of the shrimp

3.3.3.i Escapes in response to cod attacking from the anterior quadrant

Fig. 3.5 a shows 20 superimposed plots of escapes in response to cod approaching from the (normalised) right anterior quadrant.

The roll of the shrimp onto its side during the first tail-flip meant that shrimps either escaped to their contralateral or ipsilateral side with respect to the stimulus. No escapes were observed in which the shrimp tail flipped directly backwards, forwards or upwards. Of the 20 escapes observed, 11 (55%) were to the contralateral side, whilst the remaining 9 (45%) were to the ipsilateral side. This does not differ significantly from a random distribution of escapes to either side ($p > 0.5$; χ^2 test).

Among those shrimps which escaped to the contralateral side, a further dichotomy of trajectories occurred. Five of the 11 shrimps changed direction between the first tail flip and the second by introducing positive pitch during the tail flip cycle (i.e. they steered rostrally once they were swimming on their side). Therefore these 5 shrimps escaped into the anterior contralateral quadrant (with respect to the shrimp's initial position). The remaining 6 shrimps continued swimming in the direction of their first tail flip, escaping into the posterior contralateral quadrant.

Of the 9 shrimps which escaped to the ipsilateral side, 2 steered rostrally at the end of the first tail flip, and therefore escaped into the anterior ipsilateral quadrant (i.e. the quadrant

from which the cod attacked them). The remaining 7 shrimps did not deviate from their initial path, and escaped into the posterior ipsilateral quadrant.

3.3.3.ii Escapes in response to cod attacking from the posterior quadrant

The 10 *Crangon crangon* which responded to cod attacks from the posterior quadrant all escaped to their contralateral side (significantly different from random; $p < 0.01$; χ^2 test) (Fig. 3.5 b). Five of the 10 shrimps then steered towards the anterior contralateral quadrant at the end of the first tail flip, whilst the remaining 5 escaped towards the posterior contralateral quadrant.

3.3.3.iii Escape responses of non-blinded shrimps from the artificial stimulus

Fig. 3.6 shows the superimposed escape trajectories for the five artificial stimulus categories, and Fig. 3.7 summarises the proportion of escapes to the contralateral and ipsilateral sides for all attack categories.

Attacks from both 0° and 180° (Fig. 3.6 a & e) resulted in escapes to the contralateral and ipsilateral sides in approximately equal proportions (proportion to the contralateral side = 50%, $n = 12$, and 62%, $n = 13$, for 0° and 180° respectively), and these values do not differ significantly from random ($p > 0.9$ for 0° and $p > 0.5$ for 180° ; χ^2 test). Beyond the first tail flip, attacks from 0° generally resulted in shrimps escaping into the posterior quadrants, although in 3 of the 12 escapes (25%) the shrimps steered into the anterior quadrants (i.e. towards the attack direction). Conversely, attacks from 180° produced a higher proportion of escapes (62%) into the anterior quadrants, which, in this instance, represent the quadrants away from the attack direction.

Attacks from 45° resulted in 13 of the 17 escapes (76%) being directed towards the shrimps' contralateral side, whilst the remaining 4 (24%) were to the ipsilateral side (Fig. 3.6 b). This is significantly different from a random distribution to either side ($p < 0.05$; χ^2 test), and therefore indicates a preference of the shrimp to escape towards the contralateral side of the attack direction. The majority of escapes to the contralateral side continued away from the attack direction (into the posterior contralateral quadrant), but in one instance the shrimp turned abruptly at the end of the first tail flip, and steered into the anterior contralateral quadrant.

Shrimps attacked from 90° and 135° (Fig. 3.6 c & d) showed a strong preference for escaping to the contralateral side, and indeed no escapes at all were observed towards the

ipsilateral side in either instance (significant difference from random, $p < 0.001$ for both 90° and 135° ; χ^2 test). Both attack directions produced escapes which steered shrimps into the anterior and posterior contralateral quadrants.

3.3.3.iv Escape responses of semi-blinded and fully blinded shrimps

Nineteen escapes by semi-blinded shrimps in response to artificial stimulus attacks from 0° were recorded. In 9 of these, the shrimp escaped to the contralateral side of the blinded eye. In the remaining 10 escapes, the shrimp escaped to the ipsilateral side of the blinded eye (not significantly different from random escapes to either side, $p > 0.5$; χ^2 test). Therefore, inequalities in the relative amount of visual information entering each eye is not critical in determining which direction the shrimp will escape.

Fully blinded shrimps did not, except on a very small number of occasions, respond to attacks by the artificial stimulus unless the stimulus rod made direct contact with the shrimp or the base plate of the experimental arena. The trajectories of these escapes were not analysed.

3.3.3.v Escape responses after receiving an asymmetrical pre-stimulus

Twenty escape responses were recorded in which shrimps received an asymmetrical pre-stimulus before being attacked from 0° . In 18 of these, the shrimp escaped to the contralateral side of the pre-stimulus, whilst the remaining 2 escapes were to the ipsilateral side. In contrast to 0° attacks with no pre-stimulus, these responses deviated significantly from a random distribution of escapes to either side of the shrimp ($p < 0.001$; χ^2 test) (Fig. 3.7).

3.3.4 Initial $\mathcal{E}_{\text{body}}$ angles in response to the cod and artificial stimulus

For each cod or artificial stimulus attack category, the circular frequency distribution of the initial $\mathcal{E}_{\text{body}}$ angles (ipsilateral and contralateral escapes treated separately) showed strong evidence of a preferred (non-random) escape direction ($p \leq 0.001$ or 0.01 in all instances; Rayleigh's test of uniformity) (see Table 3.1).

As the attack angle of the artificial stimulus increased from 0° to 180° , the mean vector of the initial $\mathcal{E}_{\text{body}}$ angle for contralateral escapes decreased from -129° (0° attacks) to -127° (45°), -117° (90°), -102° (135°) and -97° (180°). The initial $\mathcal{E}_{\text{body}}$ angles of contralateral escapes from 0° and 45° attacks were not significantly different from one another ($p = 0.573$, Watson's F test used for all comparisons). However, the initial $\mathcal{E}_{\text{body}}$ angles of 45° attacks were significantly different from those of all other attack categories ($p \leq 0.017$ in all cases). 90° responses also differed significantly from 135° and 180° responses ($p \leq 0.009$),

but 135° and 180° responses did not differ significantly from one another ($p = 0.448$) (Fig. 3.8).

For attack directions which produced escapes to the shrimp's ipsilateral side (i.e. attacks from the anterior quadrant for cod stimuli, and artificial stimulus attacks from 0°, 45° and 180°), the plasticity of the initial $\mathcal{E}_{\text{body}}$ angle was also apparent when the symmetry of the ipsilateral versus contralateral escape responses were compared. Attacks parallel to the shrimps' longitudinal axis (0° and 180°) produced escapes in which the moduli of the ipsilateral and contralateral initial $\mathcal{E}_{\text{body}}$ angles were not significantly different from one another; in attacks from 0°, the mean vectors of the escapes were +124° and -129° (moduli not significantly different, $p = 0.330$), and in attacks from 180°, the mean vectors were +99° and -97° respectively ($p = 0.788$). However, attacks from 45° resulted in ipsilateral escapes with a mean vector of +144°, and contralateral escapes with a mean vector of -127°; the moduli of these are significantly different from one another ($p = 0.001$). The ipsilateral escapes were therefore initially directed more posteriorly than were the contralateral escapes. This pattern was also evident in attacks by cod from the shrimps' anterior quadrant, since the moduli of the ipsilateral and contralateral mean vectors were significantly different from one another (mean vectors = +126° and -106° respectively, $p = 0.005$).

3.3.5 Escape envelopes

Although *Crangon crangon* have been observed under certain circumstances to perform escapes in which the first tail flip is vertically directed (see sections 2.3.3 & 3.4.6), all of the initial $\mathcal{E}_{\text{body}}$ angles in this study were derived from horizontally orientated tail flips. However, there was clearly a lateral bias to these escapes, since initial escape angles were never directly forwards or backwards with respect to the shrimp's initial orientation, despite the wide range of attack angles used (see Fig. 3.9 a). Therefore, there appears to be an upper and lower limit to the initial $\mathcal{E}_{\text{body}}$ angle which the shrimp is able to perform.

The absolute value of the most anteriorly directed initial $\mathcal{E}_{\text{body}}$ angle was 74.5° (in response to an attack from 180°), while the most posteriorly directed one was 156° (in response to an attack from 45°). These upper and lower limits of the initial $\mathcal{E}_{\text{body}}$ angle have been used to define the shrimp's 'escape envelopes'. Each envelope (one on either side of the shrimp) comprises an initial $\mathcal{E}_{\text{body}}$ sector from |75°| to |156°| (the white areas in Fig. 3.9 b). These represent regions to the left and right of the shrimp into which it is able to escape during

the first 40-60 ms of an escape. Angles outside these sectors represent regions into which the shrimp does not, or cannot, initially escape (the grey areas in Fig. 3.9 b).

3.3.6 Initial $\mathcal{E}_{\text{attack}}$ angles in response to the artificial stimulus

Initial escape angles can also be expressed relative to the attack angle of the artificial stimulus (initial $\mathcal{E}_{\text{attack}}$ angle). Initial away responses (i.e. initial $\mathcal{E}_{\text{attack}} > |90^\circ|$) occurred in 83% of escapes ($n = 76$; significantly different from random, $p < 0.001$, χ^2 test), and the initial toward responses (initial $\mathcal{E}_{\text{attack}} < |90^\circ|$) which were observed were predominantly in response to 180° attacks (9/13 instances). The circular frequency distribution of initial $\mathcal{E}_{\text{attack}}$ angles for each attack category was non-randomly distributed (contralateral and ipsilateral escapes treated separately; $p < 0.009$ in all circumstances, Rayleigh test of uniformity; see Table 3.2), but there were considerable differences between the attack categories (Fig. 3.10 a).

A comparison was made between the initial $\mathcal{E}_{\text{attack}}$ angles of contralateral escapes in response to different attack directions. As the attack angle increased from 0° to 180° , the mean vector of the initial $\mathcal{E}_{\text{attack}}$ angles rotated from -130° (0° attacks) to -175° (45°), $+153^\circ$ (90°), $+119^\circ$ (135°) and $+80^\circ$ (180°). These were significantly different from one another in all instances ($p < 0.001$ for all comparisons, Watson's F test). The mean vectors of the ipsilateral initial $\mathcal{E}_{\text{body}}$ angles also differed significantly from one another (mean vectors = $+121^\circ$ for 0° attacks, $+96^\circ$ for 45° attacks, and -84° for 180° attacks; $p < 0.001$ for all comparisons, Watson's F test).

3.3.7 Exclusion envelope

Although a wide spread of initial $\mathcal{E}_{\text{attack}}$ angles was measured, angles were never less than $|63^\circ|$ with respect to the attack angle. This defines an 'exclusion envelope' (the black area in Fig. 3.10 b), a sector of 126° (63° either side of the attack direction) into which the shrimp never tail flipped during the first 40-60 ms of its escape, regardless of the attack direction.

3.3.8 Final $\mathcal{E}_{\text{attack}}$ angles from the artificial stimulus

The final $\mathcal{E}_{\text{attack}}$ angles in response to the artificial stimulus were more widely distributed than the initial $\mathcal{E}_{\text{attack}}$ angles because of variable steering after the first tail flip (Fig. 3.11). Escapes were non-randomly distributed when attacks were from 45° , 90° and

135° ($p < 0.001$ in each instance, Rayleigh test of uniformity), but were randomly distributed when attacks were from 0° and 180° ($p = 0.22$ and 0.36 respectively).

For each attack category, the mean vector of the final $\mathcal{E}_{\text{attack}}$ angles was always greater than $|90^\circ|$ (i.e. escapes were normally final away responses; **Table 3.3**). 19.1% of all escapes combined (or 20.2% if a correction is made for the different number of observations between each attack category) had a final $\mathcal{E}_{\text{attack}}$ angle of less than $|90^\circ|$ (i.e. final toward responses). The frequency of these final toward responses was dependent upon the attack direction, and was more common in escapes from 0° and 180° attacks, and in ipsilateral escapes from 45° attacks (**Fig. 3.12**). Conversely, contralateral escapes in response to attacks from the side of the shrimp (i.e. 45°, 90° and 135°) resulted in fewer final toward responses. The frequency of final toward responses between these two groups were significantly different from one another (11/29 in response to attacks from 45° [ipsilateral escapes], 0° and 180°, and 3/47 in response to attacks from 45° [contralateral escapes], 90° and 135°; $p < 0.001$, χ^2 test).

The mean vector of the pooled final $\mathcal{E}_{\text{attack}}$ angles from all attack categories combined was +160.0° (circular standard deviation = 60.9°; $n = 76$), and the data were non-randomly distributed ($p < 0.001$, Rayleigh test of uniformity) (**Table 3.3**). The circular frequency distribution of the pooled data (10° bins, with equal weighting applied to each attack category) reveals two main peaks, with the larger at $\pm 180^\circ$, and the smaller at +130° (**Fig. 3.13 a**). However, the apparent bimodal distribution was not significantly different from a unimodal normal circular (von Mises) distribution which was fitted to the data ($p = 0.07$, χ^2 test).

By presenting the pooled data as if attacks were from both the left or right of the shrimp, it is possible to estimate the frequency of final $\mathcal{E}_{\text{attack}}$ angles which a predator would encounter if it was unable to determine the orientation of a shrimp prior to an attack, and if it was equally likely to attack the shrimp from any direction. The final escape trajectory with the highest frequency is $\pm 180^\circ$ (**Fig. 3.13 b**).

3.4

DISCUSSION

3.4.1 Sensory stimuli mediating the escape response

Visual information was important in evoking the escape responses. *Crangon crangon* have well developed eyes, enabling shrimps to see the cod or artificial stimulus approaching

from all directions (based on personal observations of the visual field of *C. crangon*). The importance of visual stimulation was confirmed by the experiments in which shrimp had been fully blinded, since they very rarely responded to the artificial stimulus unless direct contact occurred between the rod and the shrimp's body, or between the rod and the base plate. This supports the findings of Berghahn *et al.* (1995), who, in an investigation into the escape response of *C. crangon* from fishing gear, concluded that reduced shrimp catches during periods of high underwater visibility were due to visual detection by the shrimps of the fishing gear. They demonstrated the importance of visual stimuli by accelerating an opaque disc (7 cm diameter) towards shrimps, and this elicited tail flips more often than a similarly sized transparent disc. Smith (1993) also noted a reduction in the responsiveness of *C. crangon* when a clear artificial stimulus was used in place of an opaque one.

Occasionally when a fully blinded shrimp did not escape from the artificial stimulus, it instead altered its position slightly on the substratum, indicating that it was still capable of detecting the stimulus in the absence of visual information. It is well documented that crustaceans are sensitive to water displacements occurring in the proximity of vibrating and moving objects, and that these are detected by mechanosensory hairs distributed over their body surface (e.g. Moss & Wiesenfeld, 1995; Breithaupt & Tautz, 1990; Tautz & Sandeman, 1980; Wiese, 1976; Taylor, 1968). Furthermore, some crustaceans are capable of accurately orientating themselves in response to water displacements caused by fish swimming close to them (Breithaupt *et al.*, 1995).

In *Crangon crangon*, there are a variety of mechanosensory hair types distributed over most regions of their body. Those on the uropods have been demonstrated to code stimulus directionality, and have an absolute lowest threshold of acceleration of 81 cm.s^{-1} (corresponding to $0.7 \text{ }\mu\text{m}$ amplitude of particle displacement in the surrounding water) (Heinisch & Wiese, 1987). Hairs on other regions of the body probably code directionality as well. Therefore, hydrodynamic disturbances caused either by cod swimming, or the movement of the artificial stimulus rod, are likely to be detected by the shrimps, even if this stimulus alone was not usually sufficient to initiate tail flip responses. It is interesting to note that in crayfish, sensory hairs on the abdomen which are directionally sensitive to movement have bipolar neurones which make direct electrical synapses onto the lateral giant interneurons, but their ability to initiate tail flips is lower than that of visual stimuli (Wiese, 1976; Wine & Krasne, 1982).

It is possible that chemical cues given off by approaching cod may have been detected by the shrimps, since they also have chemosensory receptors on their body surface (Heinisch & Wiese, 1987). Breithaupt *et al.* (1995) argue that it is unlikely that these are used in rapid orientation responses because, in turbulent odour plumes, the source of chemical stimuli is difficult to localise (Atema, 1988), and involves a comparatively slow search behaviour (Moore *et al.* 1991). However, chemical detection of a predator may potentially increase a shrimp's awareness of predator-presence, and prepare it for an escape.

3.4.2 Reaction distances

In general, reaction distances were small, such that the approaching stimulus reached the pre-escape position of the shrimp within 1-2 frames (20-40 ms) of it escaping. Webb & Skadsen (1980) found that during the last 80 ms of a strike, tiger muskies (*Esox sp.*) were unable to alter their attack direction. Therefore, delaying an escape until the last moment has the advantage of committing a predator to a strike, and prevents them from compensating their attack direction in response to the escape.

The reaction distances in response to the artificial stimulus were significantly greater than in response to attacks from the cod ($p < 0.001$ or 0.01 for all Tukey's pairwise comparisons). This was probably because rapid acceleration of the artificial stimulus was initiated from a distance of approximately 20 cm, whereas the cod approached the shrimp slowly, and when a feeding strike occurred, it was initiated from a range of within a few centimetres.

In pairwise comparisons between the artificial stimulus attack angle categories, the reaction distance in response to 90° attacks was significantly greater than in response to 45° attacks ($p < 0.01$, Tukey's pairwise comparison). This is perhaps surprising, since distances were measured from the shrimp's centre of mass (situated near the abdominal-thoracic joint), and therefore attacks from more anterior or posterior sectors of the shrimp might be expected to have greater measured reaction distances because of the closer proximity of the stimulus rod to the eyes and antennae (front attacks) and uropods (rear attacks).

A speculative hypothesis explaining this observation might be drawn from the neuronal pathway(s) involved in initiating the escape responses. When attacks were from a direction which induced both contra- and ipsilateral escapes, a slight delay may have been introduced by the neuronal decision-making processes which commit the shrimp to one of the two escape directions. In attacks from 90° , which unequivocally resulted in a contralateral

escape, anticipating an attack from the looming rod may have enabled the shrimp to 'pre-set' its escape direction, thereby reducing the neuronal processing time involved in initiating the escape.

3.4.3 The escape envelopes of *Crangon crangon*

The escape envelopes (Fig. 3.9 b) represent the range of initial $\mathcal{E}_{\text{body}}$ angles used by *Crangon crangon* when escaping to their left or right side.

The anterior sector into which *Crangon crangon* does not escape (i.e. initial $\mathcal{E}_{\text{body}} < |75^\circ|$) is probably dictated by anatomical constraints on the shrimp. If the first tail flip of an escape involves a rotation of the shrimp about its antero-posterior axis onto its side, then the minimum achievable initial $\mathcal{E}_{\text{body}}$ angle will depend upon the proportion of the thrust which pitches the shrimp rostrally. The temporal sequence in which the abdominal segments are activated will affect this (Newland & Neil, 1990a). However, the length of the shrimp's abdomen and the position of the shrimp's centre of mass also directly affect the moments of inertia produced by movement of the shrimp's tail fan (and head fan) (see Daniel & Meyhöfer, 1989). These morphological features limit the degree of rostral pitch which can be achieved. Evolutionary selective pressures have probably eliminated traits which give rise to excessive rotational pitch since they compromise the translatory thrust (i.e. the centre of mass remains almost stationary as the shrimp rotates about it) with the result that the shrimp will not escape from the interception path of a predator's strike.

The posterior sector into which *Crangon crangon* does not escape (i.e. initial $\mathcal{E}_{\text{body}}$ angles $> |156^\circ|$) is probably also dictated by anatomical constraints. Since *C. crangon* shelters from predators either on top of, or buried within the sediment, the normal body posture maintains the entire abdomen fully extended, with the abdomen and tail fan in close proximity, and parallel to, the sea bed. Consequently, flexion of the abdomen generates downward forces which propel the animal predominantly in a vertical direction, or to the side if the first tail flip is accompanied by a roll of the body. Therefore, the body posture adopted by *C. crangon* is probably an important feature preventing them from escaping at initial $\mathcal{E}_{\text{body}}$ angles $> |156^\circ|$. This is re-enforced by the mechanism of tail flip flexion in *C. crangon*, which is 'symmetrical' in nature (i.e. involves little or no flexion of the posterior abdominal segments and telson - see section 2.4.2), and this results in rostrally directed pitch forces.

Interestingly, the posterior region (angles $> |156^\circ|$) into which shrimps did not escape represents precisely the region exploited by many other crustacean species, particularly when

tail flips are activated by the medial giant fibres (i.e. when stimulated rostrally; Wine & Krasne, 1972; Newland & Neil, 1990a). The mud shrimp *Calocaris macandreae* demonstrates this feature well, and provides a good comparison since it is of a similar size to *Crangon crangon*. However, it differs in being burrow dwelling, and possesses no head fan. Unlike *C. crangon*, these shrimps tail flip in a posterior direction, and never incorporate body roll in their first tail flip (personal observations). However, the typical body posture adopted by these animals, and the morphology of the tail fan, differ considerably from *C. crangon*. When at rest in their burrow, *C. macandreae* adopts a posture with its abdomen raised off the bottom, and with the posterior portion curved ventrally so that the uropods are held at a large angle with respect to the sea bed. The tail fan therefore takes the form of a downwardly curved, slightly concaved scoop-like structure, with the result that, when the abdomen flexes, the attack angle is such that it propels the shrimp posteriorly. Many other burrow- or crevice-dwelling decapods adopt a similar resting posture, and they too perform posteriorly directed escapes if appropriately stimulated.

3.4.4 The exclusion envelope

The exclusion envelope is derived from considering all possible attack-escape angles between the artificial stimulus and the shrimp (Fig. 3.10). A significant feature of the exclusion envelope is that it is independent of the initial orientation of the shrimp, and can in fact include escape directions which are available to the shrimp (i.e. ones within the escape envelopes - Fig. 3.9). Therefore the exclusion envelope does not represent an anatomical constraint, but rather reflects a behavioural choice by the animal not to escape in certain directions relative to the stimulus, presumably because the perceived risk of being caught is too high.

Escaping directly towards an attacker will self-evidently result in a shrimp being caught within its first or second tail flip, since it will swim directly into the predator's mouth. As the escape angle increases, the risk of this diminishes depending upon the relative velocity of the predator and prey (Howland, 1974; Webb, 1976), the size of the predator's mouth, the magnitude and range of the negative pressure created during the predator's feeding strike (Alexander, 1970; Hart & Hamrin, 1990; Norton, 1991, 1995), and the responsiveness of the predator to the shrimp's movements (Webb, 1984).

3.4.5 Interaction of the escape and exclusion envelopes

The escape and exclusion envelopes are graphic representations of two distinct 'rules' which apply to *Crangon crangon* escape trajectories, the first deriving from an anatomical constraint and the second from a behavioural choice. The interaction of these rules for any given attack-escape angle can be represented by a graphic overlay of the escape and exclusion envelopes (Fig. 3.14). The former is referred to the anatomical axes of the animal, and remains fixed, while the latter is referred to the attack direction, and rotates. At different angles of attack, the exclusion envelope either partly (Fig. 3.14 b & e) or completely (Fig 3.14 c-d) eclipses certain areas of the shrimp's escape envelope(s), and so prevents the overlapping initial $\mathcal{E}_{\text{body}}$ angles from being used. As a consequence of this, a greater proportion of the contralateral escape envelope is available than the ipsilateral one when attacked from 45° , and the shrimp only has the option of escaping towards the contralateral side when attacked from 90° and 135° . When attacked from 0° (Fig. 3.14 a) and 180° (3.14 e), the left and right escape envelopes are equally available, although in the latter case, both escape envelopes are partially eclipsed posteriorly by the exclusion envelope.

3.4.6 Escape strategies which derive from escaping in the horizontal plane

In all of the escapes analysed here, the shrimps performed a rapid lateral rotation about their longitudinal axis at the beginning of the first tail flip. This initial re-orientation of the body enabled them to escape horizontally either towards their left or right side. Escapes of this type are also seen under more natural conditions when a shrimp on the sediment surface (i.e. not buried) is approached by a juvenile cod (personal observations).

However, laterally directed first tail flips do not occur under all circumstances. High speed video observations (section 2.3.3) reveal that when an escape is delayed until actual physical contact has been made between an approaching object and the shrimp, or when a shrimp is buried within the sediment, tail flips may be directed vertically upwards into the water column. Even in these cases, though, the shrimp usually performs a roll during the re-extension phase of a vertical tail flip so that, thereafter, it swims on its side in the horizontal plane. Alternatively, vertical tail flips may be followed by the execution of an almost complete somersault, in which the second tail flip continues to pitch the shrimp forwards. It then swims away parallel to the bottom in an upside down position, with its head lower-most and tail upper-most (see section 2.3.3.ii.a).

Therefore, regardless of whether the first tail flip is directed upwards or sideways, subsequent tail flips seem to occur predominantly in the horizontal plane, in common with many other epibenthic decapods (e.g. Wine & Krasne, 1972; Sillar & Heitler, 1985; Newland & Chapman, 1989; Spanier *et al.* 1991). Unusually though, *Crangon crangon* achieves this by swimming on its side (or upside down) rather than in an upright position.

Swimming vertically too far off the bottom is probably disadvantageous because it makes shrimps more visible to any predators which are near the seabed, since objects suspended in the water column are more easily detected when viewed from below (Thetmeyer & Kils, 1995). It may also render shrimps vulnerable to subsequent attack from pelagic predators which they would ordinarily not encounter. Conversely, when swimming horizontally close to the substratum, the shrimp presents a comparatively low contrast image to a predator viewing it horizontally, or viewing it from above against the sediment background.

As well as escaping horizontally, an additional strategy the shrimp may potentially adopt is to swim along a trajectory which prolongs the encounter until the predator abandons the pursuit. Prolonging the pursuit increases the energetic cost to the predator (i.e. it reduces the profitability of the prey item), and may also increase the likelihood of the pursuer itself being attacked by still larger predators to which they themselves are vulnerable, since movement is a strong feeding stimulus in many fish (e.g. Brawn, 1969; Ware, 1973; Kislalioglu & Gibson, 1976b; Tallmark & Evans, 1986). Therefore, a prolonged chase increases the predator's tendency to abort an attack. This conforms to the premise of the optimal evasion model of Weihs & Webb (1984), which predicts final $\mathcal{E}_{\text{attack}}$ angles $> |159^\circ|$ in order to maximise the distance between the predator and prey. However, complete reliance on this strategy is also potentially expensive for *Crangon crangon*. Shrimps probably become exhausted during a chase more rapidly than do most fish predators, since the available energy reserves in their escape muscles become depleted after about 50 tail flip cycles (Onnen & Zebe, 1983; Kamp, 1989; Smith, 1993). This corresponds to about 5-7.5 seconds for a medium sized *C. crangon*, whereas fish may perform burst swimming for as long as 20 seconds (Satchell, 1991). Therefore, a predator may be able to track an escaping shrimp until it becomes exhausted, and then capture it with little effort (especially in clear underwater conditions, since the predator does not have to keep up with the shrimp in order to visually track it). Prolonging a chase also increases the risk of the shrimp attracting the attention of

other predators. Should a second predator initiate a chase when a shrimp has just escaped from a previous attack, the shrimp would already be exhausted, and have a poor chance of survival.

A more profitable strategy for the shrimp may therefore be to reduce the duration of an encounter by re-establishing a position on the sediment where it can then rely on its crypsis and burying ability to avoid further detection by the predator. This latter strategy is analogous to the escape behaviour of various cryptic grasshoppers which jump to a new location when attacked, but then remain motionless on landing so as not to draw attention to themselves (Edmunds, 1974). In *Crangon crangon*, this strategy would be facilitated by horizontal swimming (since this keeps the shrimp in close proximity to the seabed), and by final $\mathcal{E}_{\text{attack}}$ angles which remove the shrimp from the visual field of the predator (enabling it to land on the seabed unobserved). Removal from the predator's visual field can be achieved in two ways; either by escaping to a distance equal to or greater than that of the underwater visibility (the success of this is dependent upon water turbidity and ambient light conditions), or by escaping into the predator's blind zone (fish typically have a blind zone of between 20° and 30° to their rear - Wardle, 1993). Final $\mathcal{E}_{\text{attack}}$ angles likely to be favoured with regard to the former strategy (escaping beyond the range of underwater visibility) are those which translate the shrimp directly away from the stimulus, since these angles maximise the predator-to-shrimp distance. From this, one would expect the optimal final $\mathcal{E}_{\text{attack}}$ angles to be similar to those which prolong an encounter (i.e. final $\mathcal{E}_{\text{attack}}$ angles $> |159^\circ|$; Weihs & Webb, 1984), since both strategies rely on maximising the predator-to-prey distance. Final $\mathcal{E}_{\text{attack}}$ angles likely to be favoured in translating the shrimp into the predator's blind zone are those that steer the shrimp behind the direction of attack (i.e. final toward responses). Therefore, final $\mathcal{E}_{\text{attack}}$ angles which steer the shrimp either directly behind a predator, or directly away from it, may both result in removal of the shrimp from the predator's visual field.

In *Crangon crangon*, occasional intermittent puffs of sand may be stirred up by tail flips directed along the sediment surface (Tallmark & Evans, 1986, and personal observations), and these may momentarily distract the predator's attention and allow the shrimp to land unobserved. In this respect, a further analogy may be made with the escape behaviour of grasshoppers, in that these insects display bright flashes of colour on their hind wings during flight. However, these flashes vanish the instant that the wings are closed on landing, making the grasshopper more difficult to locate against its cryptic background (Edmunds, 1974).

3.4.7 Protean behaviour: unpredictable elements of the escape response

Fish can learn to recognise particular types of prey, and improve their capture and handling ability of them with experience (e.g. Werner *et al.* 1981; Wainwright, 1986; Croy & Hughes, 1991a; Mackney & Hughes, 1996). Therefore, fish may potentially increase their predation rate upon *Crangon crangon* by becoming familiar with their escape behaviour. However, the escape response of *C. crangon* has a number of elements which incorporate unpredictability (i.e. protean behaviour; Driver & Humphries, 1988; section 1.6), and these may be important in counteracting an experienced predator's ability to anticipate a shrimp's escape trajectory.

At the beginning of an escape response, the side to which *Crangon crangon* escapes (left or right) may be unpredictable. Maximum unpredictability occurs when attacks are from 0° or 180° (Fig. 3.6 a & e). However, this unpredictability is reduced as the attack becomes more lateral (Fig. 3.6 b-d). A number of other animals have also been reported to display randomness in the side to which they escape when presented with a sudden stimulus from directly in front of, or directly behind them. In the angelfish *Pterophyllum eimekei*, Domenici & Blake (1993) found that escapes occurred randomly to the left or right when they were presented with an acoustic stimulus from angles of between 0-30°, or between 120-180°. However, when the stimulus was presented from within the 'discrimination zone' (30-120°), contralateral escapes occurred in 80-90 % of responses. The side to which the fish escapes is determined by selective excitation of the Mauthner cells on each side of the fish's body, leading to the expectation that discrimination should decrease when the stimulus is more in line with the longitudinal axis of the fish, because of the limits in the angular discrimination between two sound sources (Schuijf, 1975). By contrast, the cockroach *Periplaneta americana* appears to be more discriminative in its escape direction, since they escape to the contralateral side of a stimulus (puff of wind) presented from an angle of just 15° in 90 % of responses (Camhi & Tom, 1978). Further investigation has shown that the mechanism controlling this relies on 'directional sharpening' in the escape system at a neuronal level, and possibly at the motor level as well (Levi & Camhi, 1996).

In hatchling *Xenopus laevis* embryos, Boothby & Roberts (1995) found that a light touch on one side of the head produced random escapes to the left or right, whereas touching the side or tail of the embryo produce contralateral escapes in 80 % of cases. They attribute this to the receptive fields of the afferent sensory neurones. In the head, the receptive fields receive sensory input from both the left and right sides of the embryo, whereas in the side and

tail of the embryo, they receive unilateral sensory input. Therefore, stimulation to one side of the head can result in an ambiguous directional signal.

The period immediately after the first tail flip in *Crangon crangon* also has an intrinsic unpredictability. Shrimps which changed direction during an escape usually performed the largest steering manoeuvres within 100-200 ms of the initial escape (i.e. at the end of the first tail flip) and did so in a unpredictable manner (see Figs. 3.5 & 3.6). Therefore, if a fish fails to catch a shrimp on its first strike, it may not only have to react to whether the shrimp escapes left or right, but may have to make a further adjustment immediately afterwards (within the fish's reaction time to the first tail flip). The integration time necessary for these two closely-spaced decisions will necessarily increase its reaction time.

Unpredictable turning behaviour of the shrimp translates, from the predators view-point, into unpredictable initial and final $\mathcal{E}_{\text{attack}}$ angles. Although the general trend is for escapes to be steered away from the attack direction, an appreciable proportion (19.1% of escapes, or 20.2% if equal weighting is given to each attack category) had final $\mathcal{E}_{\text{attack}}$ angles $< |90^\circ|$ (i.e. final toward responses). The probable advantage of the latter strategy is that it steers the shrimp to the side of, and then behind the predator. In doing so, the shrimp may not only succeed in avoiding the predator's initial strike, but may also increase the time required by the cod to realign itself with the shrimp, and allow the shrimp enter the fish's rear blind zone (see section 3.4.6). Therefore, a predator may be unable to respond to manoeuvres performed by a shrimp when it is in this zone, and if the shrimp re-settles on the sediment and buries itself, the predator will be unable to visually locate it by the time it re-aligns itself with the shrimp.

Final toward responses occurred significantly more often in response to 0° and 180° attacks, and in ipsilateral escapes from 45° attacks, than in contralateral escapes from 45° - 135° attacks (χ^2 test; $p < 0.05$; Fig. 3.12). This may be because contralateral escapes from 45° - 135° attacks commit the shrimp to an initial $\mathcal{E}_{\text{attack}}$ angle which is directed away, rather than towards the side of the attack (see Table 3.2 and Fig. 3.10). The shrimp therefore needs to perform a larger turning manoeuvre in order to steer its final trajectory behind the stimulus, which may lead to a higher chance of being caught.

There was also evidence of unpredictability among the final away responses (i.e. final $\mathcal{E}_{\text{attack}}$ angles $> |90^\circ|$). Weihs & Webb (1984) calculated that the optimum trajectory for evading a predator (by maximising the distance between each participant) lies within $\pm 21^\circ$ of the line directly away from the attack (i.e. final $\mathcal{E}_{\text{attack}}$ angles $> |159^\circ|$). For normalised

attacks from the right of the shrimp, the final $\mathcal{E}_{\text{attack}}$ angle category (10° bins) with the highest frequency was $\pm 180^\circ$. In addition, the sector spanning $+159^\circ$ to -159° had the highest frequency of escapes within it for that given size sector (Fig. 3.13 a), although it still contained only 29.6% of all escapes (calculated with equal weighting given to each attack category). If the results are transformed as if attacks were from both the shrimp's left or right (Fig. 3.13 b), the proportion of escapes in this sector is 33.8%, which also represents the sector with the highest frequency (the predictability would be 11.7% if escape trajectories were totally random). Therefore, although *Crangon crangon* shows greatest preference for the escape trajectories predicted as optimal by Weihs & Webb (1984), the ability of a predator to predict whether an escape will occur within this sector is limited.

If an experienced predator is able to determine a shrimp's body position before a strike, it is possible that it may learn to modify its attack direction in order to produce a predictable initial escape direction. The most obvious way of doing this would be to attack the shrimp from between 90° and 135° , since escapes are likely to occur to the contralateral side. However, even in this situation, the fish will not be able to accurately predict the final $\mathcal{E}_{\text{attack}}$ angle. Attacks from 90° tend to lead to quite a wide spread of final trajectories, and attacks from 135° result in two prominent peaks at $+130^\circ$ and $+170^\circ$ (see Fig. 3.11 c-d). For the two categories combined, the predictability of escapes between $+159^\circ$ and -159° is still only 40.7%.

Therefore, although the highest frequency of final $\mathcal{E}_{\text{attack}}$ angles for a given sector lies within the optimal sector predicted by Weihs & Webb (1984), it is still not possible for a predator to accurately predict a shrimp's final trajectory. Attacking from 90° and 135° might have the advantage of predictably committing the shrimp to contralateral escapes, but variability in the final $\mathcal{E}_{\text{attack}}$ angle still occurs, although attacks from these directions very rarely result in final $\mathcal{E}_{\text{attack}} < |90^\circ|$. Shrimps which are attacked from 90° - 135° , and which are committed to escaping to the contralateral side, may possibly reduce the likelihood of an attack occurring if they visibly 'pre-set' their body position (Fig. 3.2), since predators which recognise signals indicating a prey's alertness sometimes abort their attack (Webb, 1982). A preparatory response prior to tail flipping has also been reported in the spiny lobster, *Jasus lalandii*, when receiving an asymmetrical stimulus from one side of the body (Cattaert *et al.*, 1988; Newland *et al.*, 1992a).

3.4.8 Comparison between the final $\mathcal{E}_{\text{attack}}$ angles of *Crangon crangon* and other animals

Domenici & Blake (1993) investigated the escape response of the angelfish *Pterophyllum eimekei*, and compared the final escape trajectories with those of the soldier crab *Mictyris longicarpus* (Nalbach, 1990a) and the cockroach *Periplaneta americana* (Camhi & Tom, 1978; Comer & Dowd, 1987) after re-analysing data from the latter two species by applying circular statistics. The unifying feature which they found for all three species was that the escape trajectories were not unimodally distributed (they differed significantly from a fitted unimodal von Mises distribution). The escape trajectories of angelfish and soldier crabs were bimodally distributed; peak frequencies (using the angular convention employed for the *Crangon crangon* data) were at $\pm 180^\circ$ and -130° for angelfish, and $+160^\circ$ and -160° for soldier crabs. The escape trajectories of cockroaches in response to a wind puff stimulus were multimodal, with the highest frequencies corresponding to inhibitory directions of the cercal hairs which detect the wind puffs (although no functional correlation has been proved between these coinciding distributions).

It has been suggested that multiple preferred escape trajectories may be adaptive in preventing predators from learning a single fixed pattern of response and compensating for it. In the case of angelfish, the peak at $\pm 180^\circ$ has the advantage of maximising the distance between the predator and the prey (Weihs & Webb, 1984). The peak at -130° may be advantageous because it enables fish to escape whilst keeping the stimulus just within its visual field and discrimination zone (the region of attack angles between 30° and 120° which resulted in non-random final escape angles). In *Crangon crangon*, little is known about the visual field of the shrimp while it is tail flip swimming. Due to the flexion of the body during the tail flip, the shrimps eyes are at the trailing edge whilst it is escaping. However, there may well be a blind region on the ventral side of cephalothorax due to obscuring of the shrimp's view by the antennal scales. Therefore, in order to be able to visually track a pursuing predator, the shrimp may have to keep it to the dorsal side of its cephalothorax during an escape. This does not seem to be an influential factor affecting the final $\mathcal{E}_{\text{attack}}$ angles in *C. crangon*. For instance, contralateral escapes in response to $45\text{-}135^\circ$ attacks from the right are biased towards positive final $\mathcal{E}_{\text{attack}}$ angles (their pooled mean is $+162.5^\circ$), which would maintain the stimulus on the abdomen side of the body. However, further work on the visual field of *C. crangon* during tail flip swimming is needed to confirm this.

It is interesting to note that, whilst the final $\mathcal{E}_{\text{attack}}$ angles of *Crangon crangon* are biased towards positive angles (mean vector = $+160^\circ$), the final escape trajectories of angelfish and cockroaches are biased towards negative angles (for example the mean vector for angelfish is approximately -160°). This probably arises as a result of the different modes of locomotion which these animals use, and in particular, due to the typically postero-lateral translation of the initial tail flip in *C. crangon* compared with the forward translation caused by angelfish and cockroach swimming and running, respectively. Therefore, for attacks from the right, the presumed anatomical constraints which determine the escape envelopes of *C. crangon* tend to commit the shrimp to positive trajectories. By contrast, an angelfish or cockroach attacked from its right would have to perform a larger turn in order to escape with a positive trajectory than they would to achieve a negative trajectory of the same magnitude (assuming that the escape is contralateral, as usually is the case).

When animals have a safe refuge to escape into, the direction of the refuge has a strong influence on the final $\mathcal{E}_{\text{attack}}$ angle. This is demonstrated in the burrowing crabs *Heloecius cordiformis* and *Uca pugilator*, which only escape directly away from a stimulus when they have no convenient burrow to flee into; otherwise, they run directly towards their burrow (Nalbach, 1990b; Land & Layne, 1995). In the blue crab *Callinectes sapidus*, escape trajectories are integrated according to the stimulus direction and the direction offshore (its 'safe' region) (Woodbury, 1986). In the experiments on *Crangon crangon*, no refuge was provided. When in their normal habitat, bias in any particular compass direction is unlikely when they are in deep water since the seabed refuge would usually be available in all horizontal directions. Localised rocky outcrops or other substrate irregularities may potentially have some influence upon the escape directions though, as may the influence of deeper water when shrimps are very close to the shore, especially during an ebbing tide.

Table 3.1 Initial $\mathcal{E}_{\text{body}}$ angles

Circular statistical analysis of the initial $\mathcal{E}_{\text{body}}$ angles (i.e. with respect to the shrimp's initial body orientation) of *Crangon crangon* in response to different attack directions. Data obtained for attacks from the left side of the shrimp have been transposed, and combined with data for attacks from the right.

Type of stimulus	COD STIMULUS		ARTIFICIAL STIMULUS											
	Right anterior quadrant		Right posterior quadrant		0°		45° right		90° right		135° right		180°	
Attack direction	Contra	Ipsi	Contra	Ipsi	Contra	Ipsi	Contra	Ipsi	Contra	Ipsi	Contra	Ipsi	Contra	Ipsi
Side to which shrimp escaped														
Number of observations	11	9	10	6	6	4	13	4	16	18	8	5	8	5
Mean vector (μ)	-105.7°	+126.3°	-98.2°	+123.9°	-129.4°	+143.6°	-127.4°	+116.9°	-102.3°	-97.2°	+99.3°			
Length of mean vector	0.98	0.97	0.98	0.99	0.99	0.99	0.99	0.97	0.96	0.98	0.98			
Concentration (k)	15.1	11.6	20.0	23.6	28.1	15.4	76.8	18.6	14.0	13.9	11.5			
Circular variance	0.03	0.03	0.02	0.01	0.01	0.01	0.01	0.03	0.04	0.02	0.02			
Circular standard deviation	12.9°	14.2°	11.0°	8.9°	8.2°	9.3°	5.8°	13.5°	15.6°	12.6°	12.0°			
Standard error of mean	4.5°	5.7°	4.1°	4.8°	4.4°	7.3°	1.8°	3.4°	3.7°	5.5°	7.7°			
Rayleigh test of uniformity (p)	< 0.001	< 0.001	< 0.01	< 0.001	< 0.001	< 0.01	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001			

Table 3.2 Initial $\mathcal{E}_{\text{attack}}$ angles

Circular statistical analysis of the initial $\mathcal{E}_{\text{attack}}$ angles (i.e. with respect to the attack angle) of *Crangon crangon* when attacked from different directions. Data obtained for attacks from the left side of the shrimp have been transposed, and combined with data for attacks from the right.

Type of stimulus	<u>ARTIFICIAL STIMULUS</u>									
	0°		45° right		90° right		135° right		180°	
Side of shrimp to which it escaped	<u>Contra</u>	<u>Ipsi</u>	<u>Contra</u>	<u>Ipsi</u>	<u>Contra</u>	<u>Ipsi</u>	<u>Contra</u>	<u>Ipsi</u>	<u>Contra</u>	<u>Ipsi</u>
Number of observations	6	6	13	4	16	18	8	5	8	5
Mean vector (μ)	-129.9°	+120.9°	-175.0°	+95.9°	+152.9°	+118.7°	+79.9°	-84.0°	+79.9°	-84.0°
Length of mean vector	0.99	0.99	0.99	0.98	0.97	0.96	0.97	0.99	0.97	0.99
Concentration (k)	38.0	20.2	47.2	12.6	16.3	13.7	11.8	18.0	11.8	18.0
Circular variance	0.01	0.01	0.01	0.02	0.03	0.04	0.03	0.01	0.03	0.01
Circular standard deviation	7.0°	9.6°	7.4°	10.3°	14.4°	15.8°	13.7°	9.6°	13.7°	9.6°
Standard error of mean	3.8°	5.2°	2.3°	8.1°	3.6°	3.7°	6.0°	6.1°	6.0°	6.1°
Rayleigh test of uniformity (p)	<0.001	<0.001	<0.001	< 0.009	<0.001	< 0.001	<0.001	<0.002	<0.001	<0.002

Table 3.3 Final \mathcal{E} attack angles

Circular statistical analysis of the final \mathcal{E} attack angles (with respect to the attack angle) of *Crangon crangon* when attacked from different directions. Data obtained for attacks from the left side of the shrimp have been transposed, and combined with data for attacks from the right.

Type of stimulus	ARTIFICIAL STIMULUS						
	0°	45° right	90° right	135° right	180°	All data combined	
Attack direction		<u>ipsi-</u> <u>and</u> <u>contra-</u> <u>escapes</u> <u>only</u>	<u>contra-</u> <u>lateral</u> <u>escapes</u> <u>only</u>				
Number of observations	12	17	13	16	18	13	76
Mean vector (μ)	183.0°	171.9°	188.1°	163.0°	143.1°	159.7°	160.0°
Length of mean vector	0.36	0.59	0.86	0.73	0.83	0.28	0.57
Concentration (k)	0.55	1.45	3.09	2.19	3.22	0.33	1.39
Circular variance	0.64	0.41	0.14	0.27	0.17	0.72	0.43
Circular standard deviation	82.3°	59.3°	31.1°	45.8°	35.4°	90.9°	60.9°
Standard error of mean	37.5°	15.1°	9.7°	11.4°	8.3°	51.7°	7.4°
Rayleigh test of uniformity (p)	0.22	<0.001	<0.001	<0.001	<0.001	0.36	<0.001

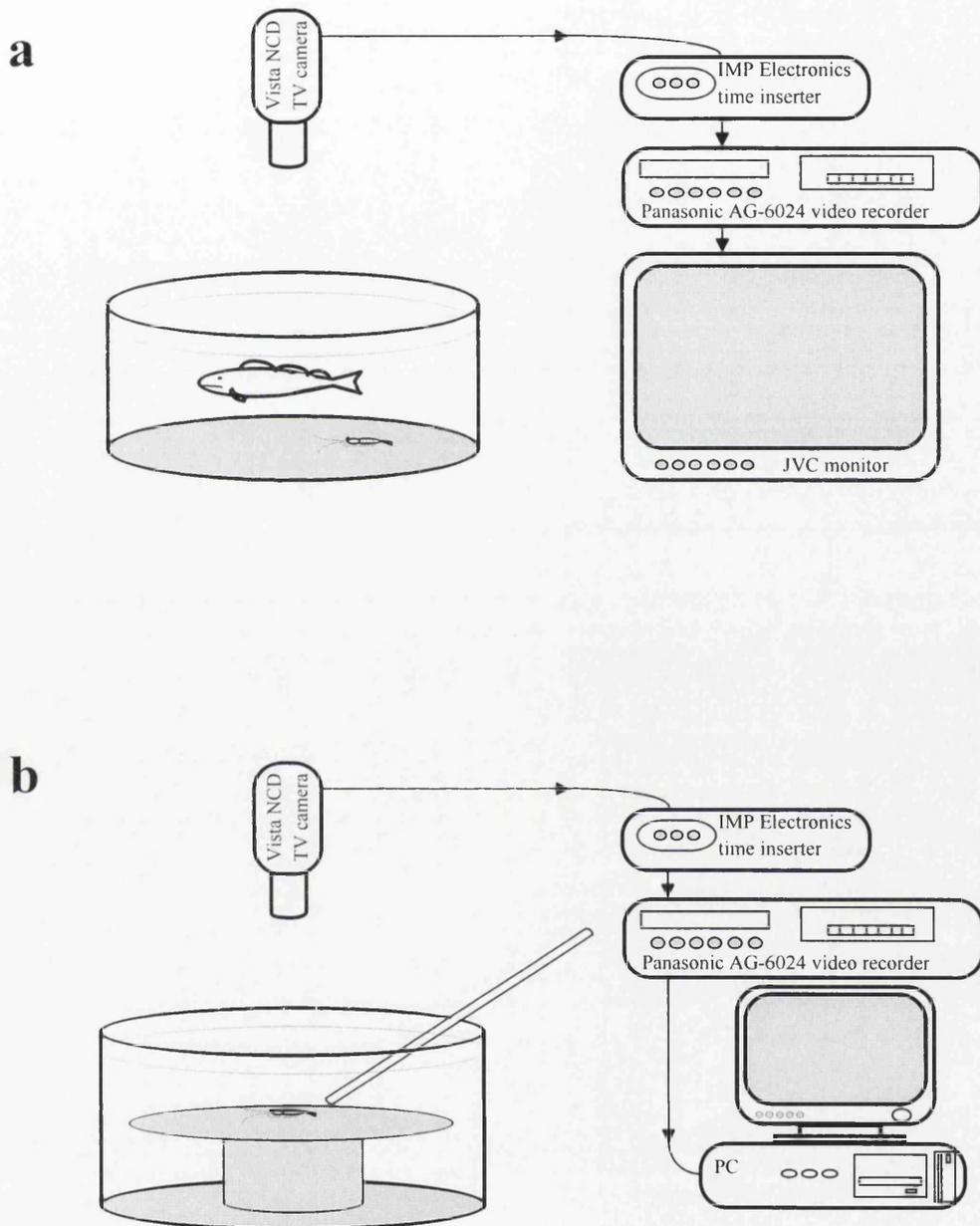


Fig. 3.1 Experimental set-up for escape trajectory experiments

Experimental set-up for filming escape trajectories in response to **(a)** attacks by cod (tank = 30 cm diameter, water depth = 20 cm), and **(b)** attacks by an artificial stimulus (tank = 1 m diameter, elevated base plate = 75 cm diameter, water depth above base plate = 25 cm).

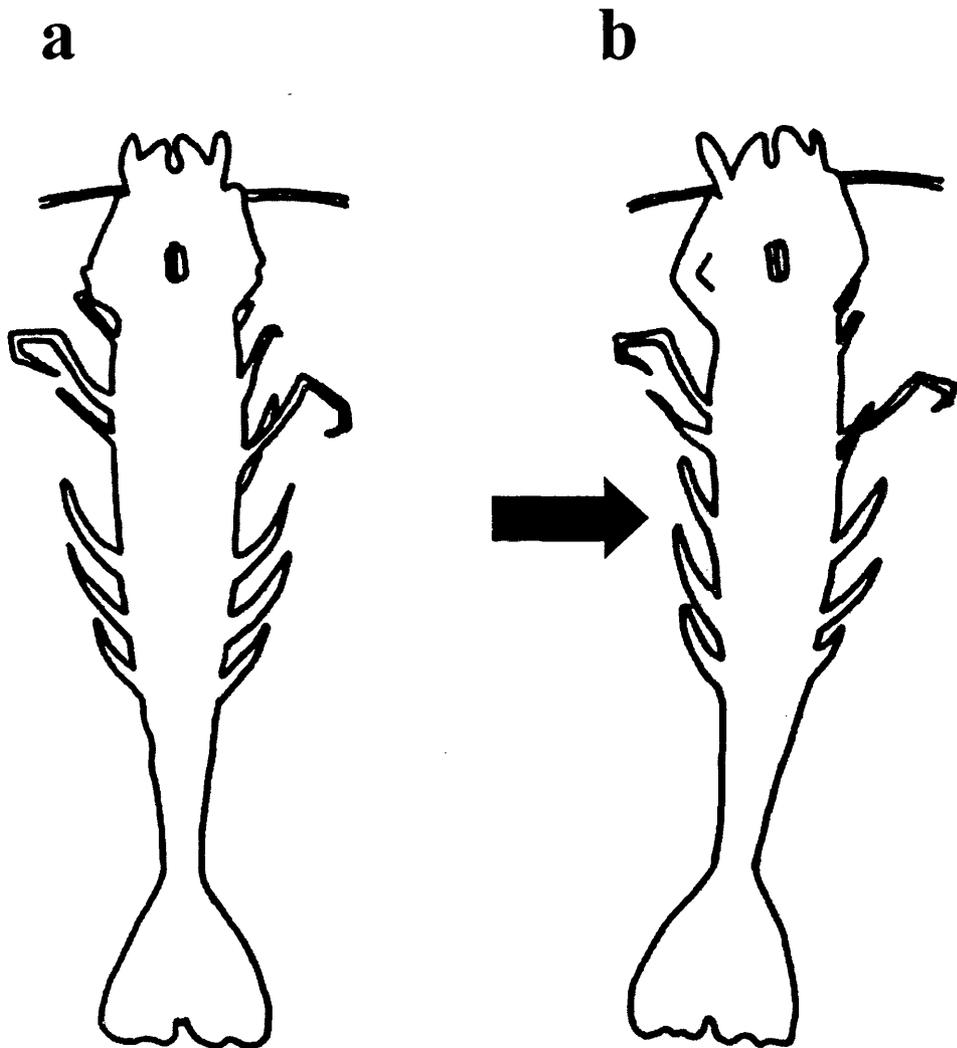


Fig. 3.2 Response of *Crangon crangon* to a pre-stimulus

(a) Typical outline tracing of *C. crangon* (viewed dorsally) in its normal resting posture. (b) Posture adopted by *C. crangon* when presented with a 'pre-stimulus' (arrow) from its left side. Note the leaning of the shrimp towards the contralateral side.

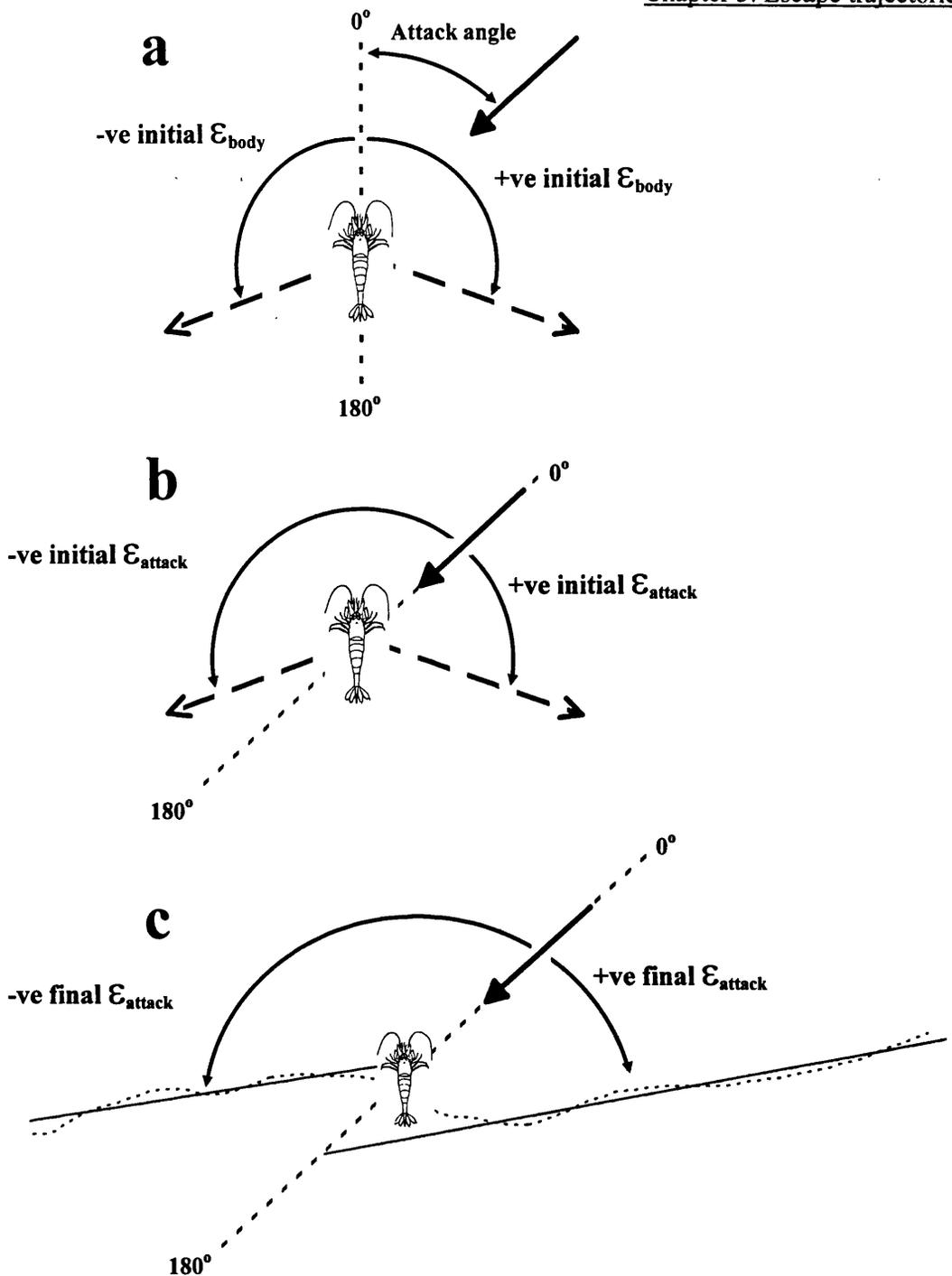


Fig. 3.3 Attack and escape angles that were measured

(a) **Attack angle and Initial $\mathcal{E}_{\text{body}}$ angle:** both measured with respect to the shrimp's pre-escape longitudinal body axis. The initial escape path of the shrimp was fitted through the position of the shrimp's centre of mass on frame 0, 2 and 3 of an escape (large-dash lines show examples of a positive and negative escape angle). (b) **Initial $\mathcal{E}_{\text{attack}}$ angle:** measured with respect to the direction of attack. Initial escape paths as in (a). (c) **Final $\mathcal{E}_{\text{attack}}$ angle:** measured with respect to the direction of attack. The final escape path was estimated by fitting a line through the position of the shrimp's centre of mass after completing initial steering manoeuvres (small dashed lines represent examples of positive and negative escapes with fitted [solid line] escape paths). All angles (a-c) were measured from artificial stimulus experiments, whereas only the initial $\mathcal{E}_{\text{body}}$ angle was measured from the cod experiments.

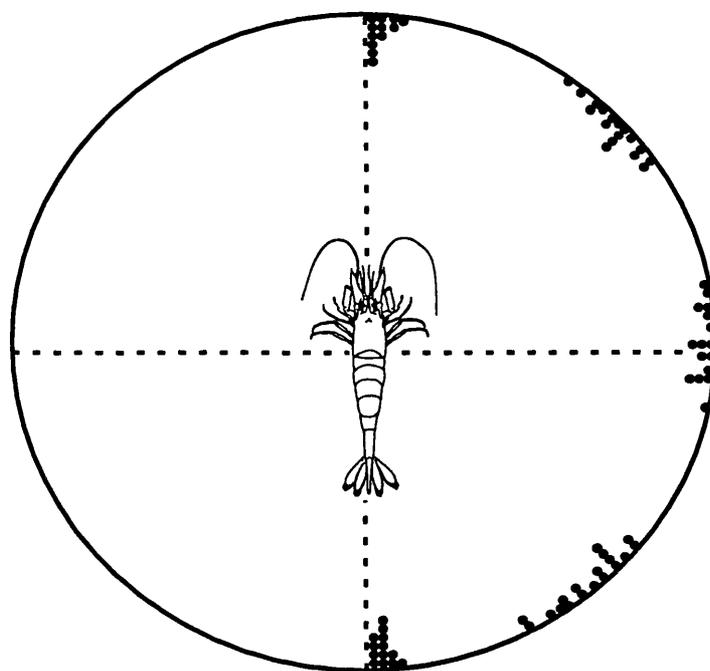


Fig. 3.4 Attack directions used for artificial stimulus experiment

Frequency of attack directions (to the nearest degree) used for the artificial stimulus experiments with non-blinded shrimps (each point represents one attack; $n = 76$). Data points for attacks from the left have been reflected so that they are depicted as if from the shrimp's right side. They fall into 5 main categories; 0° (head-on), 45° , 90° , 135° and 180° .

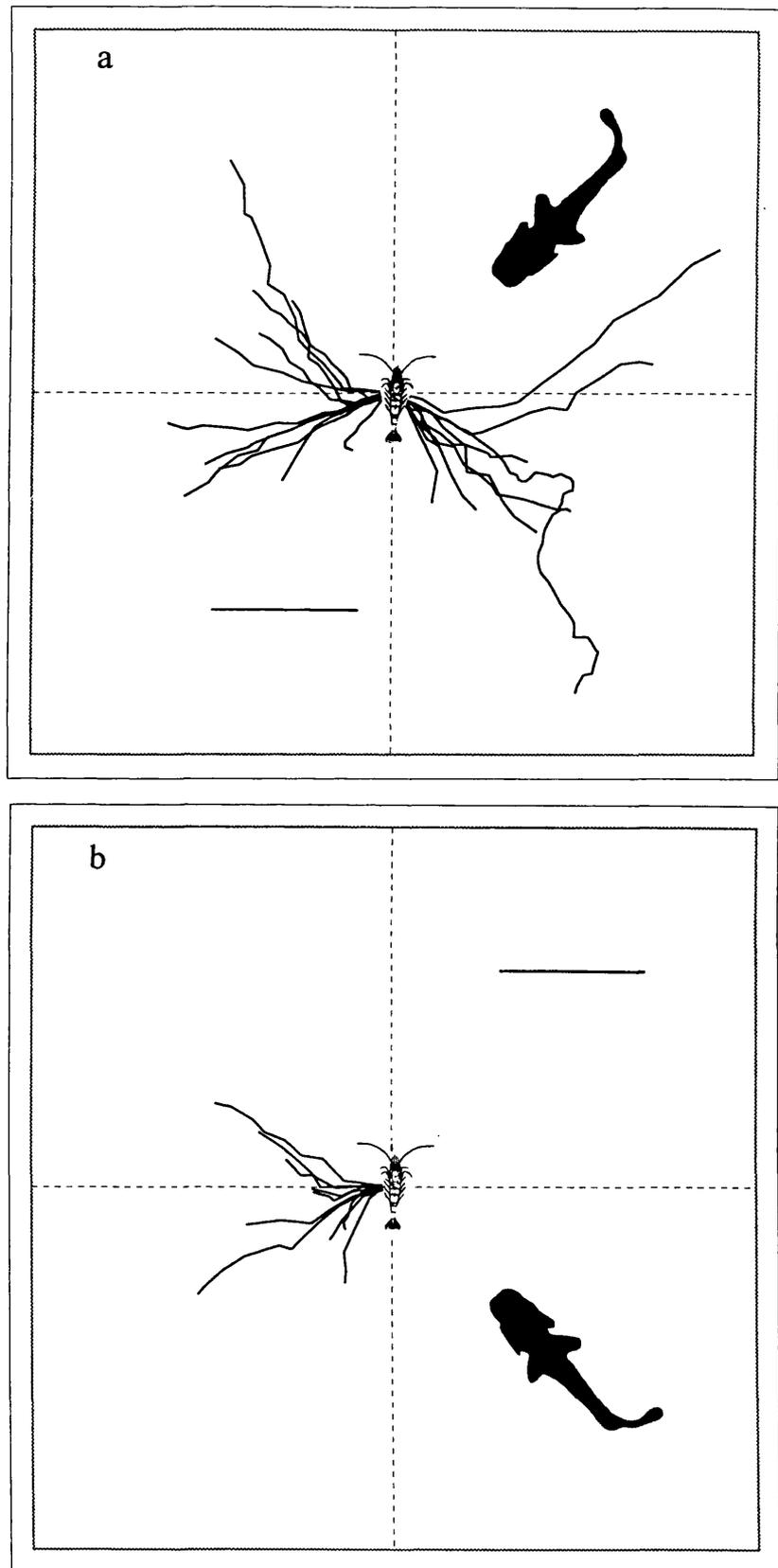
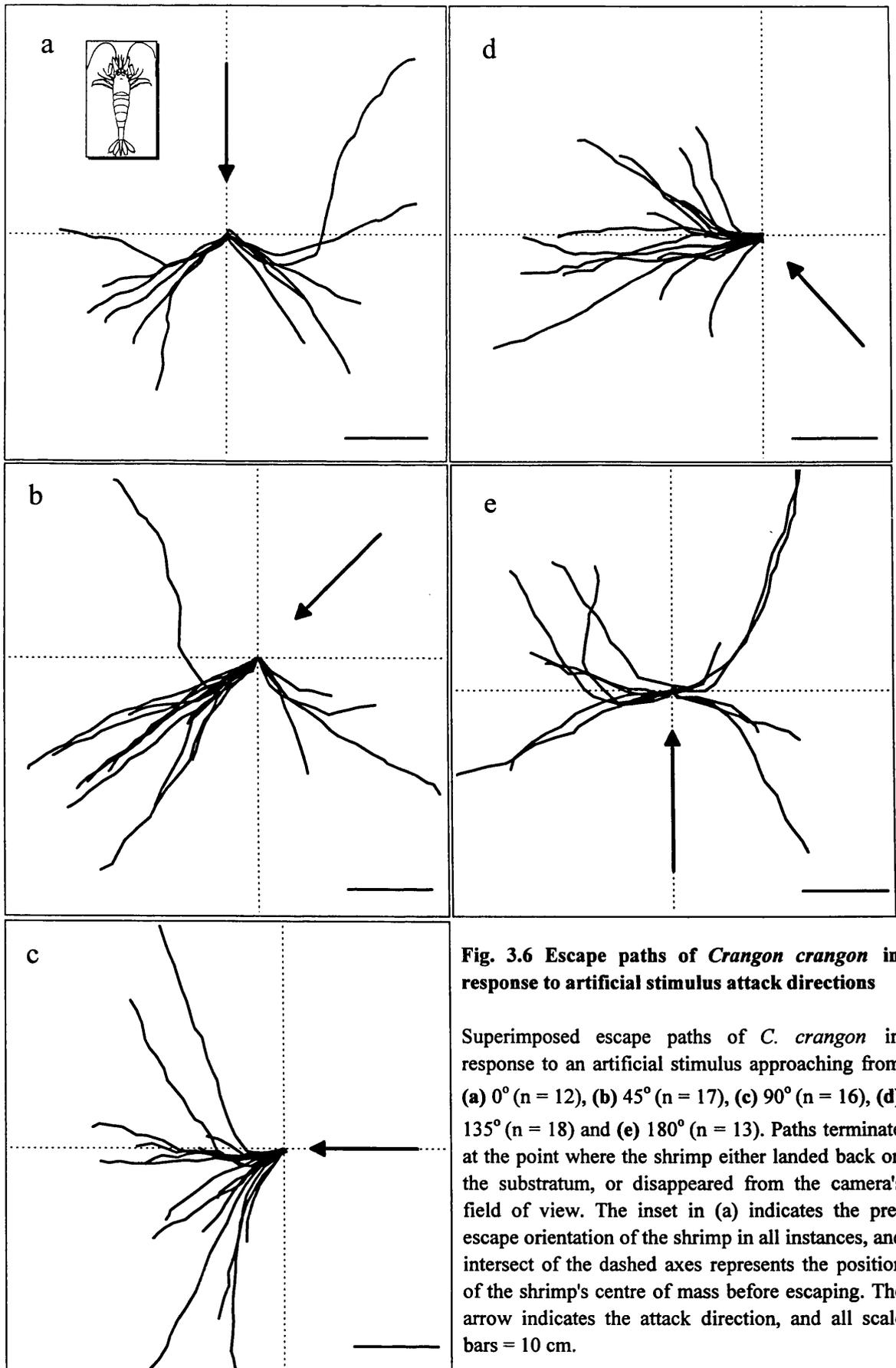


Fig. 3.5 Escape paths of *Crangon crangon* in response to attacks by juvenile cod

Superimposed escape paths of *C. crangon* in response to attacks by juvenile cod approaching from (a) the shrimp's (normalised) right anterior quadrant ($n = 20$), and (b) the shrimp's (normalised) right posterior quadrant ($n = 12$). Position of shrimp indicates its pre-escape orientation. Scale bar = 10 cm in both (a) and (b).



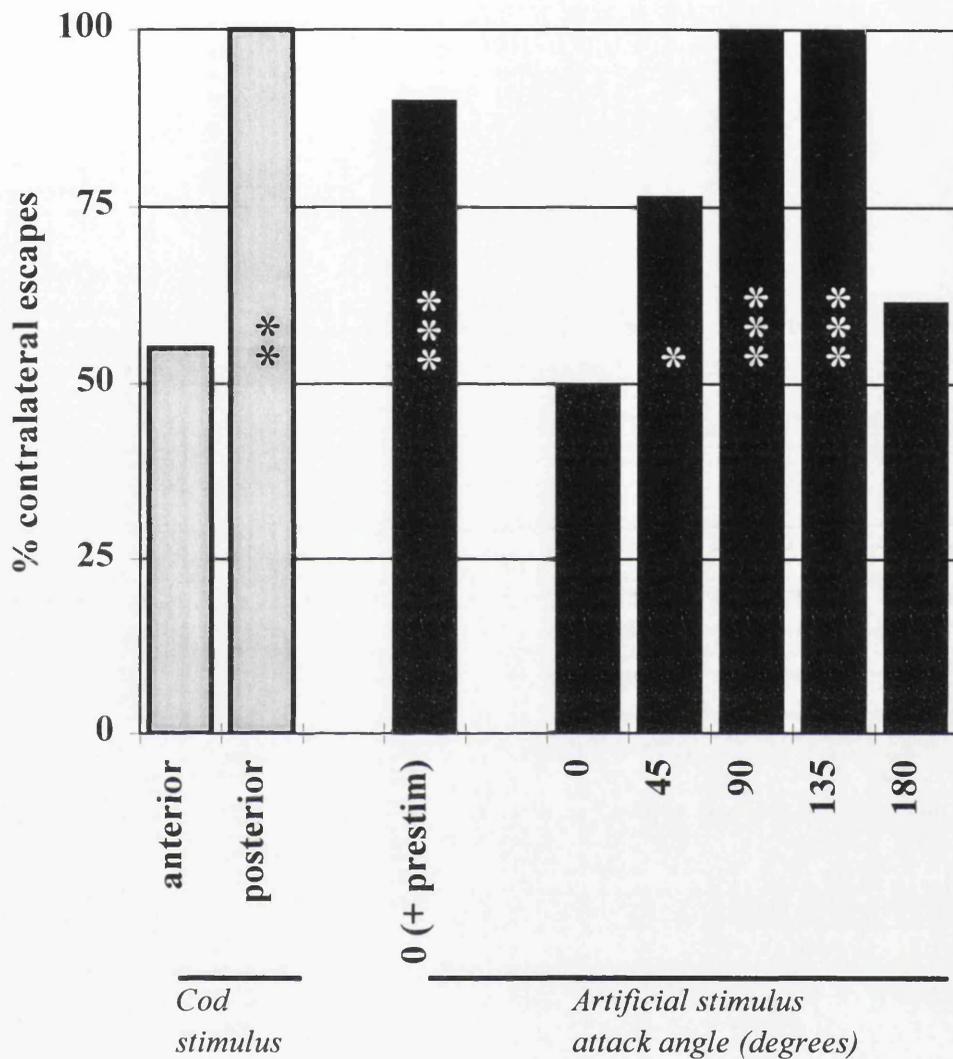
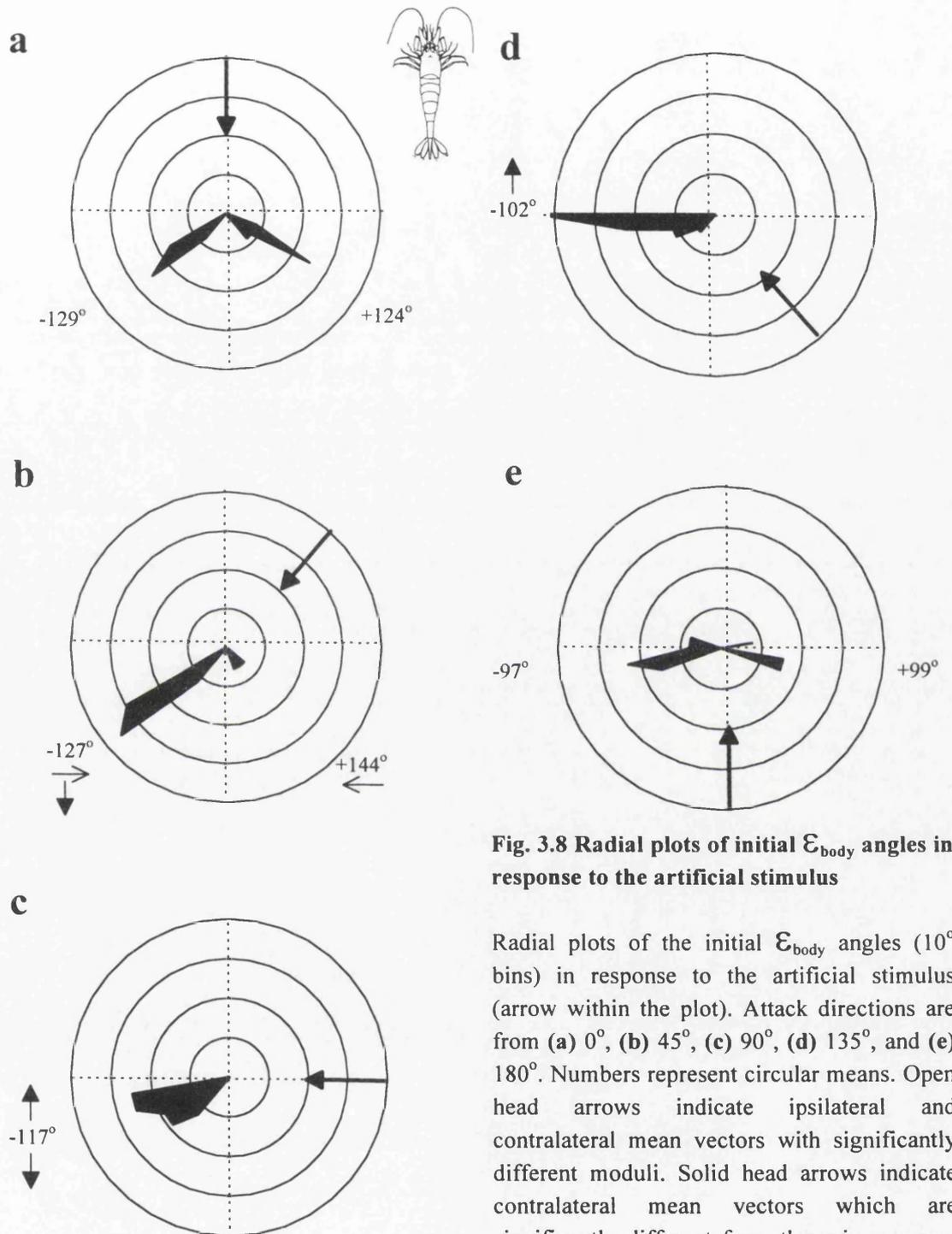


Fig. 3.7 Effect of attack angle upon the proportion of escapes to the shrimp's contralateral side

Effect of attack angle upon the proportion of escapes to the shrimp's contralateral (or left) side. Asterisks indicates values significantly different from random, i.e. 50 % (Chi squared test: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$).



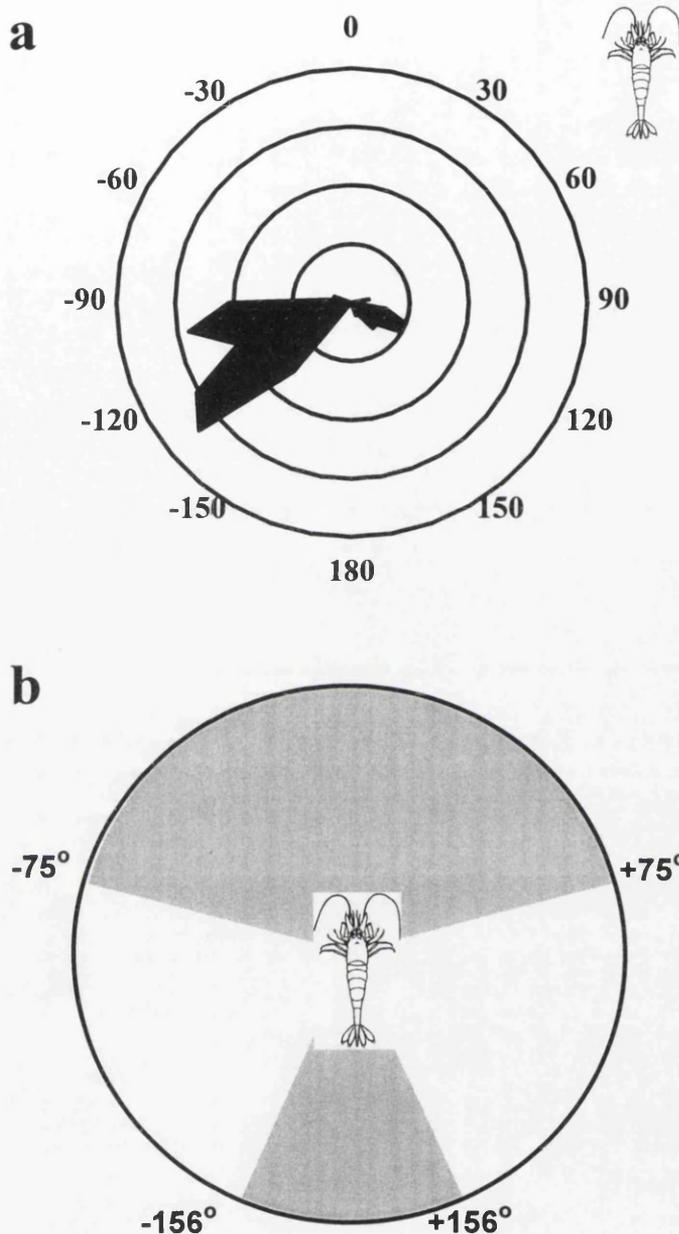


Fig. 3.9 Radial plots of all initial $\mathcal{E}_{\text{body}}$ angles combined, and escape envelopes of *Crangon crangon*

(a) Radial plot of all initial $\mathcal{E}_{\text{body}}$ angles combined (10° bins) in response to artificial stimuli from 0° to 180° (equal weighting given to each attack category). Scale : each circle = 5 %. (b) White regions represent escape envelopes (derived from the upper and lower limits of the initial $\mathcal{E}_{\text{body}}$ angle). Inserts represent the pre-escape orientation of the shrimp.

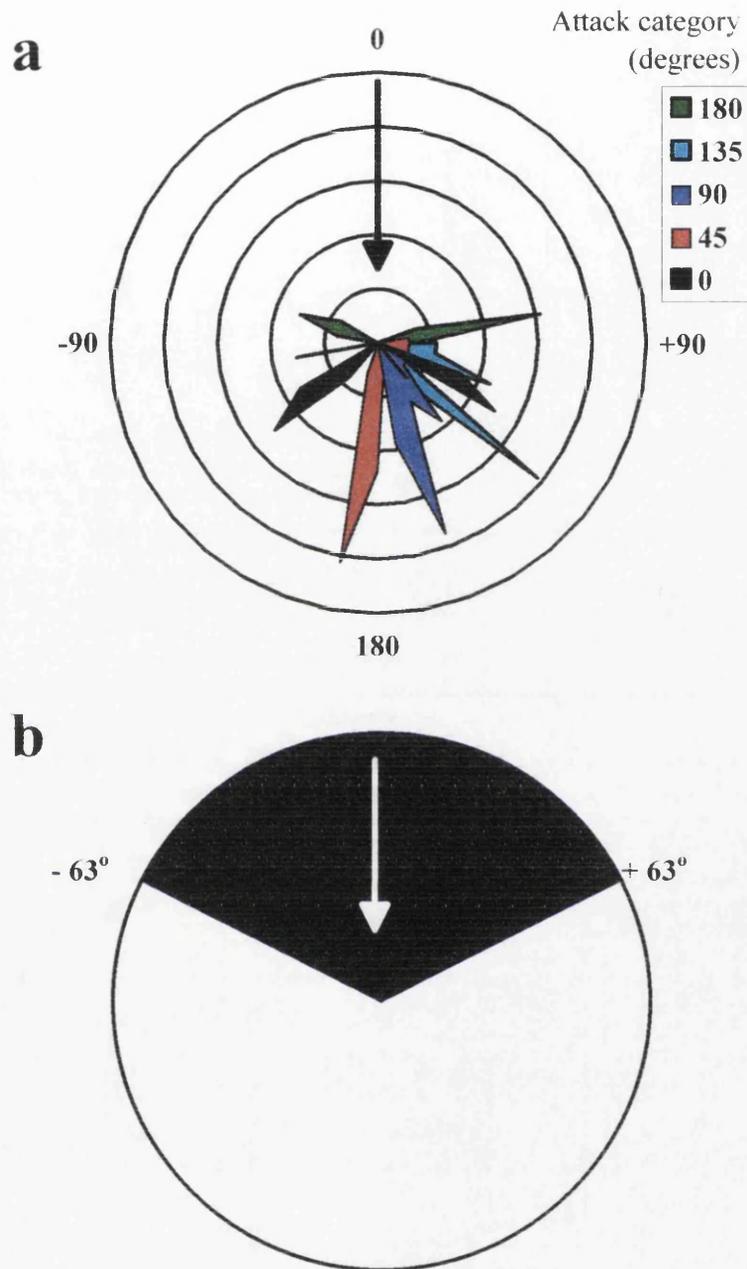


Fig. 3.10 Superimposed radial plots of all initial ϵ_{attack} angles, and exclusion envelope of *Crangon crangon*

(a) Superimposed radial plots of all initial ϵ_{attack} angles combined (10° bins) in response to artificial stimuli from 0° to 180° (equal weighting given to each attack category). Scale: each circle = 10 % **(b)** Black region represents the exclusion envelope (defined by the minimum observed initial ϵ_{attack} angle). The arrow in both plots represents the attack direction.

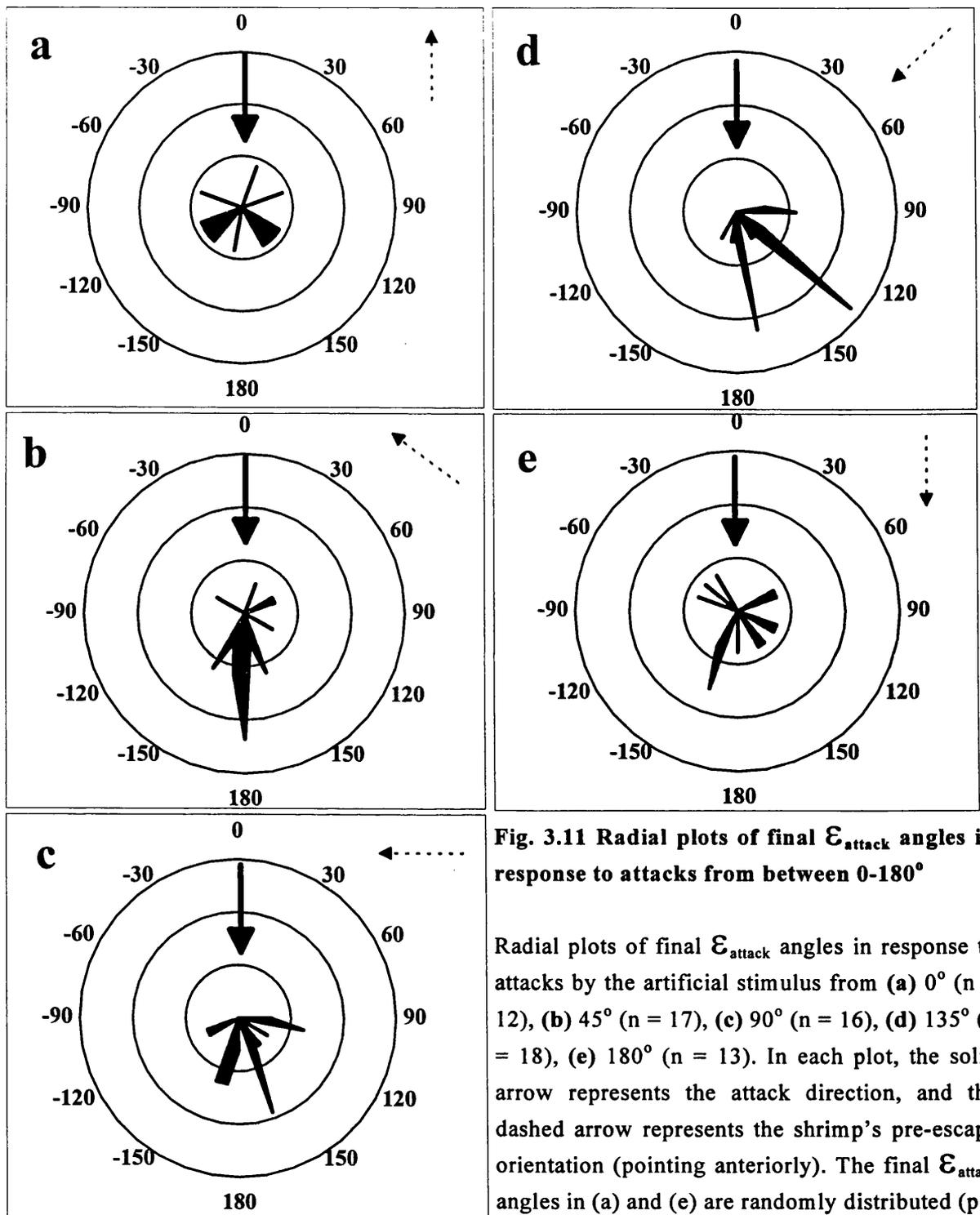


Fig. 3.11 Radial plots of final $\mathcal{E}_{\text{attack}}$ angles in response to attacks from between $0\text{-}180^\circ$

Radial plots of final $\mathcal{E}_{\text{attack}}$ angles in response to attacks by the artificial stimulus from (a) 0° ($n = 12$), (b) 45° ($n = 17$), (c) 90° ($n = 16$), (d) 135° ($n = 18$), (e) 180° ($n = 13$). In each plot, the solid arrow represents the attack direction, and the dashed arrow represents the shrimp's pre-escape orientation (pointing anteriorly). The final $\mathcal{E}_{\text{attack}}$ angles in (a) and (e) are randomly distributed ($p = 0.22$ and 0.36 respectively, Rayleigh test of uniformity), whereas those in (b), (c) and (d) are not ($p < 0.001$ in each instance). Scale in all plots: each circle = 10 %.

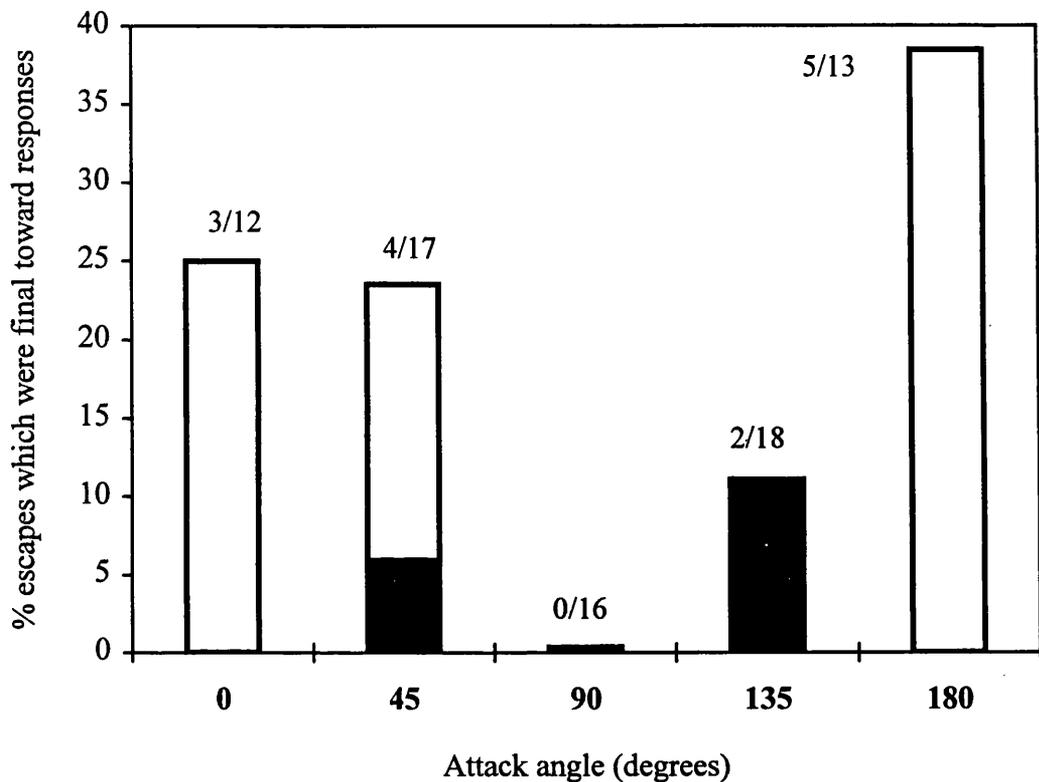


Fig. 3.12 Frequency of final towards responses with respect to attack angle

Effect of artificial stimulus attack direction upon the frequency of escapes which were final toward responses (i.e. final $\mathcal{E}_{\text{attack}} < |90^\circ|$). Final toward responses were significantly less frequent ($p < 0.001$, χ^2 test) in contralateral escapes from lateral attacks (i.e. 45° , 90° and 135°) (indicated by black) than in other escapes (indicated by white). Numbers refer to the total number of final towards responses / total number of escapes observed.

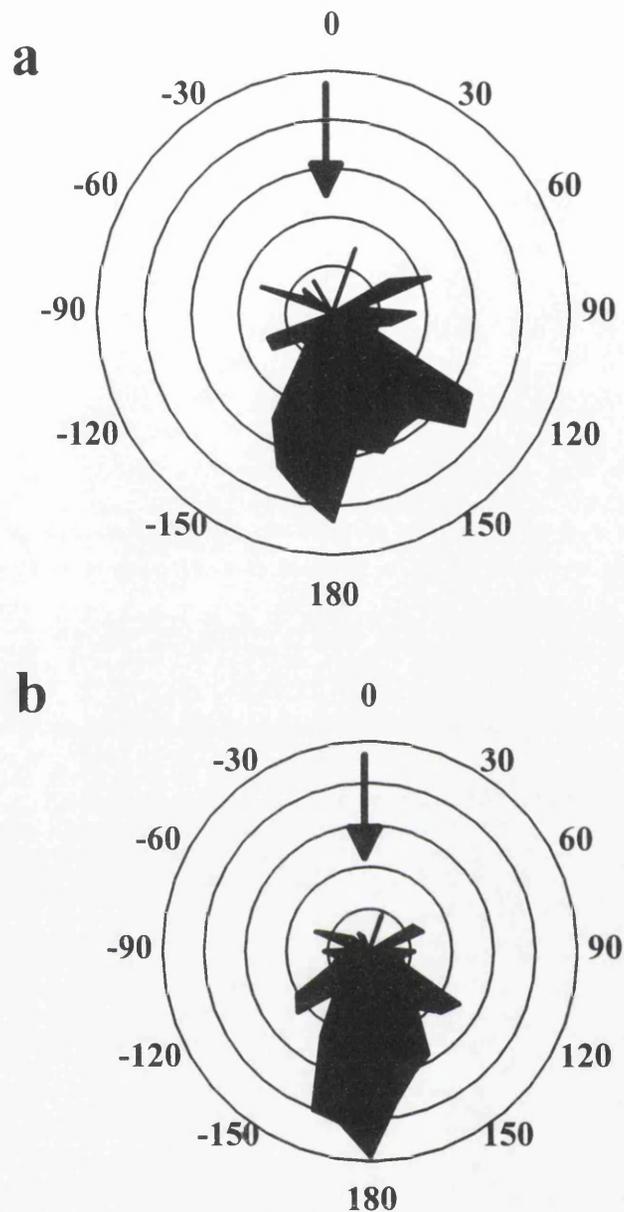


Fig. 3.13 Radial plots of combined final $\mathcal{E}_{\text{attack}}$ angles

Radial plots (10° bins) of all final $\mathcal{E}_{\text{attack}}$ angles combined (i.e. 0 - 180° artificial stimulus attack categories), with equal weighting applied to each attack category. (a) All final $\mathcal{E}_{\text{attack}}$ angles, depicted for attacks as if from the right of the shrimp only ($n = 76$). Mean final $\mathcal{E}_{\text{attack}}$ angle = 160.0° . The distribution is not significantly different from a circular normal (von Mises) distribution ($p = 0.07$, χ^2 test). (b) All final $\mathcal{E}_{\text{attack}}$ angles using the same data as in (a), but depicted for attacks from all directions (shrimp's left and right - see section 3.2.8 for details). Arrows indicate attack direction. Scale in both plots: each circle = 2 %.

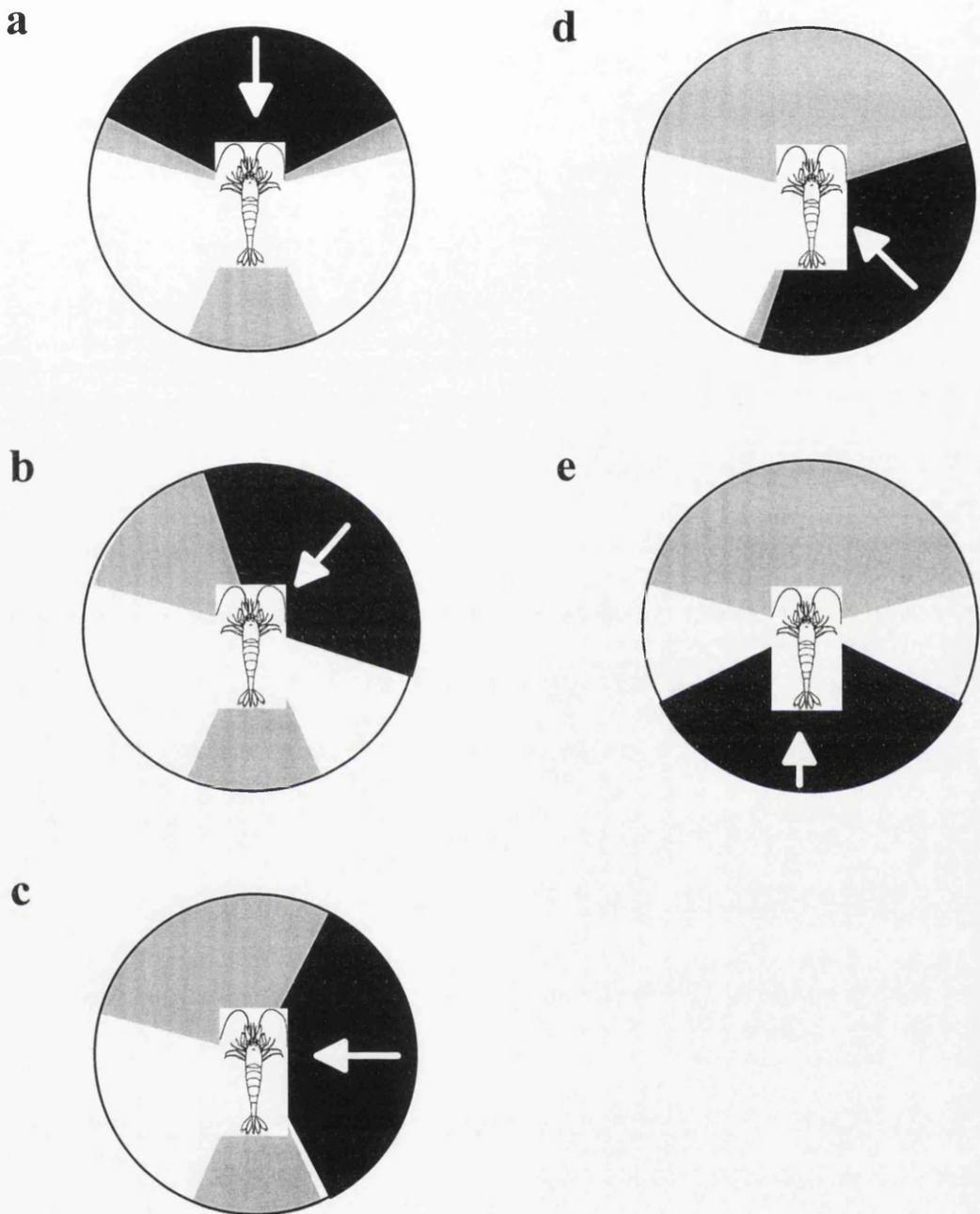


Fig. 3.14 Superimposition of the escape and exclusion envelopes

Superimposition of the escape envelopes (white regions) and exclusion envelope (black region) when shrimps are attacked from (a) 0° (b) 45° (c) 90° (d) 135° (e) 180° . Arrow indicates the attack direction; shrimp outline indicates its pre-escape orientation.

Chapter 4

Laboratory studies of predator-prey interactions between *Crangon crangon* and juvenile cod

Predation can be considered as a sequence in which feeding proceeds from prey detection → attack → capture, and for the prey to survive, they must intercept this sequence using a combination of primary and secondary defence mechanisms (see section 1.1). The effectiveness with which prey can defend themselves against predation will affect the amount of effort required by a predator to find, capture and consume them, and according to optimal foraging theory (OFT), this will affect the energetic profitability of the prey to the predator (see section 1.4). In this investigation, behavioural aspects of predator-prey interactions between *Crangon crangon* and predatory juvenile cod (*Gadus morhua*) have been examined. From these data, the effectiveness of the tail flip escape response of *C. crangon* has been determined, as well as the impact that it has on the profitability of shrimps to juvenile cod.

In Chapter 2, it was shown that the kinematic performance of tail flip swimming in *Crangon crangon* significantly improves as shrimps increase in size from their post-larval length (c. 5 mm) up to 50-60 mm (section 2.3.6). On the basis of this finding, it may be hypothesised that, for a predator feeding upon *C. crangon*, the probability of capture will decline as shrimp length increases, whilst the number of attacks required to capture the shrimp, and time spent pursuing it, will both increase. This study tests these hypotheses in the laboratory by filming interactions between *C. crangon* and predatory juvenile cod over a range of shrimp:cod (S:C) body length ratios.

Juvenile cod were chosen as the predatory species for experimental purposes because this species is known to feed heavily upon *Crangon crangon* in various European nursery areas such as the Firth of Forth (McLusky, University of Stirling, pers. comm.), the Severn Estuary (Bamber, Fawley Environmental Consultants, pers. comm.), and the Wadden Sea (Berghahn, 1996). Also, on the basis of previous investigations (Ellis, 1994, pers. comm.), it has been shown that, of those fish species feeding upon *C. crangon* at Tralee Beach (the field location studied in Chapter 5), juvenile cod are present in large numbers, and contain a comparatively high proportion of shrimps in their diet. Furthermore, they are more amenable to laboratory experimentation than some of the other *C. crangon* predators available, such as whiting (*Merlangius merlangus*).

A large number of studies on feeding selectivity in fish have used optimal foraging theory as a tool for evaluating the species composition and size range of prey items found in fish stomachs (see Hart, 1993). Classical OFT assumes that fish feed in a manner which

maximises their net energy gain. Given a range of prey items to feed upon, the optimal diet will therefore be dependent upon the energy content of each prey type, and the rate and efficiency with which a fish is able to locate, capture, consume and digest the prey. Handling time (here defined as the time taken to fully consume an item once it has been caught) is a commonly used parameter for estimating the relative profitability of prey items, and in some situations, correlates well with the diet of types of animals in their natural habitat (e.g. Kislalioglu & Gibson, 1976a; Hughes, 1980). This parameter has the advantage that it can be measured with relative ease in the laboratory. In this investigation, the handling time of cod feeding upon shrimps of different lengths has been measured and used to estimate, for a given size of cod, the length of shrimp which can be consumed with optimal profitability once it has been captured.

Three separate sets of experiments were conducted. The aim of Experiment 1 was to determine the effectiveness with which shrimps of different lengths (6-36 mm) are able to escape from various lengths of cod (61-107 mm), and to measure the handling time required by cod to consume shrimps of different S:C ratios. This initial set of experiments was conducted in a small arena with a hard, white substratum. The aim of Experiment 2 was to determine the effectiveness of tail flip escapes under more natural conditions, using a larger arena, and a sand substratum. A sand substratum is important because *Crangon crangon* are able to bury within sand in order to avoid detection by predators (Pinn & Ansell, 1993), and they are also cryptic against it.

Both of these series of experiments were conducted under light which was visible to both the cod and the shrimps. However, *Crangon crangon* and juvenile cod are also active at night-time. In a further experiment (Experiment 3), some data were acquired on the effectiveness with which cod are able to feed upon *Crangon crangon* in the absence of visible light. This was achieved using infrared illumination, which is beyond the visible wavelength spectrum of both *C. crangon* (Waterman, T.H., 1960; Fernandez, 1973; Ghidalia, 1985) and cod (Blaxter, 1970).

The results of these experiments suggest that the tail flip escape response of *Crangon crangon* is an effective secondary defence mechanism against predation, and significantly reduces the probability of a shrimp being caught and consumed once it has been detected by a predator. Furthermore, the effectiveness of the escape operates in a size-dependent manner, and reduces the profitability of *C. crangon* to predators.

4.2

MATERIALS & METHODS

4.2.1 Experimental work

All experimental work was conducted at the Dunstaffnage Marine Laboratory, Oban.

4.2.1.i. Animals used for experiments

All animals used in experiments were collected in less than 2 m of water in Dunstaffnage Bay on the west coast of Scotland (a few kilometres south of the field site studied in Chapter 5), and were maintained at ambient sea water temperatures during the experimental period (approximately 12-14°C). Animals were kept for a minimum of 2 weeks before being used in experiments, and for a maximum of 2 months.

The majority of *Crangon crangon* were collected at low tide using a hand-held trawl net, but small shrimps (< 10 mm total length; i.e. tip of rostrum to tip of telson) were collected by sieving sand collected from intertidal pools through a 1 mm mesh sieve. After capture, shrimps were transferred to holding tanks supplied with continuously flowing sea water which was aerated by an air-stone. A layer (1-2 cm) of sand was placed on the bottom of the holding tanks to allow the shrimps to bury. Shrimps were fed *ad.lib.* every day on mysids and chopped mussels (*Mytilus edulis*).

0-group cod (*Gadus morhua*) were caught during nocturnal spring low tides in Dunstaffnage Bay using a beach seine net. Those used in Experiment 1 were caught in June 1993, and those in Experiments 2 and 3 were caught in July 1994. Cod were transferred to circular holding tanks (diameter = 1 m, depth = 0.55 m) supplied with continuously flowing sea water aerated with an air-stone. During the first 24 hours after capture, a small number of cod (< 3 %) died, but mortalities were rare after this period. The cod were fed *ad. lib.* between 10 a.m. and 12 noon every day on mysids which were caught in a hand-net in Dunstaffnage Bay. For convenience, cod were usually fed on frozen mysids, but twice a week they were fed on a mixture of live mysids and *Crangon crangon* in order to expose them to elusive prey items. All experiments were conducted between 10 a.m. and 5 p.m. using cod which had been starved for between 22-31 hours.

4.2.2 Experimental protocol

A summary of the procedures used in Experiments 1, 2 and 3 is provided in **Table 4.1**.

4.2.2.i Experiment 1

Experiment 1 was conducted between 25 July and 25 August 1993. Individual trials were conducted using either 'small' or 'large' cod. The mean total length (tip of snout to tip of tail) of the small group was 66.4 mm (range = 61-71 mm, $n = 23$), whilst that of the large group was 100.3 mm (range = 92-107 mm, $n = 26$). Ten cod of intermediate length (71-92 mm) were used, in addition to the small and large cod, for determining handling times.

All trials were conducted in an air-conditioned room maintained at 13°C. An experimental arena (30 cm diameter, 20 cm water depth) with a white base was illuminated from a distance of *c.* 3 m with fluorescent lighting (light levels not determined), and filmed (50 f.s^{-1}) from directly above with conventional video equipment (Vista NCD 360 TV camera, IMP Electronics V9000 time inserter, Panasonic AG-6024 VHS recorder; see **Fig. 4.1 a**). Before each trial, a single shrimp and a single cod were placed in the arena and kept separate from one another for 15 minutes by covering the shrimp with an upturned perforated container. Aeration was provided at this stage with an air stone. At the start of the trial, the air stone was removed, and the container was lifted remotely with an attached string from behind a screen in order not to startle the animals (in particular, the more excitable cod). A total of 59 trials were conducted, each lasting 1 hour or until the shrimp was consumed. Shrimp lengths ranging between 6-36 mm were used to achieve S:C ratios of between 0.09 and 0.41.

4.2.2.ii Experiment 2

Experiment 2 was carried out between 25 July and 1 September 1994. The investigation consisted of a series of trials in which individual cod were exposed to 8 shrimps of equal length under more natural conditions (larger arena, sand substratum, lower light levels) than in Experiment 1. Nevertheless, the area of the arena was limited to a size which enabled the investigator to see the shrimps reliably against the sediment background during video replay.

All trials were conducted in a circular fibre-glass tank with a diameter of 1 m and a height of 0.55 m, kept in an air conditioned room maintained at 13°C. An elliptical cylinder made of transparent plastic was placed on its edge inside the tank to form a central arena with

a long axis of 0.85 m and short axis of 0.65 m (area $\approx 0.4 \text{ m}^2$) within which trials were conducted (see Fig. 4.1 b). This set-up reduced the shadows formed around the edges of the arena, which otherwise attracted the cod, and also made it difficult for the investigator to see shrimps during video analysis. The arena had an even covering of sand 2 cm deep on its base, and was filled to a depth of 30 cm with sea water which had been filtered through a gauze made of artificial fibre. The sand was collected from a nearby intertidal location (Tralee Beach), and the infauna was removed by passing the sand through a 1 mm mesh sieve, flushing it thoroughly with a high pressure water jet, incubating it for 24 hours in an oven at 60°C, and then re-washing it.

In order to encourage the cod to venture over the entire area of the arena (rather than remaining just around the periphery), 5 obstacles were arranged on the surface of the sand. These consisted of a vertical solid cylinder and four boulders, all of between 5 and 10 cm in diameter.

Trials were filmed in a manner similar to Experiment 1, with the exception that two cameras were used to film trials with shrimps of 20 mm or less. With this arrangement, each camera filmed opposite halves of the arena, thereby increasing the detail visible on the monitor during analysis. Illumination was provided by two shaded fluorescent strip lights located 2 m above the arena, and 0.5 m to each side of it. Light levels on the sand surface varied between 1.6 and 2.0 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, similar to levels found in Scottish shallow water locations around the hours of dusk (Burrows, pers. comm.), the time at which field work in **Chapter 5** was conducted.

Thirteen separate trials were conducted. In each trial, a single cod (length = 100-103 mm) was placed in the arena with 8 shrimps of a given length (total lengths measured to the nearest millimetre). Trials were conducted with 4 shrimps lengths: 14 mm (3 trials), 20 mm (3 trials), 30 mm (4 trials) and 38 mm (3 trials). It was not possible to conduct trials with smaller shrimps because they could not be seen on the TV monitor reliably during video re-play.

Animals were placed in the experimental arena 1 hour before the start of each trial, with aeration provided by an air-stone. During this period, the cod was confined to a portion of the arena using a fine mesh separator to prevent it from feeding upon the shrimps. At the beginning of the trial, the recording equipment was turned on and the separator and air-stone were removed. Each trial lasted for 2 hours, and at the end of this period, the cod was sacrificed and its stomach contents were examined to confirm the number of shrimps which it

had eaten. Shrimps which had been eaten during the trial were still mostly whole, and were the only food items found in the stomach, although food from previous day's meal was clearly visible in the intestines.

If shrimps were not eaten during a trial, they were removed from the arena and not used again. Between trials, the sand in the arena was raked, and half of the water was renewed. After every third trial, the sand was siphoned into a bucket and flushed thoroughly with filtered sea-water before being used again in order to reduce the build up of chemicals emitted by shrimps or cod over the duration of the experiment. Trials were conducted in a random order with regard to the length of shrimps used in each trial.

4.2.2.iii Experiment 3

A single trial was conducted in the same arena, and with the same equipment as that described for Experiment 2, with the exception that an alternative illumination source was used. Illumination was provided by 2 underwater lights (Osprey OE 1132, 300 W), each fitted with an infrared filter (Farnell Electronic Components) which allowed only wavelengths of greater than 750 nm to pass through. The lights were placed in the outer enclosure of the experimental holding tank (see Fig. 4.1 b). Cod are insensitive to infrared light (Blaxter, 1970 - p.282), as are most crustaceans (Waterman, T.H., 1960; Fernandez, 1973; Ghidalia, 1985), but the video camera was sensitive to the wavelengths emitted by the lights. This allowed observations to be made of interactions between cod and shrimps in the absence of visual behaviour.

A single cod (102 mm) and eight 30 mm shrimps were placed in the arena, and the same experimental procedure was followed as in Experiment 2. The infrared lighting was not switched on during the 1 hour settling period because of the heat generated by the lights (the animals were kept instead in complete darkness). To minimise this effect during the actual trial, the water in the outer area of the holding tank was circulated using 2 air-stones. During the 2 hour experimental period, when the lights were switched on, the temperature in the inner arena increased from 13°C to 15°C at the points nearest the light source.

4.2.3 Video analysis

4.2.3.i Experiment 1

Interactions between cod and shrimps were viewed from video tape on a TV monitor (JVC). Encounters were identified in which the cod aligned itself with the shrimp, approached it, and either caught the shrimp, or caused the shrimp to escape with a tail flip response. From these encounters, $P[\text{capture}]_{\text{approach}}$ (the probability of being caught per approach by the cod) was calculated for each trial, in which:

$$P[\text{capture}]_{\text{approach}} = \frac{\text{number of captures}}{\text{number of approaches}}$$

If a shrimp was caught, the handling time taken by the cod to eat it was measured. Handling time was measured from the time of capture until the time when the shrimp was judged to have been fully consumed. With small shrimps, this was often short, and in such cases, a minimum value of 1 second was assigned. In the case of a large shrimp, it was often difficult to judge precisely when consumption was complete, but a characteristic swallowing action was evident during which an exaggerated expansion of the opercula occurred (described by Ellis, 1994), and this was taken as the end of consumption. If the cod was ejected from the cod's mouth, and then re-ingested before consumption, the time taken to do this was included in the handling time.

Cod sometimes performed a rapid head-shaking motion after capturing a shrimp, and for each capture, the number of head-shakes was recorded (1 head-shake = 1 full cycle of head movement; e.g. left to right to left). Occasionally, shrimps were able to escape from the cod's mouth after capture (secondary escapes), and the probability of a secondary escape occurring per capture ($P[\text{secondary escape}]_{\text{capture}}$) in each trial was determined as:

$$P[\text{secondary escape}]_{\text{capture}} = \frac{\text{number of secondary escapes}}{\text{number of captures}}$$

4.2.3.ii Experiment 2

In Experiment 2, shrimps usually buried within the substratum, and therefore the cod was not able to locate them as easily as in Experiment 1. However, if it did locate a shrimp and attack it, an encounter ensued. An encounter is defined as an attack by the cod which either

resulted in a tail flip escape response, or resulted in capture of the shrimp. During a single encounter, a cod was able to perform more than 1 feeding strike at a shrimp if it pursued it. The duration of an encounter was measured from the start of the cod's first feeding strike to the time when it either caught the shrimp, or stopped pursuing it. Buried shrimps only tail flipped when a cod performed a feeding strike (*cf.* Experiment 1, where shrimps often responded to an approaching cod). Therefore, P[capture]_{strike} (the probability of capture per strike by the cod) was used as measure of capture success in each trial, where:

$$P[\text{capture}]_{\text{strike}} = \frac{\text{number of captures}}{\text{number of strikes}}$$

Since encounters sometimes consisted of numerous strikes, P[capture]_{encounter} (the probability of capture per encounter) was also recorded in each trial, where:

$$P[\text{capture}]_{\text{encounter}} = \frac{\text{number of captures}}{\text{number of encounters}}$$

4.2.3.iii Experiment 3

Experiment 3 was analysed in the same manner as Experiment 2.

4.2.4 Statistical Analysis of laboratory experiments

All statistical tests were carried out using Minitab 10X computer package (Minitab Inc., 1995), except for logistic regressions, which were carried out using SPSS 5.0.2 (SPSS Inc., 1993).

For data from Experiment 1, logistic regressions were fitted to the relationships P[capture]_{approach} versus S:C ratio, and P[secondary escape]_{capture} versus S:C ratio. For Experiment 2, logistic regressions were also fitted to the relationships P[capture]_{strike} versus S:C ratio, and P[capture]_{encounter} versus S:C ratio.

A quadratic equation was fitted to the number of head-shakes performed by cod after capturing shrimps with an S:C ratio > 0.19 in Experiment 1 (section 4.3.1.iv).

Handling times measured in Experiment 1 were analysed initially by multiple regression. To test whether the relationship between handling time versus S:C ratio differed between small and large cod, separate linear regressions were fitted to log-transformed data

(Fig. 4.6 b), and differences between their respective slopes and elevations were tested by analysis of covariance.

Chi squared tests were used for comparing the accuracy of feeding strikes by cod at the sediment (section 4.3.2.ii). A Goodness of Fit test was used for comparing $P[\text{capture}]_{\text{strike}}$ and $P[\text{capture}]_{\text{encounter}}$ values derived from Experiments 2 and 3 (section 4.3.3.ii).

A Kruskal-Wallis test was used for comparing the number of strikes in an encounter (section 4.3.2.iii) and the duration of pursuits (section 4.3.2.iv) between shrimps of different lengths in Experiment 2.

4.3

RESULTS

4.3.1 Experiment 1 (small arena, hard substratum, visible lighting)

4.3.1.i Description of encounters between cod and shrimps

During experiments, shrimps spent the majority of time stationary on the substratum of the arena, although they occasionally walked about. A minimal amount of time ($< 1\%$) was spent pleopod swimming in mid-water.

When the screen between the cod and the shrimp was lifted at the beginning of a trial, the cod usually remained motionless for a period (probably a defensive behaviour in response to the movement of the screen, as described by Brawn, 1969), before starting to swim about the arena.

An encounter was initiated by the cod swimming directly towards the shrimp and approaching to within a few centimetres of it. An escape response by the shrimp was either initiated before the cod performed a feeding strike or was delayed until one occurred, and consisted of either a single or multiple tail flip response (reaction distances from some trials are presented in section 3.3.2). A feeding strike consisted of a rapid lunge forward by the cod, accompanied by a rapid opening of the mouth and expansion of the buccal apparatus (see Fig. 4.2 for an example of this). If no escape occurred, or the escape was too late, the shrimp was caught by the cod. In the event of a successful escape, the cod sometimes pursued the shrimp until it had captured it, but in other instances it terminated the encounter without a capture.

After 1 hour, trials with both the small (61-72 mm) and large (92-107 mm) cod resulted in 100 % of shrimps with an S:C ratio < 0.20 being consumed, compared with

approximately 85 % of those with an S:C of between 0.20-0.30, and approximately 25% of those with a ratio > 0.30. Shrimps were either consumed immediately, or in the case of larger shrimps, they were consumed after a period of manipulation within the cod's mouth. An increasing amount of manipulation was required as the S:C ratio increased. Often, this served the purpose of re-orientating the shrimp in the cod's mouth to facilitate swallowing. Small shrimps were swallowed immediately, but large shrimps were usually swallowed by grasping the shrimp dorsally on the cephalothorax or at the abdominal-thoracic joint, with the long axis of the shrimp across the cod's mouth. This caused the shrimp to fold in half as it was swallowed. However, a proportion of large shrimps were also swallowed either head- or tail-first.

Some shrimps, particularly relatively large ones, managed to escape from the cod's mouth (secondary escape) as the cod was manipulating them into position for swallowing. In addition to this, shrimps with an S:C ratio greater than 0.20 were increasingly likely to be dropped or forcibly ejected from the fish's mouth. When this occurred, the cod returned to the shrimp either to consume it, or to perform short biting actions before eventually rejecting it altogether. Such rejections after capture only occurred with two shrimps, and these had S:C ratios of 0.35 and 0.41. The largest shrimps which cod were observed to consume had S:C ratios of 0.36 (small cod) and 0.30 (large cod).

When a relatively large shrimp was caught, the cod sometimes performed an extremely rapid 'head-shaking' motion. These head-shakes occurred in a series of one or more bouts, between which the cod carried the shrimp in its mouth, or deposited it on the substratum. In some cases, head-shakes resulted in physical damage sufficient to incapacitate the shrimp if it was released, and also resulted in the loss of various of the shrimp's appendages.

4.3.1.ii Probability of shrimps being caught

A total of 344 individual approaches by cod (including those which involved a strike) resulting in an escape or capture of a shrimp were observed. The probability of capture per approach ($P[\text{capture}]_{\text{approach}}$) was found to decline as the S:C ratio increased for both the small (61-72 mm) and large (92-107 mm) cod (Fig. 4.3 a). The results for small and large cod are in close agreement with one another, and a logistic regression was fitted to the combined data sets such that:

$$P[\text{capture}]_{\text{approach}} = \frac{e^{(0.82 - 11.55S:C)}}{(1 + e^{(0.82 - 11.55S:C)})} \quad (4.1)$$

(Chi-squared test, $p < 0.0001$; model accounts for 87 % of the variation in $P[\text{capture}]_{\text{approach}}$). Therefore, for a given length of cod, there is a significant trend for small shrimps to be caught more readily than larger ones.

4.3.1.iii Probability of shrimps escaping once they had been caught (secondary escapes)

Above an S:C ratio of 0.19, shrimps were sometimes able to escape from the cod's mouth once they had been caught (secondary escape), although if this happened, cod were still able to re-capture the shrimp with further strikes. The probability of a secondary escape occurring per capture ($P[\text{secondary escape}]_{\text{capture}}$) increased with S:C ratio for both the small and large cod, and the relationship for the combined data (see Fig. 4.3 b) was described by the logistic regression:

$$P[\text{secondary escape}]_{\text{capture}} = \frac{e^{(11.24S:C - 4.11)}}{(1 + e^{(11.24S:C - 4.11)})} \quad (4.2)$$

(Chi-square test; $p = 0.004$; model accounts for 76 % of variation).

4.3.1.iv Head-shake behaviour

Head-shake behaviour was only observed in cod (both small and large) feeding on shrimps with S:C ratios equal or greater than 0.19. Each head-shake had a duration of approximately 80-240 ms. If they occurred, the total number head-shakes performed by a cod varied in number between 1 and 24, and generally increased as the relative length of the shrimp increased. For S:C ratios > 0.19 , the number of head-shakes which the cod performed on shrimps which were consumed was described by the quadratic equation:

$$\text{Number of head-shakes} = 185(S:C)^2 - 30.6(S:C) \quad (4.3)$$

where S:C is the shrimp:cod length ratio (Analysis of variance, $p < 0.0001$; see Fig. 4.4).

4.3.1.v Handling time required to consume shrimps of different lengths

Analysis of handling times included 10 trials using cod of an intermediate length (71-92 mm), in addition to the trials using small and large cod. In cases where shrimps were fully consumed ($n = 48$), handling time (which included time spent head-shaking) varied between 1 and 194 seconds. For a given cod length, small shrimps required a shorter handling time than did large ones and, for a given shrimp length, small cod took longer to handle the prey than did large ones (Fig. 4.5 a). Above an S:C ratio of about 0.2, handling times started to increase notably, and became increasingly variable.

In order to determine whether the handling time required to consume a shrimp of a given S:C ratio varied between cod of different lengths, two tests were performed. In the first test, the estimated handling time for a given combination of cod and shrimp lengths was predicted by fitting the multiple regression:

$$\log(\text{HT}) = 3.56 - 3.71 \log(L_C) + 3.87 \log(L_S) \quad (4.4)$$

where HT is the handling time (seconds), and L_C and L_S are the cod length (mm) and shrimp lengths (mm) respectively (Analysis of variance, $p < 0.0001$, $r^2 = 0.62$; see Fig. 4.5 b). From this equation, it was also possible to plot the predicted handling times against S:C ratio for given lengths of cod. This model predicted that cod length had very little effect upon the predicted handling time for shrimps of a similar S:C ratio, and the differences which did occur were considerably less than the observed variability in handling times (see Fig. 4.6 a).

In the second test, a linear regression was fitted to the \log_{10} (handling time) versus S:C ratio for cod lengths of 61-82 mm, and a separate regression for cod lengths of 89-110 mm (Fig. 4.6 b). The slope and elevation of these regressions did not differ significantly from one another (Analysis of covariance; for slope, $F_{1, 34} = 0.6$, $p = 0.8$; for elevation, $F_{1, 35} = 0.55$, $p = 0.46$), again indicating that the handling time for a shrimp of a given S:C ratio did not differ significantly with cod length.

Therefore, it is possible to describe handling times for all cod of between 61-107 mm by the simple regression equation:

$$\log_{10}(\text{HT}) = 8.63(\text{S:C}) - 0.657 \quad (4.5)$$

where both the coefficient and constant are significant (Analysis of variance, $p < 0.0001$, $r^2 = 0.65$; see Fig. 4.6 c).

4.3.1.vi Effect of handling time upon the profitability of shrimps

The effect of handling time upon the profitability of shrimps to cod was calculated by dividing the dry weight of the shrimp by the measured handling time in each instance in which a shrimp was fully consumed, such that:

$$\text{Observed profitability (g.s}^{-1}\text{)} = \text{DW/HT} \quad (4.6)$$

where DW is the dry weight of the shrimp (g), and HT is the measured handling time (s). Dry weight of *Crangon crangon* of different lengths was estimated from the equation derived for *C. crangon* by Kils (1982), whereby:

$$\text{DW} = 1.32 \times 10^{-6} (\text{L}_s^{3.18}) \quad (4.7)$$

where L_s is the total shrimp length (mm) (r^2 of regression = 0.97).

Fig. 4.7 a shows that the profitability of shrimps of different lengths fed to cod of between 61 and 107 mm is highly variable (due to variability in the measured handling times). However, shrimps towards the middle of the S:C range were more profitable, on average, than either shrimps with a very small S:C ratio, or those approaching the maximum length consumable for a particular length of cod.

Fig. 4.8 shows the same data, with the mean profitabilities plotted against 6 categories of S:C ratios for cod of 61-82 mm, ($n = 25$), and cod of 89-107 mm ($n = 23$). For 61-82 mm cod, the S:C category with the greatest mean profitability had a range of 0.13-0.17. For 89-107 mm cod, the greatest mean profitability also occurred at an S:C category with the range 0.13-0.17, although the profitability at an S:C of 0.18-0.20 was very similar. In neither case could the peak in the curve be explained by the appearance of disproportionately large cod within the optimal S:C category (disproportionally large cod within any one category would lead to spuriously high profitabilities because they are able to consume larger shrimps).

These data were compared with the profitabilities to cod of different lengths which were derived by dividing shrimp weight by the handling time predicted by the regression shown in **equation 4.5**, such that:

$$\text{Predicted profitability (g.s}^{-1}\text{)} = (\text{DW}) / (\text{predicted HT}) \quad (4.8)$$

where dry weight was calculated from **equation 4.7**, and the predicted handling time from **equation 4.5**. The results generated by this model are shown in **Fig. 4.7 b**; for all lengths of cod between 60-110 mm, it predicts that the peak profitability of shrimps occurs at an S:C ratio of 0.16.

Therefore, although profitabilities are naturally very variable due to the inconsistent nature of the shrimp handling times, the observed profitabilities and the predicted profitabilities suggest that, on average, shrimps with an S:C ratio of approximately 0.16 are the most profitable in terms of handling time once they have been caught. The profitability of very small shrimps is constrained by their low dry weights, whilst the profitability of very large shrimps is constrained by their disproportionately long handling times.

4.3.2 Experiment 2 (large arena, sand substratum, visible lighting)

4.3.2.i Description of shrimp and cod behaviour

Shrimps spent the majority of time (> 90 %) during experiments buried within the sediment, only rarely emerging unless they were attacked by a cod. Therefore, unless caught by a cod, or provoked into performing an escape response, they were not normally visible on the video monitor during analysis.

The behaviour of the cod when it was not engaged in an encounter with a shrimp could be grouped into 3 categories; it either remained motionless near the bottom of the arena, swam in mid-water, or swam slowly near the substratum with the barbel on its lower jaw close to the sand, and its caudal fin raised off the bottom. This third behavioural category resembles the foraging behaviour of cod described by Brawn (1969) & Døving & Selset (1980) (see **Fig. 4.9**).

During foraging behaviour, a cod moved its head from side to side across the sediment, and often searched around the edges (or underneath) obstacles within the arena. When it

detected a shrimp, its activity typically increased, and this was often followed by 1 or more feeding strikes directed towards the sediment. Immediately preceding a strike, the angle of the cod with respect to the substratum increased so that the bite was directed almost vertically downwards. The actual strike consisted of a rapid lunge forward, accompanied by an opening of the mouth, and a rapid expansion of the buccal apparatus. Strikes were not always aimed directly at a shrimp. If no encounter resulted from a strike (i.e. the shrimp was not caught, or no escape occurred), the cod subsequently cleared any ingested sediment from its mouth over a period of several seconds using a combination of jaw and operculum movements. This sediment clearing behaviour was also observed when a small shrimp was caught, enabling the shrimp to be consumed, whilst any ingested sediment was rejected.

It was also observed that when a shrimp emerged from the sediment and moved to a different area of the arena, the cod remained interested in the shrimp's initial location, reversing to re-inspect the patch and perform feeding strikes if it passed over the area. This suggests that chemical cues are important in enabling cod to detect buried shrimps. However, recent chemical cues from shrimps were not essential for a strike to occur. In a few trials in which an individual cod was placed in the arena with cleaned sand and no shrimps, some strikes at the sediment were still observed.

The time to the first feeding strike of a trial (an indication of willingness and motivation of the cod to feed) varied between 2 and 60 minutes, except in one of the experiments with 14 mm shrimps in which virtually no foraging behaviour or strikes were observed during the entire 2 hour period of the trial.

Although shrimps rarely emerged from the sediment, when they did, the cod was able to detect them visually, and some encounters were initiated as a result of this, particularly when shrimps were mobile on the sediment surface. Therefore, an encounter could be initiated in one of two ways: either by a foraging cod striking at a buried shrimp, or by a cod (not necessarily foraging) striking at an emerged shrimp in response to predominantly visual cues.

Following the initial strike of an encounter, the shrimp was either caught by the cod, or it escaped. If a shrimp successfully evaded the initial strike, the cod sometimes responded by pursuing it. During a chase, the cod attempted to capture the shrimp with further strikes, either whilst the shrimp was tail flipping, or more often, once it had re-settled on the sediment. If a shrimp was not caught at the end of an encounter, this was either because the cod had lost sight of the shrimp (e.g. it sometimes escaped behind the cod), or because the cod terminated

the chase. It was usually not possible to distinguish with confidence between these two causes, but chase termination was evident in encounters with large (38 mm) shrimps which, having become exhausted by tail flip swimming, reverted to a much slower form of pleopod swimming. In such an event, the cod was able to track the shrimp at close quarters, leaving or returning to it at will, until it finally abandoned the encounter.

On some occasions, shrimps managed to perform a secondary escape whilst being handled by a cod, and the likelihood of this occurring agreed well with the results from Experiment 1 (section 4.3.1.iii).

Head-shaking behaviour was observed when shrimps of between 20-38 mm were caught. The number of head-shakes in relation to S:C ratio agreed well with the observations in Experiment 1 (section 4.3.1.iv), with the exception that fewer were performed than predicted by equation 4.3 when feeding on 38 mm shrimps (all of which were rejected after capture).

During the 13 trials within Experiment 2, a total of 73 encounters consisting of 166 strikes were observed, and the outcome of these are described below, and summarised in Table 4.2.

4.3.2.ii Accuracy of feeding strikes at buried shrimps

The majority of encounters (71-95 % - some could not be confirmed) started with a cod locating a buried shrimp rather than one which was on the surface of the sediment (Fig. 4.10 a), and the frequency of this did not differ significantly between trials in which shrimps of different lengths were used (Chi-square test; $\chi^2 = 3.02$, $df = 3$, $p > 0.25$). However, when the cod was foraging, only a small proportion of strikes towards the sediment resulted in an encounter. In experiments with 14 mm shrimps, the mean frequency was only 3.9 % of strikes (s.e. = 3.9, $n = 2$ trials, 131 strikes), compared with 19.9 % (standard error = 7.2, $n = 3$ trials, 99 strikes) with 20 mm shrimps, 30.3 % (s.e. = 7.8, $n = 4$ trials, 68 strikes) with 30 mm shrimps, and 21.0 % (s.e. = 6.8, $n = 3$ trials, 98 strikes) with 38 mm shrimps (Fig. 4.10 b). These frequencies were not equal between the different length categories of shrimps (Chi-squared test; $\chi^2 = 14.31$, $df = 3$, $p < 0.01$).

4.3.2.iii Number of strikes in an encounter

The proportions of encounters which resulted in a pursuit by the cod were 33 % (14 mm shrimps, $n = 12$ encounters), 67 % (20 mm, $n = 21$), 80 % (30 mm, $n = 20$), and 75 % (38 mm, $n = 20$), and the median numbers (and ranges) of strikes per encounter were 1 (1-3), 2 (1-5), 2 (1-8) and 1.5 (1-7) respectively (**Fig. 4.11**). The number of strikes per encounter with 14 mm and 30 mm shrimps were significantly different from one another (Kruskal-Wallis test adjusted for ties, $H = 8.16$, d.f. = 3, $p = 0.043$, followed by multiple comparison test in which $p < 0.05$), whilst differences between the other groups were not significantly different.

For those shrimps which were caught at the end of an encounter ($n = 7, 12, 7$ and 5 for 14-38 mm shrimps respectively), the median number of strikes (and range) required to capture them increased with shrimp length from 1 (1-3) to 1 (1-3), 3 (1-8) and 3.5 (1-6) for, 14, 20, 30 and 38 mm shrimps respectively. The values for 14 mm versus 30 mm shrimps, and 14 mm versus 38 mm shrimps were significantly different from one another (Kruskal-Wallis adjusted for ties, $H = 16.33$, d.f. = 3, $p = 0.001$, followed by multiple comparison test in which $p < 0.05$ in both instances).

4.3.2.iv Duration of encounters

In accordance with the number of strikes per encounter increasing with shrimp length, the duration of encounters also increased (**Fig. 4.12**). Pursuit times ranged from < 1 s to 20.7 s (0 s was allocated to single strike encounters with no subsequent chase), with median (and range) pursuit times of 0 s (0-3.2 s), 2.1 s (0-5.8 s), 2.9 s (0-14.5 s), and 3.8 s (0-20.7 s) for 14, 20, 30 and 38 mm shrimps respectively. The differences in the pursuit times between 14 mm versus 30 mm, and 14 mm versus 38 mm shrimps were significant (Kruskal-Wallis test adjusted for ties, $H = 9.95$, d.f. = 3, $p = 0.019$, followed by multiple comparison test in which $p < 0.05$ in both instances).

4.3.2.v Behaviour of shrimps and cod during a pursuit

Shrimps which were buried within the sediment very rarely tail flipped in response to a cod foraging nearby, even when feeding strikes were directed towards the sediment within a few centimetres of them. Therefore, escapes only occurred when a feeding strike either made direct contact with a shrimp, or was directed immediately adjacent to it. Cod responded to an escape in a variety of ways, although in some situations (but only with 14 and 20 mm

shrimps), no visible reaction by the cod was observed. On other occasions, the cod rapidly turned toward the direction in which the shrimp escaped, and either proceeded no further, or started to pursue the shrimp.

The shrimp's escape consisted of a series of multiple tail flips. The initial escape translated the shrimp to a new location on the sediment surface where, upon landing, it would usually start to re-bury itself. When a chasing cod was able to see where the shrimp landed, it swam directly towards the location and attempted to catch the shrimp with another strike before the shrimp was able to bury itself. This resulted in a further tail flip swimming bout if the shrimp was not caught, and the chase continued in this manner until the cod either lost sight of the shrimp, terminated the pursuit, or caught the shrimp. Sometimes when a cod appeared to lose sight of an escaping shrimp, it would approach the vicinity where the shrimp landed at the end of a chase and start foraging actively in that area.

An example of the trajectories followed by a 20 mm shrimp being pursued by a 102 mm cod during Experiment 2 is shown in **Fig. 4.13 a**. From this sequence, it is evident that both the relative velocity (**Fig. 4.13 b**) and manoeuvrability of the shrimp and cod during a pursuit have a strong influence upon the shrimp-to-cod distance (**Fig. 4.13 c**), and that the shrimp is able to exploit the reaction time of the cod in responding to manoeuvres made by the shrimp. The sequence starts at the beginning of an escape swimming bout in which, after tail flipping for 80 ms (\cong 6.5 cm, or approximately 1-2 tail flips - see **section 2.3.4**) the shrimp abruptly changed its trajectory by 50° and continued along a new, roughly linear, trajectory. The cod chased the shrimp in a series of rapid ballistic bursts. The first burst was initiated 120 ms after the shrimp escaped from the sediment, and was directed towards the shrimp's concurrent position at the beginning of the cod's burst. The cod's trajectory intersected that of the shrimp after a further 120 ms, but by this time, the shrimp had escaped beyond the interception path of the cod. Therefore, the cod had to reassess the shrimp's position, and turn a full 90° in order to re-align itself before the next burst. The velocity of the cod declined to zero during this manoeuvre, and therefore the relative distance separating the two increased. The time taken by the cod between missing the shrimp (i.e. intersecting its path) and initiating its second burst was between 160 and 200 ms. The cod then accelerated once more towards the shrimp, but the shrimp had swum out of the camera's field of view by the time that their paths intersected again.

During the pursuit, the velocity of the shrimp fluctuated between 0.4 and 0.9 m.s⁻¹ (mean = 0.64, sd = 0.15) according to the flexion and re-extension phases of the tail flip swimming action (Fig. 4.13 b). The velocity of the cod was much more variable, ranging between 0 and 1.3 m.s⁻¹, and although it was capable of achieving a greater maximum velocity than the shrimp, it had a lower overall mean velocity (mean = 0.49 m.s⁻¹, sd = 0.35). Therefore, if a cod performs an unsuccessful strike, the shrimp is able to exploit the time taken by the cod in realigning itself in order to maximise the distance separating the two (Fig. 4.13 c) before landing on the sediment and re-burying itself. Re-burial was usually achieved within 10 seconds of landing (see Fig. 4.14).

4.3.2.vi Probability of shrimps being caught

The probabilities of a shrimp being caught per strike (P[capture]_{strike}) were 0.47 (14 mm shrimps), 0.26 (20 mm), 0.13 (30 mm), 0.10 (38 mm). The relationship between shrimp length and P[capture]_{strike} is described by the logistic regression:

$$P[\text{capture}]_{\text{strike}} = \frac{e^{(0.69 - 8.17S:C)}}{(1 + e^{(0.69 - 8.17S:C)})} \quad (4.9)$$

(Chi-square test, $p = 0.001$, model accounts for 81 % of the observed variation in P[capture]_{strike}).

Fig. 4.15 a shows the observed P[capture]_{strike} data, and the line predicted by equation 4.9. Both the observed and predicted values are greater than values predicted for P[capture]_{approach} in Experiment 1 (equation 4.1), and this difference was significant (Goodness of Fit test, $\chi^2 = 13.71$, $df = 2$, $p < 0.005$).

The probabilities of being caught during an encounter (P[capture]_{encounter}) were 0.58 (14 mm shrimps), 0.57 (20 mm), 0.35 (30 mm) and 0.25 (38 mm). The relationship between shrimp length and P[capture]_{encounter} was described by the logistic regression equation:

$$P[\text{capture}]_{\text{encounter}} = \frac{e^{(1.47 - 6.76S:C)}}{(1 + e^{(1.47 - 6.76S:C)})} \quad (4.10)$$

(Chi-square test, $p = 0.034$; model accounts for 61 % of the observed variation; see Fig. 4.15 b).

4.3.2.vii Probability of shrimps being consumed

Fig. 4.16 shows the number of shrimps consumed by cod during each 2 hour trial in Experiment 2. Shrimp consumption varied considerably between the 3 fish exposed to 14 mm shrimps, since one of the cod foraged very actively and consumed 7 shrimps, whilst the remaining two did not forage extensively, and consumed no shrimps. All shrimps of this length that were caught were consumed. The 3 cod feeding on 20 mm shrimps consumed between 2 and 6 individuals, and again, all captures resulted in the shrimp being consumed. However, in the 4 trials with 30 mm shrimps, cod consumed only 1-2 individuals each, and 1 shrimp was rejected after it had been captured. With both 20 and 30 mm shrimps, the greatest number of shrimps eaten by a single cod (6 and 2 respectively) represent approximate maxima which the cod were able to consume, since their stomachs were very full when they were examined at the end of each respective trial. The incident in which a 30 mm shrimp was rejected probably occurred because the cod had consumed a similarly sized shrimp 23 minutes earlier, although in one of the other trials, a cod was observed to consume a second 30 mm shrimp within 14 minutes its first.

Five 38 mm shrimps were captured by cod, but none was consumed whole, and they were instead rejected. However, two of the three cod managed to remove appendages from a 38 mm shrimp by performing head-shakes and biting actions. Consequently one of these cod consumed 2 uropods, and the other consumed 1 cheliped and 1 pereopod.

4.3.2.viii Handling time

For cod feeding upon 14 and 20 mm shrimps, there was no obvious change in handling time as cod became more satiated. Handling times of between 1-14 s (mean = 5.0 s) were observed with 14 mm shrimps, and between 4-36 s (mean = 15.1 s) with 20 mm shrimps (*cf.* 4 s and 12 s respectively in Experiment 1, as predicted by **equation 4.5** for a cod feeding upon a single shrimp). The 36 s handling time recorded for a 20 mm shrimp was for the first in a series of 6 shrimps which were eaten; the cod required only 4 seconds to consume a second shrimp.

However, for cod feeding upon 30 mm shrimps, the two trials in which cod consumed 2 shrimps each indicated that handling time did increase considerably for the second shrimp. In one of these instances, the cod required approximately 10 minutes to consume the second shrimp. The mean handling time per shrimp was 338.7 s (*cf.* 86 s predicted by **equation 4.5**).

At the end of the two trials in which cod consumed two 30 mm shrimps, it was evident that the cod's stomach was completely full; in one instance the telson and uropods of one shrimp were protruding into the cod's oesophagus, and were visible through its mouth.

These observations suggest that the effect of satiation upon handling time becomes particularly marked only when the volume of the food item being consumed approaches or exceeds the available stomach capacity. Prior to this, the natural variability in handling time (section 4.3.1.v) is a more important factor causing variability in the time required to consume successive shrimps.

4.3.2.ix Effect of handling and pursuit times upon the profitability of shrimps

The effect of pursuit time on the profitability of shrimps was estimated for each cod (except those feeding on 38 mm shrimps) using the equation:

$$P = \frac{(\text{Total DW consumed}) / (\text{Total HT} + \text{Total PT})}{(\text{Total number of shrimps consumed})} \quad (4.11)$$

where P = the profitability ($\text{g}\cdot\text{s}^{-1}$), Total DW = the total dry weight of shrimps consumed (derived from equation 4.7), Total HT = the total handling time required to consume all shrimps, and Total PT = the total time spent pursuing all shrimps (including those that were not caught). These results were compared with the profitabilities calculated by the same method, but omitting the pursuit times (see Fig. 4.17).

In the single trial in which a cod successfully located and consumed 14 mm shrimps, all 7 shrimps which it consumed were included in the calculation of equation 4.11. However, for the 3 trials in which cod which fed upon 20 mm shrimps, only the first 2 shrimps consumed in each trial were evaluated. Therefore, at this stage, both categories of cod had consumed a similar mass of food (approximately 0.04 g dry weight). For the 4 cod which fed upon 30 mm shrimps, only the first shrimp consumed was evaluated (total dry weight consumed each \approx 0.07 g).

When pursuit times were omitted, the mean profitability of shrimps (\pm s.e.) was estimated to be $1.15 \text{ mg}\cdot\text{s}^{-1}$ (± 0 , $n = 1$ cod), $1.41 \text{ mg}\cdot\text{s}^{-1}$ (± 0.44 , $n = 3$) and $0.35 \text{ mg}\cdot\text{s}^{-1}$ (± 0.08 , $n = 4$) $\text{mg}\cdot\text{s}^{-1}$ for 14, 20 and 30 mm shrimps respectively. When pursuit times are included, profitabilities decline, but their ranking with respect to shrimp length remained unchanged (mean \pm standard error for 14 mm shrimps was $0.86 \pm 0 \text{ mg}\cdot\text{s}^{-1}$; for 20 mm

shrimps, $0.91 \pm 0.13 \text{ mg.s}^{-1}$; and 30 mm shrimp, $0.34 \pm 0.08 \text{ mg.s}^{-1}$). Therefore, pursuit time reduces the profitability of 14 mm shrimps by approximately 25 %, and the profitability of 20 mm shrimps by approximately 35 %. The profitability of 30 mm shrimp remains virtually unchanged (3 % difference) because pursuit times are negligible compared to the very long handling times.

4.3.3 Experiment 3 (large arena, sand substratum, infrared lighting)

4.3.3.i Description of shrimp and cod behaviour

In the single trial conducted under infrared lighting, shrimps were more likely to emerge from the sediment than those under visible lighting in Experiment 2, and several shrimps were sometimes visible on the video monitor simultaneously, either motionless on the sediment surface, or moving about it. Consequently, the proportion of shrimps which were buried at the beginning of an encounter was lower than in Experiment 2; in the dark, the proportion of encounters in which shrimps were buried was between 27 and 45 % ($n = 22$; in some cases, it was not possible to confirm whether they were buried or not), compared with 90 % ($n = 20$) in Experiment 2 (Chi squared test on closest estimates; $\chi^2 = 9.35$, d.f. = 1, $p < 0.005$).

The cod in Experiment 3 foraged very actively in the absence of visible light. Encounters were initiated only when the cod had approached to within a few centimetres of a shrimp, regardless of whether the shrimp was buried or not; there was no indication that the cod was able to detect shrimps visually. In a few instances, when the cod approached a shrimp which had emerged from the sediment, the shrimp tail flipped 1 frame (20 ms) before the cod initiated a feeding strike, suggesting that the strike by the cod may have occurred at least partly in response to the water-borne vibrations caused by the tail flip itself. Following an escape, the cod occasionally responded by rapidly turning towards the point from which the shrimp had escaped, but a subsequent chase never occurred.

4.3.3.ii Probability of shrimps being caught in the dark

The outcome of encounters in Experiment 3 are summarised in **Table 4.2**. A total of 22 encounters were observed, all consisting of just a single strike by the cod towards the shrimp. As a result of these encounters, 1 shrimp was caught and consumed during the trial.

Although the probability of being caught per strike in the dark was not significantly different from that of the same sized shrimps in the light (Experiment 2) (Chi squared test; $\chi^2 = 1.18$, 1 d.f., $p > 0.10$), the probability of being caught per encounter was significantly lower (Chi squared test; $\chi^2 = 6.30$, 1 d.f., $p < 0.025$) because no pursuits occurred.

4.4

DISCUSSION

4.4.1 The role of tail flip swimming in *Crangon crangon* as an anti-predation mechanism

Tail flip swimming is energetically demanding because it requires vigorous activity of large anaerobic muscles, and these constitute a large proportion of the shrimp's biomass. The abdominal muscles used for tail flipping become energetically depleted after about 50 tail flips, and although ATP levels are restored within minutes, full recovery takes considerably longer, with lactate levels remaining elevated for a number of hours after exhaustive swimming (Onnen & Zebe, 1983; Kamp & Juretschke, 1987; Kamp, 1989; Gruschczyk & Kamp, 1990). Therefore, the cryptic colouration of *Crangon crangon*, and their ability to bury within sediment (Pinn & Ansell, 1993), are also important defences in avoiding predation because they reduce the likelihood of an encounter with a predator occurring.

As reported previously by other workers (e.g. Hagerman, 1970; Al-Adhub & Naylor, 1975; van Donk & de Wilde, 1981; Burrows *et al.*, 1994), the activity of *Crangon crangon* on the sediment surface coincided with periods when they were least likely to be detected by visual predators. Shrimps under visible light (Experiment 2) spent the majority of time buried, whilst those in the dark (Experiment 3) emerged more frequently. This is made more important by the fact that the chelae of *C. crangon* are comparatively small, and although they are used for capturing prey items (Gibson *et al.* 1995), they are ineffective weapons against predators (in contrast to some larger crustaceans, e.g. Wahle, 1992; Mather & Stein, 1993; Garvey *et al.*, 1994).

Burying behaviour in *Crangon crangon* affects the distance from a predator at which they will initiate a tail flip response. When shrimps had no sediment in which to bury (Experiment 1), tail flips were initiated when cod were between 1 and 5 cm away (see section 3.3.2) and often occurred before the cod had begun a strike, but when shrimps were buried (Experiments 2 and 3) tail flips were usually suppressed until an actual strike occurred, even

when the cod was foraging in the immediate vicinity of the shrimp. This agrees with the findings of Smith (1993), who also observed an inverse relationship between the degree of burial and the reaction distance in *C. crangon*.

An analogous situation has been reported by Heatwole (1968) in the two lizard species *Anolis stratulus* and *A. cristatellus*. When these species are perched upon the bark of a tree, individuals may differ in their degree of crypsis, and those that are more visible flee earlier in response to an approaching person than do the less visible ones. Ydenberg & Dill (1986) have suggested that well-camouflaged animals have reduced reaction distances because, at a given distance from an approaching predator, they are less likely to be detected, and can conserve energy by remaining stationary. The high energetic cost of tail flipping in *Crangon crangon* highlights the importance of this strategy. Furthermore, by escaping too soon, concealed prey may increase their vulnerability by revealing their location to an otherwise unaware predator. This would certainly appear to be true in the case of *C. crangon*, since movement by a shrimp was a strong stimulus in provoking an attack by a cod. Brawn (1969) also reported that cod were more willing to accept moving rather than stationary food items, and numerous other fish predators also initiate feeding in response to movement (e.g. Kislalioglu & Gibson, 1976b; Holmes & Gibson, 1986; Croy & Hughes, 1991b).

An additional (or opposing) argument explaining the late responses of buried shrimps to approaching cod may be that burying impairs the sensory perception of shrimps, and so escape thresholds are only exceeded once a predator has approached more closely. Visual cues are important in eliciting escape responses in *Crangon crangon* (Smith, 1993; Berghahn *et al.*, 1995; section 3.4.1), but it seems unlikely that a buried shrimp's view of an approaching cod is obscured because the eyes of *C. crangon* protrude above the sediment surface when they are buried (Pinn & Ansell, 1993; personnel observations). Water-borne mechanosensory cues may also be important in provoking an escape, and these are detected by sensory hairs dispersed over various regions of the shrimps body (Heinisch & Wiese, 1987; Berghahn *et al.* 1995). It is possible that these hairs are less sensitive in response to an approaching predator when shrimps are buried, because many of the body parts which possess sensory hairs, such as the uropods, are concealed within the sediment. However, the antennae, and sometimes the antennules, remain exposed above the sediment surface when a shrimp is buried (Pinn & Ansell, 1993), and these possibly assume the main mechanosensory role when in this state.

An internal (physiological) adjustment to the tail flip threshold level of *Crangon crangon* offers a further possible mechanism explaining the reduced reaction distances of buried shrimps, and is supported by the observation that physical contact with other objects can result in an adjustment to the tail flip threshold in other decapods (Krasne & Wine, 1975). Similarly, the escape response of the cockroach *Periplaneta americana* is suppressed when their antennae are in contact with surrounding objects (indicating that they are in a confined space), and this is believed to be due to an internal adjustment of the escape threshold level (Watson & Ritzmann, 1994).

The benefit to buried shrimps of remaining stationary in the presence of a predator is further highlighted by the comparatively low proportion (4-30 %) of strikes directed towards the sediment that result in an encounter. The ability of cod to accurately locate shrimps may be even lower than this in natural situations, because the sediment used in the experiments was regularly cleaned, whereas natural sediments, with constant faunal activity on and within them, probably have a higher chemical loading which would partially mask any chemical attractants released by the shrimps (discussed below in **section 4.4.2**).

4.4.2 Location of shrimps by cod

Fish are able to use a variety of senses for detecting prey, and those employed depend upon the fish's morphological and physiological characteristics, the prevailing habitat conditions, and the type of prey that is being sought. As particular circumstances change with time and space, the reliance upon different sense(s) may shift (Jobling, 1995).

When no sediment was present (Experiment 1), encounters occurred as a result of the cod detecting shrimps primarily by vision, since the shrimps were conspicuous upon the white substratum of the arena. In experiments with sediment, the cod were usually unable to see the shrimp before the first strike of an encounter, either because the shrimp was buried (Experiment 2; **Fig. 4.10 a**), or because there was insufficient visible light available (Experiment 3). Therefore, the cod were only able to locate shrimps whilst foraging, probably using a combination of olfactory, gustatory, and tactile senses. During foraging behaviour, the cod adopted a position with its head-down, and its barbel and pectoral fins in contact with the sediment, as described by Brawn (1969) and Døving & Selset (1980; see **Fig. 4.9**). Both the barbel and pectoral fins possess gustatory and tactile sensory organs. Innervation of these in various species of fish, including cod, was first examined by Herrick (1900, 1907), who

concluded that feeding strikes were initiated by tactile and gustatory stimuli acting together, but that a gustatory stimulus alone was also sufficient for this to occur. Brawn (1969) tested the gustatory response of the barbel and pectoral fins by offering cod fabric bags containing either mussels or an inert substance. Contact between a mussel-filled bag and the barbel or pectoral fins resulted in a feeding response in 70-80 % of trials, compared with no responses when control bags were encountered.

The function of olfactory senses during feeding by cod was studied by Døving & Selset (1980). Teleost fish possess a pair of nasal cavities on the dorsal side of their head, and the olfactory epithelia which line them are folded into a series of lamellae to form sensory rosettes (Hara, 1993). These are innervated, via the olfactory tracts, by four neural bundlets which originate from various locations in the brain (implying different functions). The experiments of Døving & Selset demonstrated that electrical stimulation of isolated nerve bundlets brought about specific behavioural responses. In particular, one of the bundlets, when stimulated, resulted in the cod adopting a head down position against the substratum, and caused it to move backwards over the surface. Higher stimulation intensities resulted in the fish swimming in a more vertical (head-down) position, and induced rapid turns. Other bundlets caused the cod to perform biting actions when they were stimulated at high intensities. Brawn (1969) also demonstrated the importance of olfactory cues by blocking the nasal cavities of a cod. This fish ceased to perform typical foraging behaviour until trained to do so by dropping large pieces of food, which could be located visually, on to the substratum.

Døving & Selset (1980) suggest that the food search behaviour elicited by olfaction is due to the presence of substances including and resembling amino acids, and these have also been implicated in stimulating feeding behaviour in a variety of other fish species (Carr, 1982; Hidaka, 1982; Mackie, 1982; Marui & Caprio, 1992; Takeda & Takii, 1992; Jones, 1992). Pawson (1977) found that cod were attracted particularly by the glycine and alanine in concentrations found in natural food sources.

The information above, and the observations made from video recordings of Experiments 2 and 3, provide compelling evidence that cod rely on chemosensory cues whilst foraging. In particular, this explains the attraction of cod towards patches of sediment recently vacated by shrimps, and the fact that a considerable proportion of strikes towards the sediment resulted in no encounter (Fig. 4.10 b), either because a shrimp had vacated the patch, or

because strikes were directed with poor accuracy at a shrimp when using chemosensory cues alone.

In Experiment 2, the virtual lack of feeding responses observed in two of the three trials in which cod were presented with 14 mm shrimps may have arisen because these smaller shrimps emitted insufficient chemical cues within the two hour period of each trial to stimulate foraging behaviour.

4.4.3 Size-dependent variability in P[capture]_{approach} and P[capture]_{strike}

The probability of a predator capturing a prey item once an encounter occurs depends upon a balance between the characteristics of both participants. In teleosts, mouth morphology plays an important role in determining the range of available prey species which they are able to feed upon, because this affects their feeding behaviour and the size of organisms they are able to consume. The mechanisms used by various types of fish to strike at prey form a spectrum, ranging from suction feeding to ram feeding (Norton, 1995), and in addition to this, many fish modify their strike in response to situation-specific circumstances such as prey type and position (e.g. Nyberg, 1971; Elshoud-Oldenhave & Osse, 1976; Janssen, 1976; Lauder & Norton, 1980; Liem, 1980; Rand & Lauder, 1981; Vinyard, 1982; Lauder, 1983; Wainwright, 1986; Wainwright & Lauder, 1988). Suction feeding relies upon maximising the drag force on the prey (Denny *et al.*, 1985), and is favoured by a small mouth gape as this increases the pressure differential between the buccal cavity and the ambient water (van Leeuwen & Muller, 1983; Lauder & Clark, 1984). By contrast, ram feeders initiate attacks from a greater distance, and typically have streamlined bodies, and a large gape that improves the capture probability by increasing the catching area of the mouth. Norton (1995) has shown that ram feeding fish with large gapes are more successful at catching elusive shrimps than fish with a small gape feeding by suction alone.

Cod may be classified as intermediate between suction and ram feeders (Mattson, 1990), and therefore may be expected to have a relatively high capture success when feeding on shrimps. Over a range of shrimp and cod lengths, a significant decline in P[capture]_{approach} was demonstrated as the S:C ratio increased (Experiment 1). Therefore, for a given length of shrimp, the probability of being caught increased with cod length, possibly because larger cod are able to achieve greater maximum velocities than smaller ones (Wardle, 1975), thereby reducing the time available for the shrimp to escape. In addition, the

size of the cod's gape and the volume of its buccal cavity increase with cod length (Robb & Hislop, 1980), thus increasing both the capture area of the mouth and the suction region created by expanding the buccal apparatus (Alexander, 1970). Therefore, the 'zone of interception' (a field with decreasing probability of capture from the centre outwards - Hart & Hamrin, 1990) will occupy a greater volume of water extending from the predator's mouth.

From the perspective of a cod of given length, the probability of capture declines as shrimps become larger (Figs. 4.3 a & 4.15 a). This can be explained, over the size range of shrimps used, by the increase in acceleration and velocity of tail flip escape responses as shrimps become larger (see Chapter 2). Therefore, shrimps are more likely to escape from the suction region and capture area of the mouth within the time taken to perform a strike (Hart & Hamrin, 1990). A similar size-dependent relationship was demonstrated by Buskey (1994), who, using a standardised artificial suction device, found that the probability of copepod nauplii (*Acartia tonsa*) being caught decreased exponentially as their escape ability improved during growth.

An interesting aspect of this relationship with respect to the tail flip performance of *Crangon crangon* (Chapter 2), is that above a length of approximately 40 mm, the tail flip velocity of shrimps starts to level off, and declines above a length of 50-60 mm (see Figs. 2.17 & 2.19). However, the maximum velocity of cod continues to increase with length (Wardle, 1975), as does their jaw size. Therefore, one would predict that, for cod which are large enough to feed upon shrimps of 40 mm and above, the $P[\text{capture}]_{\text{strike}}$ for a given S:C ratio would be greater than in smaller cod feeding upon shrimps less than 40 mm, but with the same S:C ratio.

The balance between strike and escape capabilities is more complex when shrimps are able to bury within sediment (Experiment 2), since escapes are delayed until the cod approaches within a closer distance than when they are not concealed (see section 4.4.2). Ydenberg & Dill (1986) recognised that there is a trade-off between concealment and the risk of capture. The results obtained from Experiment 2 show that although $P[\text{capture}]_{\text{strike}}$ declined exponentially, values for a given S:C ratio were significantly greater than $P[\text{capture}]_{\text{approach}}$ in Experiment 1 (Fig. 4.15 a). Therefore, although burying reduces the probability of an encounter occurring, by allowing predators to approach closer, a greater risk of being caught is incurred if the first strike is accurately directed towards the shrimp.

However, if a buried shrimp successfully evades the first strike of an encounter, the presence of sediment probably then reduces the chances of it being caught during a pursuit because it enables the shrimp to exploit its crypsis and burying ability to prevent it being seen by the pursuing predator when it lands back on the sediment. If the predator does see where the shrimp lands, an entire encounter may consist of a series of tail flip bouts interspersed with short periods when the shrimp is stationary on the sediment surface, as described by Tallmark & Evans (1986). An analogous strategy has been observed in a variety of cryptic animals; for instance, juvenile lizards of the species *Psammodromus algirus* flee only a short distance when attacked by a predator before they stop and resort to crypsis, but they keep the predator under surveillance in case another attack occurs (Martín & López, 1995).

Norton (1995) investigated the capture success of four species of cottid fish feeding upon the pandalid shrimp *Pandalus borealis*. He found $P[\text{capture}]_{\text{strike}}$ values in the region of 0.1-0.3 (he does not specify shrimp:fish length ratios, but from his data, mean ratios can be estimated to lie between 0.12 and 0.17). Therefore, his values are similar to, or lower than the values determined for cod feeding on *Crangon crangon*, although differences in experimental protocol make it unfeasible to draw direct comparisons between the two sets of data.

Beddow *et al.* (1995) found a $P[\text{capture}]_{\text{strike}}$ of 0.73 for short-horned sculpin (*Myoxocephalus scorpius*) attacking *Crangon crangon* at 15°C (shrimp:predator length ratios were approximately 0.12-0.20). *M. scorpius* is a ram feeder, and this may explain the higher strike success of this species in comparison to that of cod. The importance of strike velocity in determining the capture success was also revealed in a further set of experiments in which sculpin of the same size were acclimated at 5°C, but tested at 15°C. These fish achieved lower maximum strike velocities, and correspondingly, the $P[\text{capture}]_{\text{strike}}$ value fell to 0.23.

Rademacher & Kils (1996) found a $P[\text{capture}]_{\text{strike}}$ value of only 0.25 for 100 mm sticklebacks (*Spinachia spinachia*) feeding upon 10 mm individuals of the mysid *Neomysis integer* (shrimp:predator length ratio = 0.10). Mysids of this length have a similar maximum tail flip velocity to that of 10 mm *Crangon crangon* (see Table 2.3), but *S. spinachia* have a lower strike velocity than cod, and are also suction feeders.

4.4.4 Size-dependent variability in $P[\text{capture}]_{\text{encounter}}$

If the initial strike in an encounter was unsuccessful, cod sometimes pursued shrimps and caught them on subsequent strikes of the encounter. In Experiment 2, $P[\text{capture}]_{\text{encounter}}$

values were therefore greater than $P[\text{capture}]_{\text{strike}}$ values (Fig. 4.15), because the former represents an accumulating probability of the latter in encounters comprising more than 1 strike.

There was a significant decline in $P[\text{capture}]_{\text{encounter}}$ as S:C ratio increased, but the slope was considerably less steep than the decline in $P[\text{capture}]_{\text{strike}}$. Several factors probably contributed to this decline. Firstly, as shrimps increase in length, the reduction in $P[\text{capture}]_{\text{strike}}$ increases the likelihood that the shrimp will avoid capture during an entire encounter. However, the motivational state of the cod probably also played a significant role, especially with the largest (38 mm) shrimps, since all shrimps of this length that were captured were subsequently rejected. As a consequence of this, cod may reduce the effort invested in capturing 38 mm shrimps compared to shrimps of a consumable length. This is indicated by their chase behaviour, which transformed from a rapid pursuit into a much slower swim ('tracking behaviour') when 38 mm shrimps became exhausted whilst tail flipping.

Overall, $P[\text{capture}]_{\text{encounter}}$ values were probably overestimates of those that occur *in situ* because of the space-restriction imposed by the arena on the shrimps' escape swimming (the area of the arena was a compromise between providing sufficient space to allow shrimps to escape, and maximising video replay resolution for analysis purposes). Space restrictions affect the trajectory of a prey's escape from a predator, which is crucial in determining the outcome of an encounter (Howland, 1974; Weihs & Webb, 1984; also see section 1.6 and Chapter 3). However, many of the encounters resulted in shrimps making contact with the retaining wall, and once this occurred, shrimps were constrained to swimming along sub-optimal trajectories around the edges of the arena. This is more likely to have influenced large shrimps, because encounters with them were more likely to result in a pursuit.

4.4.5 Behaviour during pursuits (Experiment 2)

In Experiment 2, there was a general trend for pursuits to consist of more strikes and last longer as shrimp length increased (Figs. 4.11 & 4.12 respectively). This is attributable to the higher tail flip velocities achieved by larger shrimps, and their greater likelihood of evading each strike. Larger shrimps may also be more easy to visually track during a pursuit. No significant differences were found between 14 mm and 20 mm shrimps in duration of pursuit, number of strikes per pursuit, or, for those encounters leading to a capture, the number of strikes required by the cod to achieve a capture. This is probably because of the limited

number of observations made, the comparative similarity in lengths between the two shrimp groups, and the constraints imposed by being in a confined space. From the trend observed, one would expect shrimps smaller than 14 mm to be caught with less effort by the cod, but this was not testable because it was impossible to see shrimps of less than 14 mm reliably on the monitor during video analysis. It is possible that, *in situ*, pursuits between relatively large (100 mm) cod and the smallest shrimps available (4-5 mm) to them rarely, if ever, occur because (a) shrimps are increasingly likely to be caught on the first strike of an encounter, and (b) if they do escape, the shrimp's small size may make them increasingly difficult to track visually, except in the clearest of waters.

During a pursuit, cod typically proceeded in a series of rapid ballistic bursts, and hence their velocity fluctuated considerably more than that of the shrimp. Each burst was directed along an approximately linear trajectory determined by the position of the shrimp at the beginning of the burst, and the velocity achieved by the cod was in excess of $1 \text{ m}\cdot\text{s}^{-1}$. Maximum velocities recorded for 100 mm cod were similar to theoretical maximum burst speeds reported by Wardle (1975). This differs from the findings of Webb (1984), in which four species of fish predators were found to pursue prey at velocities which were considerably lower than their maximum capability, possibly in order to reduce the probability of being out-manoeuvred by the prey.

The chase sequence shown in Fig. 4.13 reveals the effectiveness of the sudden turn which *Crangon crangon* sometimes performs at end of the first tail flip of an escape response (reported in sections 2.3.3.ii & 3.3.3). The change of direction occurs at approximately the same time as the cod initiates its first acceleratory burst in response to an escape of the shrimp from the sediment. Webb & Skaden (1980) observed that during the last 80 ms of a strike, tiger muskies (*Esox* sp.) were unable to modify their attack direction, and a similar refractory period appears to exist for cod. Therefore the turn at the end of the first tail flip occurs at a time when the predator is unable to respond. This enables the shrimp to exploit the response latency (approximately 120-200 ms) required for the cod to re-align itself and prepare for its next burst, thereby increasing the distance between the shrimp and the cod (Fig. 4.13 b), and maximising the effort required by the predator in order to achieve a successful capture. Webb (1984) also noted that the relatively long (81-133 ms) response latencies of fish during chases accounted for their poor ability to capture prey escaping along unpredictable trajectories.

4.4.6 Secondary escapes and head-shake behaviour

Lima & Dill (1990) state that few, if any, studies in behavioural ecology have assessed secondary escapes during predator-prey interactions. In this investigation, secondary escapes by *Crangon crangon* were only observed when S:C ratios were equal or greater than 0.19, and the probability of them occurring increased as the S:C ratio increased. A similar type of behaviour in which crayfish (*Pasifastacus leniusculus*) were able to escape from perch (*Perca fluviatilis*) during prey-handling has also been reported by Blake & Hart (1995).

The S:C ratio at which secondary escapes first appear in *Crangon crangon* coincides with the ratio at which the handling time begins to increase steeply (reflecting the degree of manipulation required before ingestion of shrimps). A causal link may exist between these two events. Manipulation of larger shrimps is required by the cod in order to re-orientate them into a position where they can be swallowed more easily, and this presents the shrimp with an opportunity of tail flipping if the cod momentarily releases its grasp.

Interestingly, in both *Crangon crangon* (personal observations) and crayfish (Krasne & Wine, 1975), tail flip behaviour is suppressed when an animal is held between one's fingers, but the instant the grip is relaxed, a tail flip will often occur. Krasne & Wine (1975) suggest that this is an adaptation which produces a response at times most opportune for a successful escape. In *C. crangon*, this is borne out by their secondary escape responses from cod. This may therefore represent a physiological mechanism by which shrimps of a relatively large S:C ratio are able to exploit the fish's manipulation period in order to increase their chances of survival.

Head-shake behaviour by cod appears to serve the purpose of reducing the shrimp's ability to perform secondary escapes, since vigorous shaking often results in appendage loss, leaves the shrimp in an incapacitated state, and may possibly cause internal injuries as well. Indeed, cod which had performed head-shakes were often observed to spit out a shrimp onto the substratum, and grasp it in a different position without the shrimp attempting to escape. When shrimps were too large to ingest whole, the cod was still able to consume one or two appendages removed during head-shakes or by biting, but the profitability of this type of feeding is very low. Brawn (1969) describes head-shake behaviour in cod feeding on pieces of mussel tissue attached to shell, which enabled them to remove the edible portion of food. Eels (*Anguilla anguilla*) have also been reported to perform head-shakes when feeding upon crayfish, causing the crayfish to lose its large chelae before being ingested (Behrendt, 1987),

and similar types of head-shaking behaviour also occur in a number of other animal groups (e.g. crocodiles; Harris, 1996).

4.4.7 Probability of shrimps being eaten or rejected once caught

Above an S:C ratio of approximately 0.30, it became increasingly likely that shrimps would be rejected rather than consumed once they had been caught. Shrimps above a ratio of 0.36 were never consumed in the laboratory, and the extreme difficulty with which cod deal with shrimps of this length indicates that their mouth gape prevented the shrimp from being swallowed. The rejection of shrimps of between 0.30 and 0.36 also reflects their decline in profitability as handling time rises. Stein (1977) found a similar relationship to this as the length of crayfish (*Orconectes propinquus*) approached the maximum size edible by predatory bass (*Micropterus dolomieu*). Sticklebacks (*Gasterosteus aculeatus*) also reject isopod prey (*Asellus aquaticus*) more often as they approached the edible size limit of the fish, and this is modified by the degree of predator satiation (Hart & Gill, 1992; Gill & Hart, 1994). Indeed, satiation probably accounted for the single rejection of the 30 mm shrimp in Experiment 2, because the cod had already consumed one 30 mm shrimp, and in 2 other trials where cod consumed two 30 mm shrimps, the fish showed signs of difficulties in consuming them (reflected by the very long handling times). This indicates that the size of shrimps which cod are able to consume will decline as satiation increases according to the remaining free stomach space.

4.4.8 Summary of predator-prey interactions between *Crangon crangon* and juvenile cod (with a sediment substratum and visible light)

Fig. 4.18 summarises the predator-prey events observed during Experiment 2 for juvenile cod preying upon *Crangon crangon* on a sediment substratum, and under illumination similar to natural dusk lighting levels. The probabilities associated with various feeding events in the diagram highlight the influence of shrimp length upon their likelihood of being eaten. The escape behaviour of shrimps has an important influence on predator-prey interactions, with its effect upon the probability of capture increasing as a function of shrimp length. Once a capture has occurred, the probability of a secondary escape also increases as a function of shrimp length, but the probability of being eaten is then determined by the size of the shrimp with respect to the mouth gape of the cod, and the available stomach volume.

4.4.9 Comparisons between shrimps feeding in the dark versus in the light

The single trial conducted on cod feeding upon *Crangon crangon* under infrared light suggests that $P[\text{capture}]_{\text{encounter}}$ is severely reduced by the fish's inability to see and pursue shrimps. This agrees with the findings of Moore & Moore (1976a), who found that $P[\text{capture}]_{\text{encounter}}$ of flounder (*Platichthys flesus*) feeding upon *C. crangon* (mean shrimp:fish length ratio estimated to be > 0.18), fell from 0.45 in clear water to almost 0 in turbid water. However, since Experiment 2 indicates that the probability of being caught on the first strike of an encounter increases as shrimps become smaller (Fig. 4.12), it might be expected that, when cod feed in the dark, their diet will consist of a higher proportion of small shrimps compared cod feeding in the light. In their natural habitat, the influence of this effect may shift continuously with space and time, depending upon the visual threshold of cod, the time of day, phase (i.e. brightness) of the moon, the degree of cloud cover, the depth at which fish are feeding, the turbidity of the water, and other factors which affect the visibility of prey items. Batty *et al.* (1990) for instance, found that the size selectivity of herring (*Clupea harengus*) feeding upon planktonic organisms was modified by light intensity.

4.4.10 Handling time of shrimps

For a given length of cod, handling time increases exponentially with shrimp length. This relationship is typical, not only for teleost predators (e.g. Kislalioglu & Gibson, 1976a; Hoyle & Keast, 1987; Hart & Ison, 1991), but for other types of predators as well (e.g. crabs: Elner & Hughes, 1978; snakes: Webb & Shine, 1993).

As shrimps become larger, the handling time required by cod to consume them not only becomes greater, but also becomes increasingly variable (Fig. 4.6 c). This is because, although small shrimps were consumed almost immediately, larger ones required re-orientating in the fish's mouth, and the amount of time needed to manipulate them depended upon the position in which the cod caught the shrimp, the ease with which the cod was able to re-orientate it, and the number of secondary escapes which the shrimp was able to perform.

An increase in cod length from 61 to 107 mm had no significant effect upon the handling time of shrimps for a given S:C ratio (Fig. 4.6). Maximum consumable prey size and handling times of predators are usually determined by the maximum width of the prey, and the mouth gape of the predator (Hambricht, 1991). In juvenile cod, there is evidence that jaw dimensions increase isometrically with total length (Robb & Hislop, 1980), as do the body

dimensions of *Crangon crangon* (personal observations; also see **Appendix 1**), and this probably explains the result.

In some fish, the handling time for a given prey size increases with satiation (Werner, 1974; Kislalioglu & Gibson, 1976a; Croy & Hughes, 1991a). However, there was no discernible relationship between the order with which shrimps were eaten and the handling time required to consume them, except in cases when the volume of the shrimp being eaten approached the remaining available stomach capacity of the cod. This conclusion must be treated with caution because of the limited amount of data available, but is supported nevertheless by findings of Ellis (1994), who detected no significant relationship between handling time and the number of plaice (*Pleuronectes platessa*) or dab (*Limanda limanda*) being eaten by juvenile cod. Likewise, Gill & Hart (1994, 1996) were unable to significantly correlate handling time and satiation in 3-spined sticklebacks (*Gasterosteus aculeatus*) feeding upon isopods (*Asellus aquaticus*), and in this case, the authors suggested that the awkwardness in dealing with crustacean prey possessing various appendages and protrusions may mask the effect that hunger has on handling time. This explanation may also apply to cod feeding on *Crangon crangon*.

If the handling times of cod feeding upon *Crangon crangon* are compared with the values derived by Ellis (1994) for juvenile cod feeding upon plaice and dab, in both instances, flatfish were consumed more quickly than shrimps for a given predator:prey length ratio. For instance, whilst cod are able to consume a shrimp with an S:C ratio of 0.19 within 10 seconds, they can consume plaice and dab with a length ratio of approximately 0.28 within the same time. This is probably because of the more bulky nature and hard exoskeleton of shrimps compared with the comparatively soft, distortable features of flatfish. Greater handling times were also observed by Hoyle & Keast (1987) when largemouth bass (*Micropterus salmoides*) were fed crayfish rather than a range of fish species.

4.4.11 Profitability of shrimps

Profitability estimates for cod of all lengths between 61 and 107 mm feeding upon different lengths of *Crangon crangon*, based on handling time alone (Experiment 1), indicate that the optimal S:C ratio with regard to this parameter lies between 0.15 and 0.20. The assignment of a minimum handling time of 1 second in the calculations has an important effect upon this, because it takes into account the fact that there is a minimum cost in time

required to perform a feeding strike. The value of $1/s$ limits the maximum profitability of a shrimp to a value equal to or lower than its total dry weight. The minimum time measured between two feeding strikes directed towards the sediment (neither of which resulted in an encounter) was 1.5 s (measured from Experiment 2), and values were usually considerably greater than this. The experiments do not take into account the effect upon profitability of a cod capturing more than one shrimp during a single strike at the sediment, but this is presumably a rare occurrence in their natural habitat.

In Experiment 2, shrimps with an S:C ratio of between 0.14 and 0.20 were more profitable than shrimps with an S:C ratio of 0.30 and 0.38, agreeing with the values derived in Experiment 1. Pursuit times in Experiment 2 reduced the profitability of shrimps in the optimal S:C ratio range by between 25-35 % (Fig. 4.17). This will have an important effect upon the profitability of *Crangon crangon* compared to other, non-elusive prey items (e.g. amphipods) available to cod *in situ*, since it will affect their relative ranking in profitability, and hence may result in the omission of *C. crangon* from the cod's diet (Stephens & Krebs, 1986; Hart, 1993; also see section 1.4). The true impact upon profitability of having to pursue *C. crangon* is probably even greater than this, because burst swimming requires a considerable investment in energy by fish, and also may make the cod themselves more vulnerable to larger predators by attracting attention to themselves. An encounter not resulting in a capture will also have the effect of increasing the search time required to successfully locate shrimps (i.e. consume them). Therefore, the escape response of *C. crangon* will increase the effective search time for S:C ratios of greater than 0.14 by at least 42 %, because $P[\text{capture}]_{\text{encounter}}$ for shrimps with S:C ratios of 0.14-0.38 were between 0.58 and 0.25 (Fig. 4.15 b). Since an increase in search time reduces the profitability of a prey item (Stephens & Krebs, 1986), the profitability values which have been derived here by measuring handling time represent absolute maximum values.

A further aspect not taken into account by the profitability calculations is the time and energy required by cod to digest and absorb *Crangon crangon* with respect to shrimp length and with respect to other types of prey items. Variation in these factors may have a significant effect upon prey profitability (Kaiser *et al.*, 1992b). Cod are able to digest fish and polychaete prey more rapidly than *C. crangon* (Jones, 1974; Singh-Renton & Bromley, 1996), and this may reduce the relative profitability of *C. crangon*. Cod can also digest crustaceans with thin exoskeletons more rapidly than those with thick exoskeletons (Jones, 1974). Therefore, one

might expect large shrimps (with comparatively thicker exoskeletons) to be digested and eliminated more slowly than small ones. Singh-Renton & Bromley (1996) have shown that, in whiting (*Merlangius merlangus*), there is no significant difference in the digestion rate of different sizes of *C. crangon*, although the shrimp:whiting length ratios they tested were only between 0.14 and 0.26. Soofiani & Hawkins (1982) have also shown that, in cod, meal size does not affect the relative amount of energy required for digestion.

The calculated profitability values are not intended as a direct prediction of the S:C ratios expected to be eaten by cod in their natural habitat. This is because there are many factors, that are not included in the calculations, but which affect their diet selection (e.g. the relative availability of shrimps of different lengths; also see **sections 1.4 & 5.4**). The values derived do, however, allow S:C ratios found in the field to be compared with the efficiency with which shrimps of certain lengths are able to be consumed, and reveal possible influences of other factors affecting the profitability of different S:C ratios.

Table 4.1 Summary of experimental procedures used in Experiments 1, 2 and 3

Summary of experimental procedures used in Experiments 1, 2 and 3. All trials were video filmed from directly above using conventional video equipment. * = addition trials used only for determining handling time.

	Experiment 1	Experiment 2	Experiment 3
Date conducted	July - August 1993	July - Sept 1994	August 1994
Temperature	13°C	13°C	13-15°C
Dimensions of experimental arena	30 cm diameter	85 cm x 65 cm ellipse (area $\approx 0.4 \text{ m}^2$)	85 cm x 65 cm ellipse (area $\approx 0.4 \text{ m}^2$)
Water depth	20 cm	30 cm	30 cm
Substratum	Hard white base plate	Cleaned sand	Cleaned sand
Lighting	Visible	Visible (1.6-2.0 $\mu\text{E}\cdot\text{m}^{-2}\text{s}^{-1}$)	Infrared
Number of trials conducted	59	13	1
Total length of cod	'small' (n=23): 61-71 mm 'large' (n = 26): 92-107 mm ['intermediate']* (n = 10): 71-92 mm] (1 cod used per trial)	100-103 mm (1 cod used per trial)	102 mm (1 cod used per trial)
Total length of shrimps	6-36 mm (1 shrimp used per trial)	14 mm, 20 mm, 30 mm & 38 mm (8 shrimps of equal lengths used per trial)	30 mm (8 shrimps of equal lengths used per trial)
Range of shrimp:cod (S:C) ratios in trials	0.09-0.41	0.14, 0.20, 0.30 & 0.38	0.30

Table 4.2 Outcome of encounters in Experiments 2 and 3

Outcome of encounters in Experiment 2 (+ sediment and visible light,) and Experiment 3 (+ sediment and infrared light). A chase duration of zero indicates that an encounter consisted of just a single strike by the cod, with no subsequent chase. Values in brackets represent percentages.

	Experiment 2				Exp. 3
	14 mm	20 mm	30 mm	38 mm	30 mm
Shrimp length					
Light regime	visible	visible	visible	visible	infrared
Number of experimental trials	3	3	4	3	1
Total number of encounters	12	21	20	20	22
Median pursuit duration (seconds)	0	2.08	2.87	3.82	0
Encounters resulting in a capture	7 (58)	12 (57)	7 (35)	5 (25)	1 (5)
Encounters resulting in an eaten shrimp	7 (58)	12 (57)	6 (30)	0 (0)	1 (5)
Encounters resulting in a rejected shrimp	0 (0)	0 (0)	1 (5)	5 (25)	0 (0)
Encounters resulting in an escape	5 (42)	9 (43)	13 (65)	15 (75)	21 (95)
Total number of strikes	15	47	54	50	22
Median number of strikes per encounter	1	2	2	3	1
Strikes resulting in a capture	7 (47)	12 (26)	7 (13)	5 (10)	1 (5)
Strikes resulting in escape	8 (53)	35 (74)	47 (87)	45 (90)	21 (95)
Median # strikes in encounters resulting in a capture	1	1	3	3.5	1

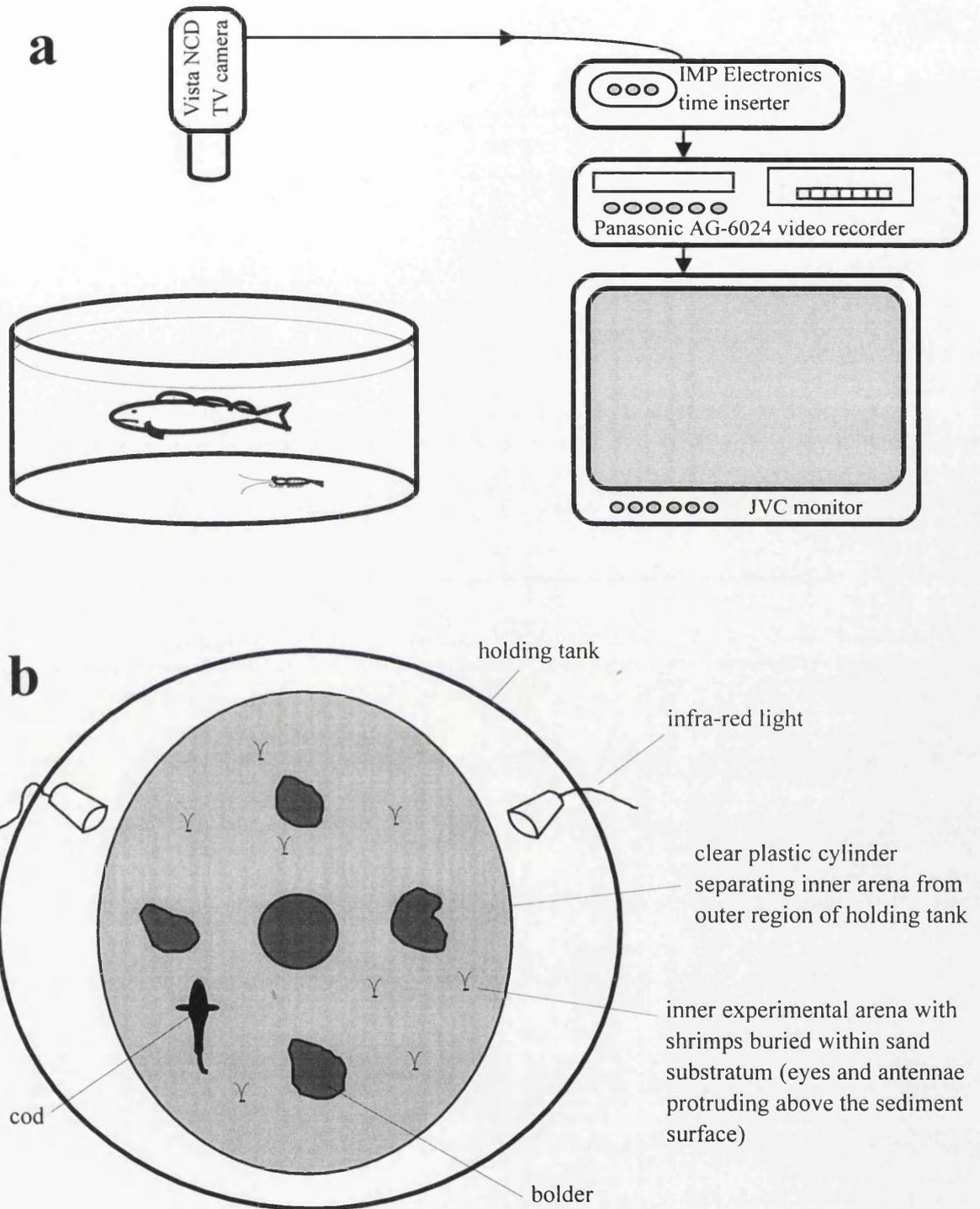


Fig. 4.1 Experimental set-up

(a) Set-up used for Experiment 1 (illumination provided by overhead fluorescent lighting). Diameter of holding tank = 30 cm, water depth = 20 cm. (b) Plan view of set-up for experiments 2 and 3. Filming was conducted from above in a similar manner to Experiment 1. Diameter of holding tank = 1 m; inner arena = eclipse measuring 85 cm x 65 cm; water depth = 30 cm. Illumination was provided by overhead fluorescent lighting in Experiment 2 ($1.6\text{--}2 \text{ uEm}^{-2}\text{s}^{-1}$), and by the infra-red lights in Experiment 3.

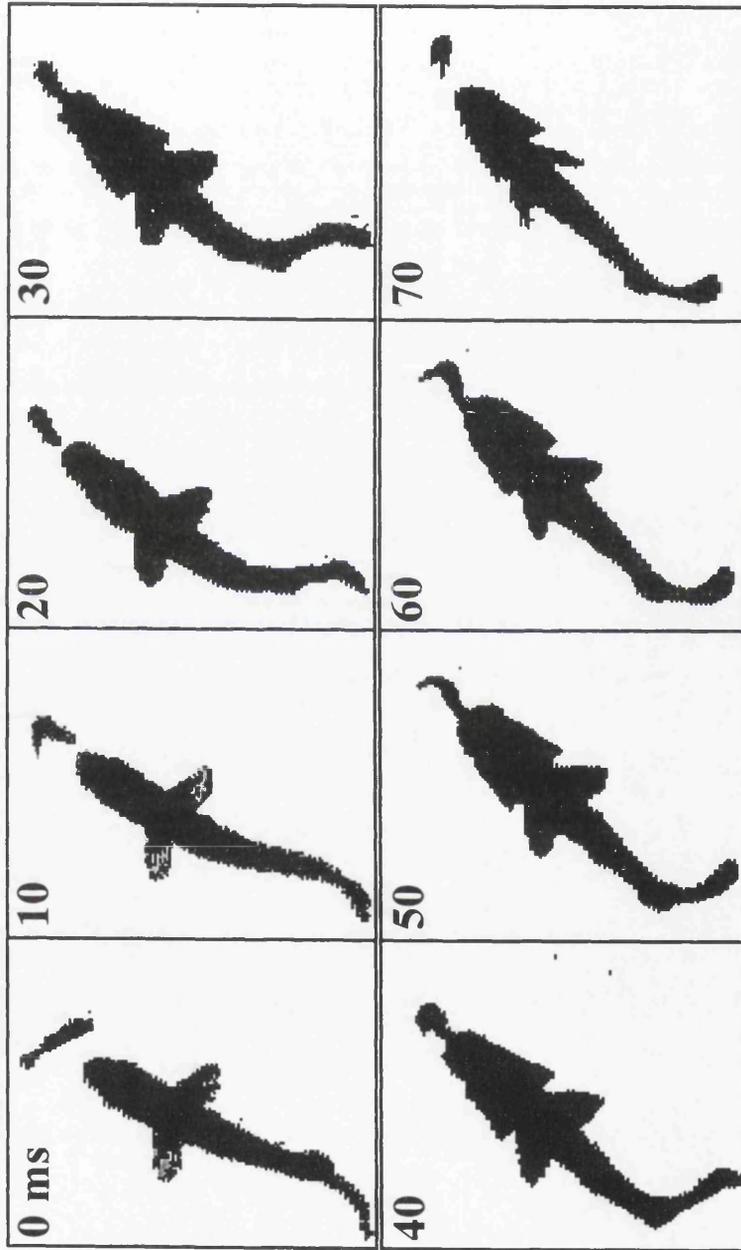


Fig. 4.2 High speed video sequence of *Crangon crangon* escaping from cod

Video images (recorded on high speed video, separate to Experiments 1, 2 & 3) showing every second frame of an escape response by *Crangon crangon* from an approaching cod (numbers refer to elapsed time in ms). The feeding strike by the cod consists of rapid lunge forward, an opening of the mouth, and an expansion of the buccal apparatus. The shrimp performs two tail flips. The first flexion (10-20 ms) conveys the shrimps laterally from a stationary position on the substratum. The second flexion (60-70 ms) incorporates a change of direction, off-set from that of the first tail flip.

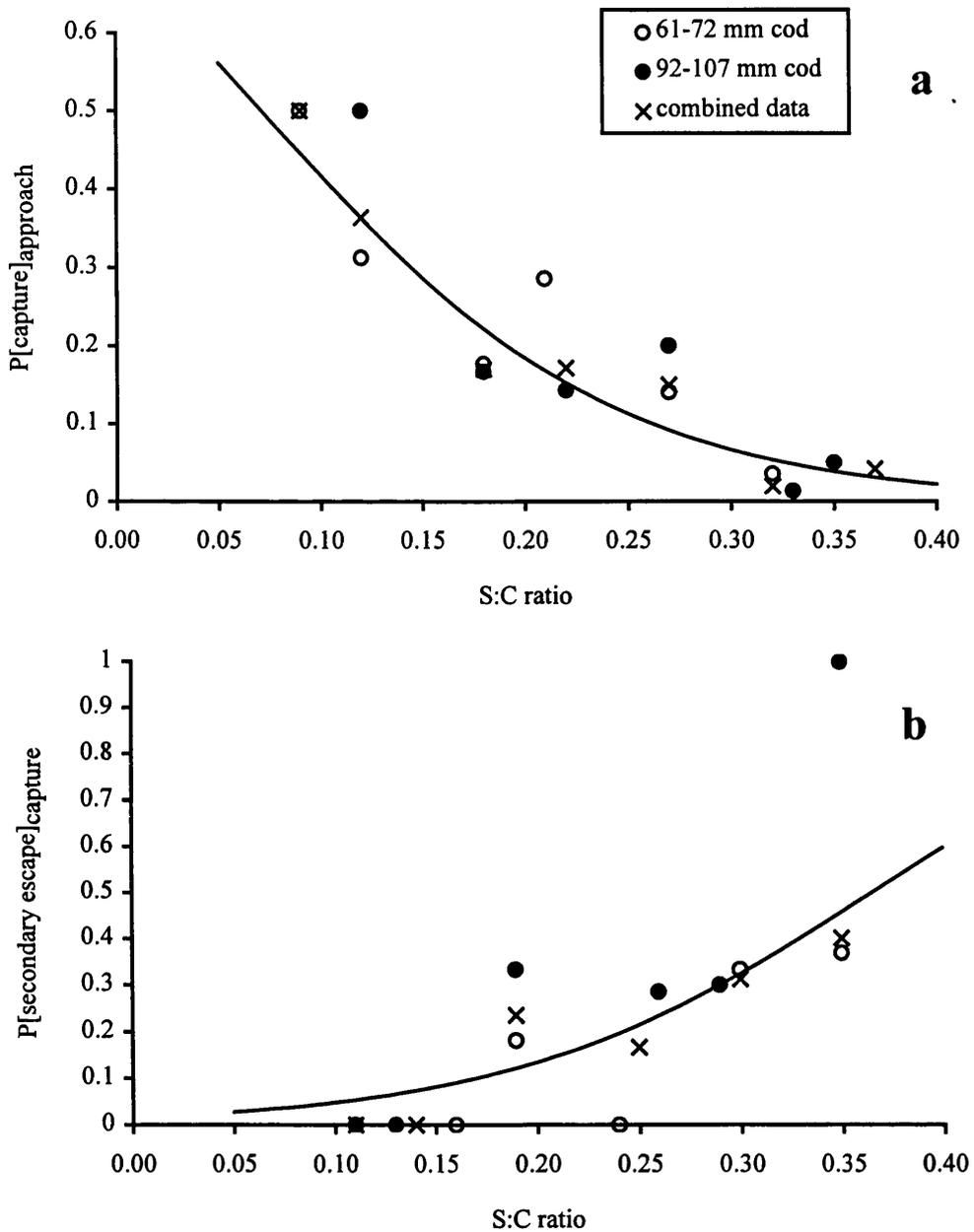


Fig. 4.3 Probability of *Crangon crangon* being caught per approach in Experiment 1, and of a secondary escape if caught

The effect of the S:C ratio on (a) the probability of *C. crangon* being caught per approach by a cod in Experiment 1 ($n = 344$ approaches by 49 cod), and (b) the probability, per capture, of a secondary escape occurring from the cod's mouth ($n = 78$ captures) in Experiment 1. Open circles represent values for small (61-72 mm) cod, filled circles represent values for large (92-107 mm) cod, and crosses represent the combined data sets. Data points represent mean values for different S:C ratio categories. Fitted lines were derived from logistic regression equations (equations 4.1 and 4.2).

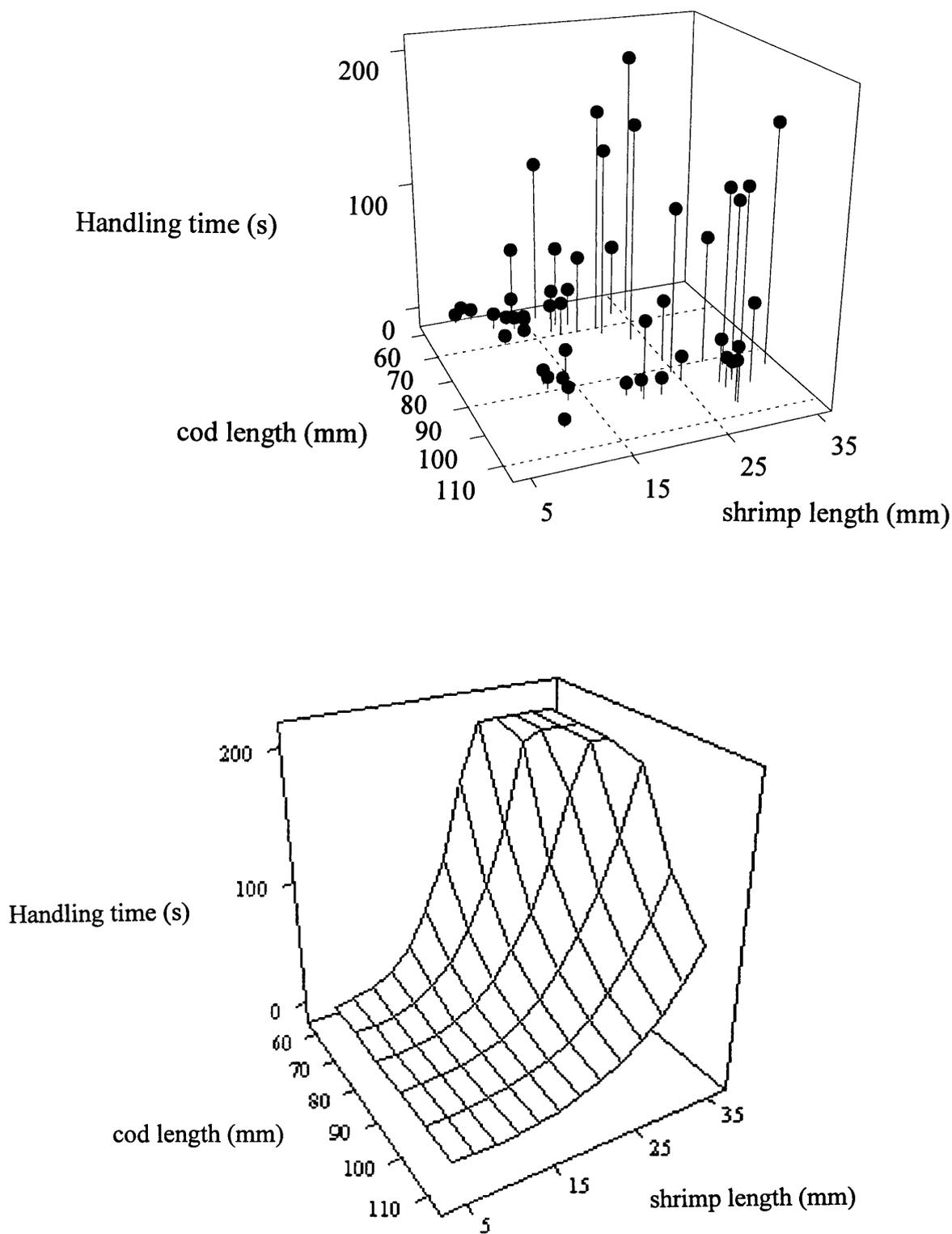


Fig. 4.5 Handling times of cod consuming *Crangon crangon* in Experiment 1

(a) Handling times determined for juvenile cod consuming *C. crangon* in Experiment 1. (b) Handling times predicted from fitting a multiple regression (equation 4.4) to the data in (a).

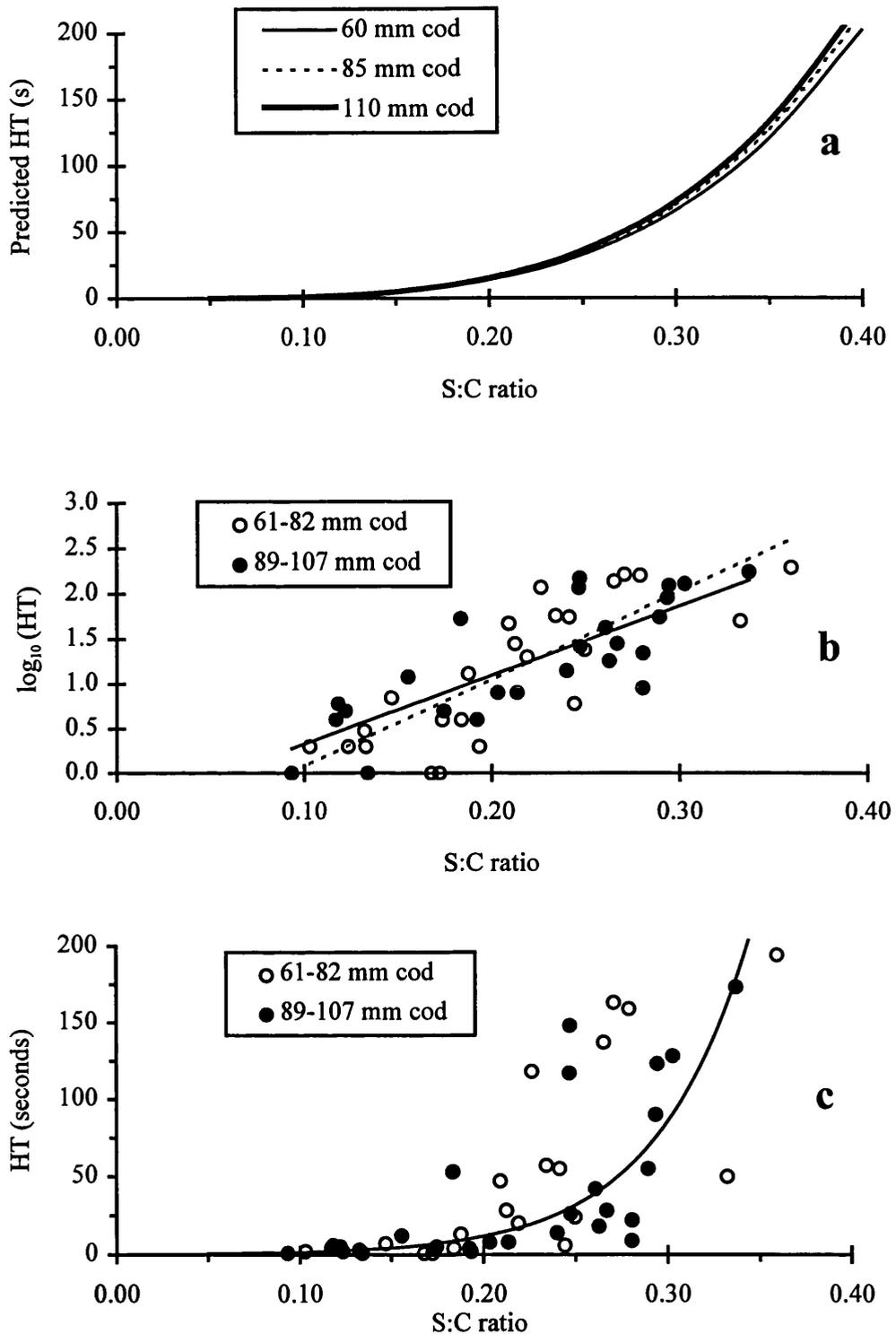


Fig. 4.6 Relationship between S:C ratio and handling time

(a) Comparison of handling times predicted by multiple regression equation 4.4 for cod of 60 mm, 85 mm and 110 mm. (b) Comparison of linear regressions fitted to $\log(\text{HT})$ against S:C ratio for small (61-82 mm; dotted line) and large (89-107 mm; solid line) cod. The slope and elevation of the regressions were not significantly different from one another ($p = 0.8$ and 0.46 respectively). (c) Handling times for all cod lengths between 60-110 mm, fitted with a simple regression (from equation 4.5; $p < 0.0001$, $r^2 = 0.65$).

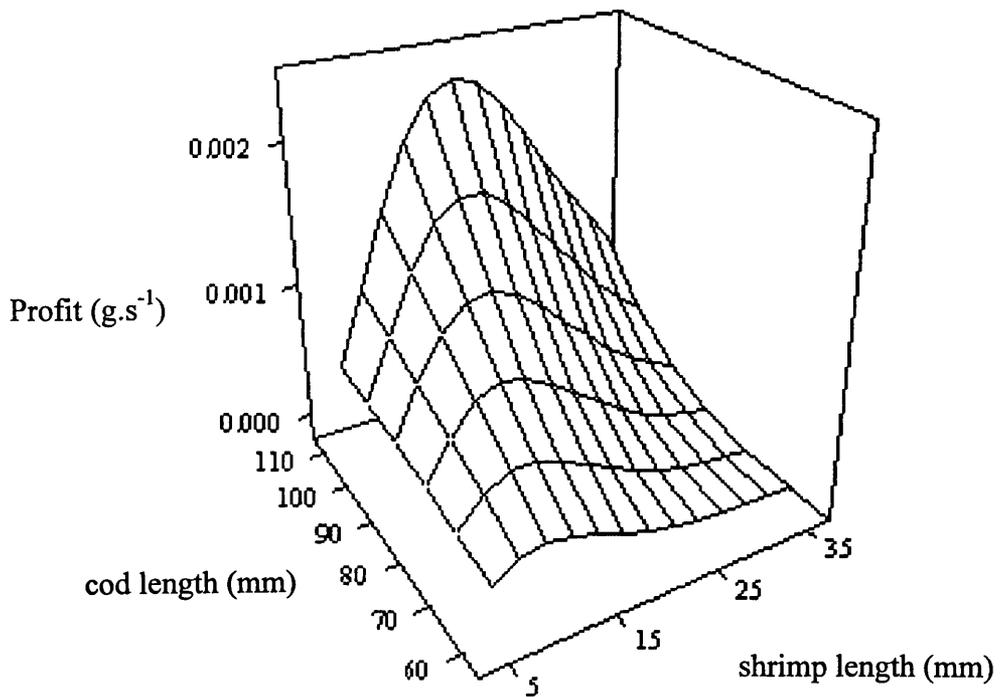
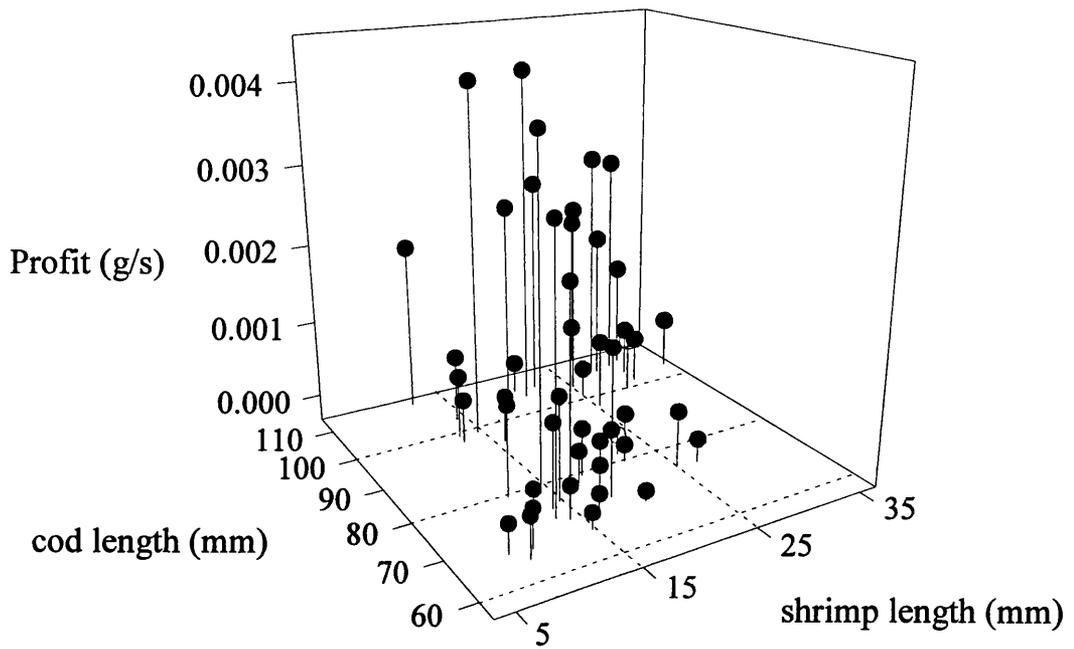


Fig. 4.7 Profitability of *Crangon crangon* to cod in Experiment 1

(a) Observed profitability (see equation 4.6) of *C. crangon* to juvenile cod in Experiment 1. (b) Predicted profitabilities (fitted from equation 4.8).

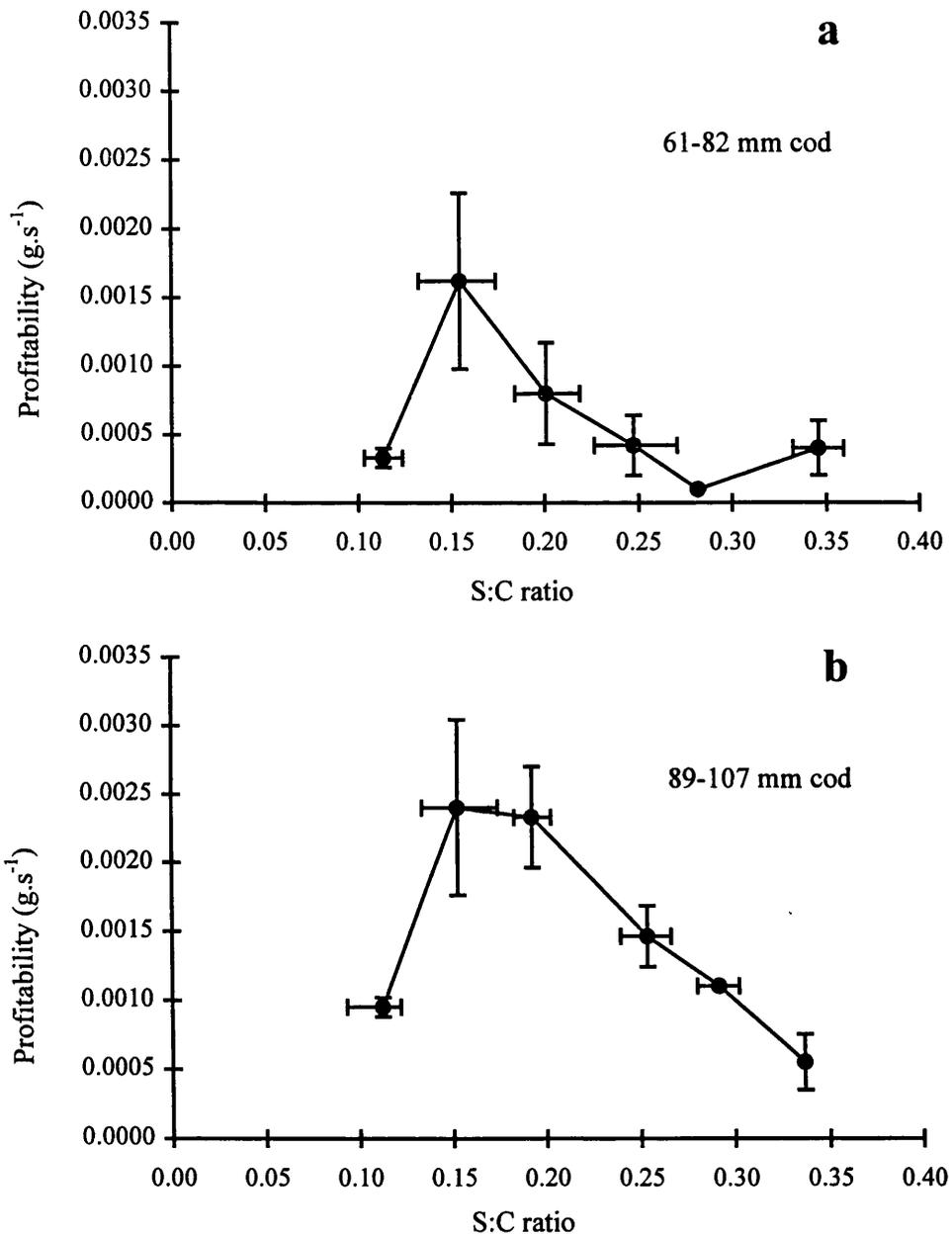


Fig. 4.8 Profitability of *Crangon crangon* to cod with respect to S:C ratio

Profitability of different S:C ratios for (a) cod of between 61-82 mm ($n = 25$), and (b) cod of between 89-107 mm ($n = 23$). Each point represents mean values for a particular shrimp:cod length ratio category. X-error bars represent the range of S:C ratios from which the mean profitability was calculated; Y-error bars represent the standard error of the mean profitability.

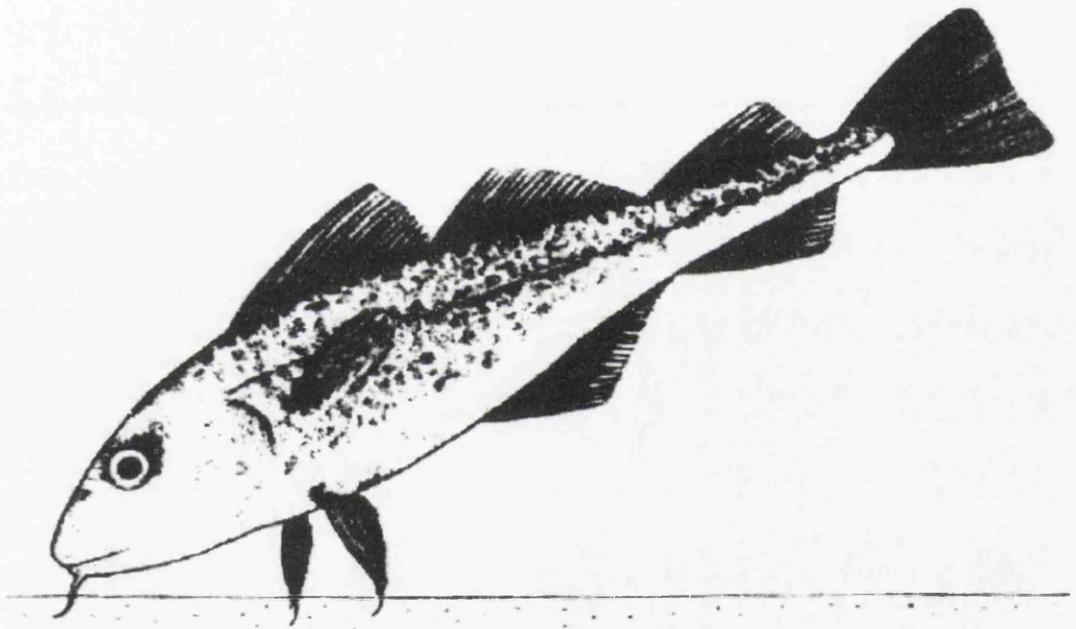


Fig. 4.9 Typical position adopted by cod when foraging

Typical position adopted by cod whilst performing foraging behaviour on a sediment substratum (Taken from Doving & Selset, 1980).

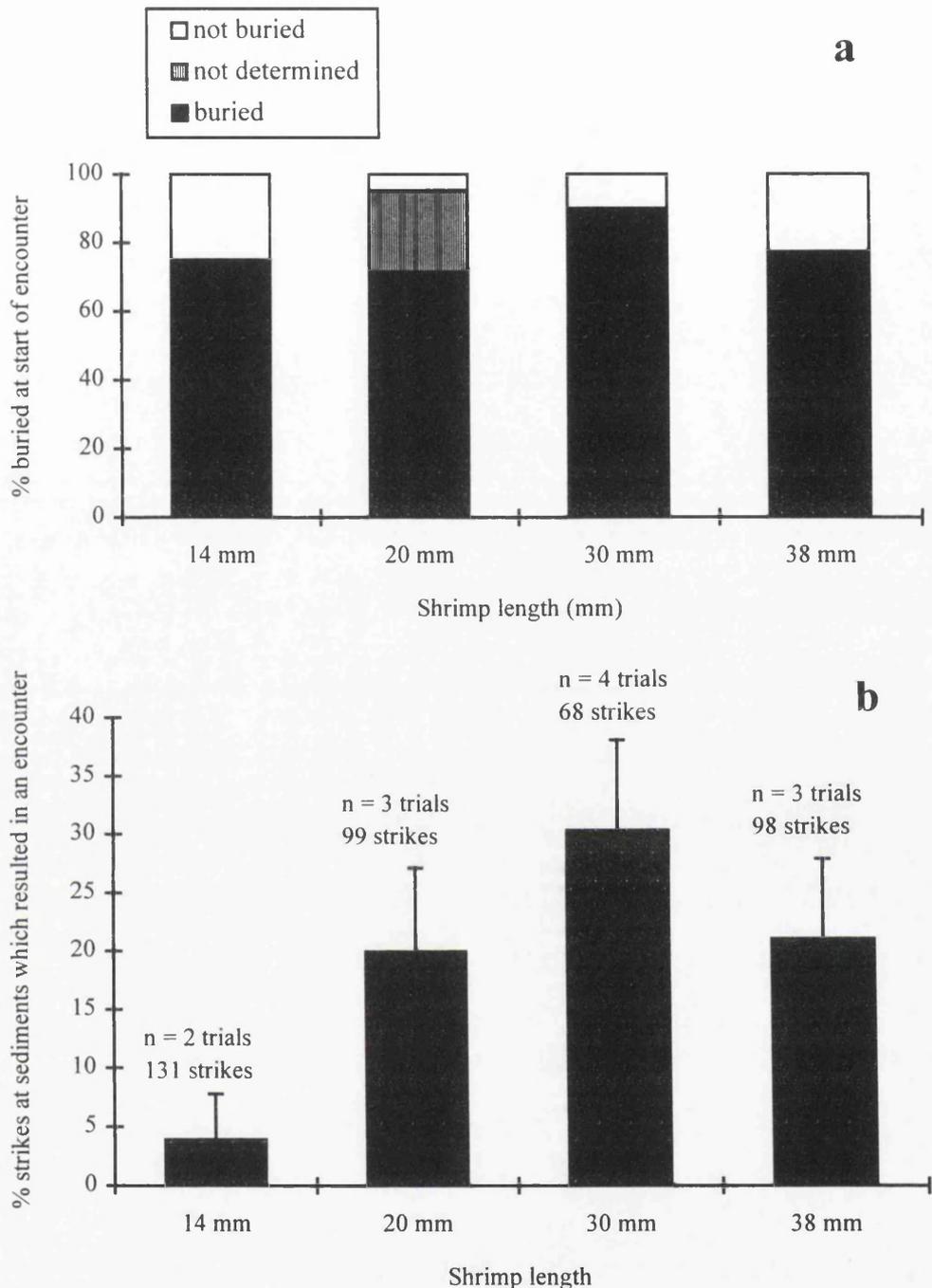


Fig. 4.10 Percent of shrimps buried at the start of an encounter, and the accuracy of feeding strikes by cod at buried shrimps

(a) Frequency of shrimps which were buried within the sediment at the start of each encounter in the light (Experiment 2). In some cases it was not possible to determine with confidence whether the shrimp was buried or not ('not determined'). Variation between shrimps of different lengths was insignificant (Chi-square test, $p > 0.25$). (b) Percent of strikes (+ s.e.) directed towards the sediment by cod during foraging behaviour which resulted in an encounter with a shrimp. The frequencies were not uniform between shrimps of different lengths (Chi-square test, $p < 0.01$).

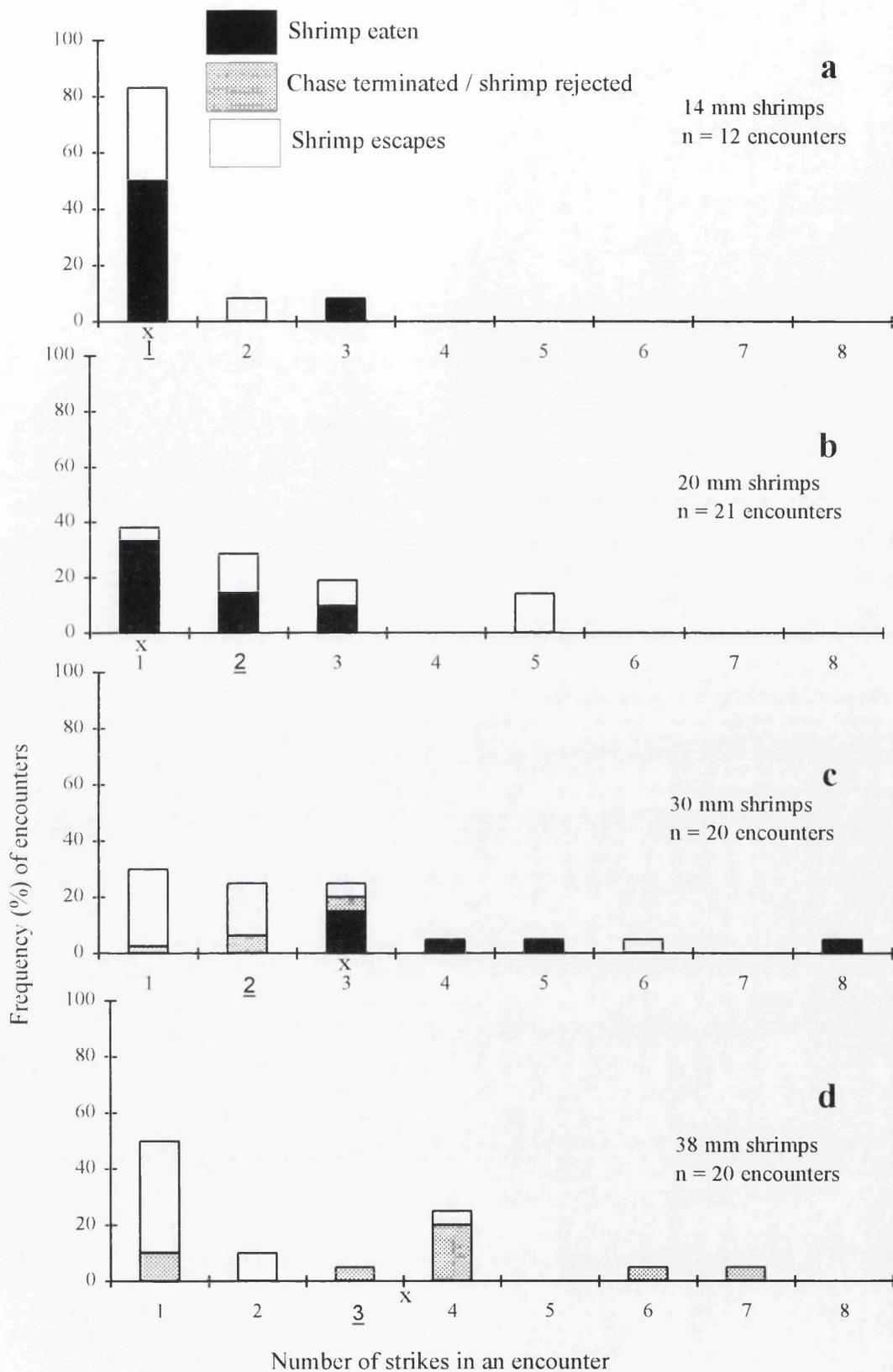


Fig. 4.11 Number of strikes per encounter with shrimps on sediment

The number of strikes occurring per encounter with (a) 14 mm shrimps, (b) 20 mm shrimps, (c) 30 mm shrimps, (d) 38 mm shrimps. The key in (a) indicates the fate of shrimps at the end of an encounter. Underlined values represent median number of strikes per encounter; x represents median number of strikes until capture.

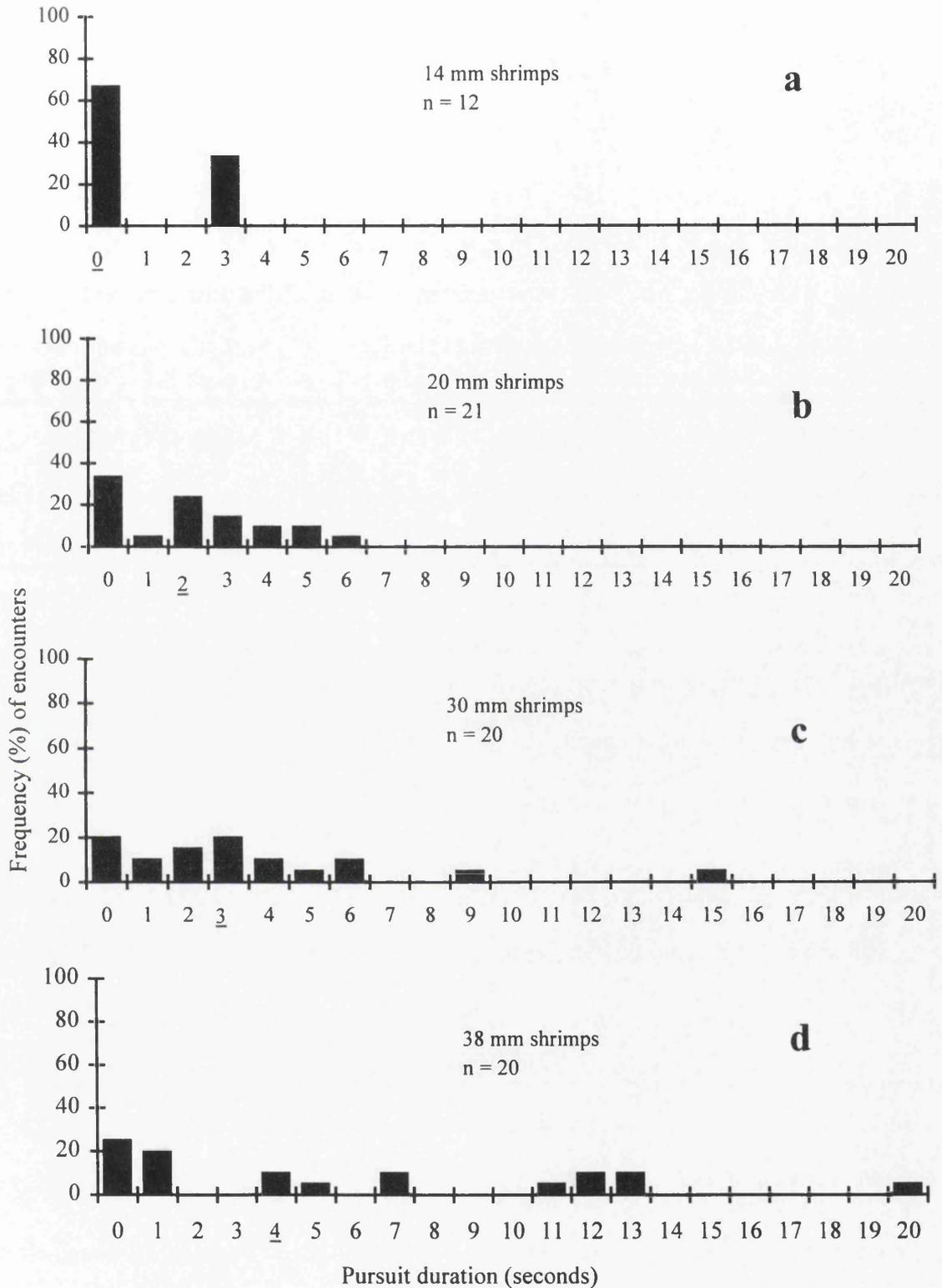


Fig. 4.12 Frequency of pursuit durations between cod and shrimps

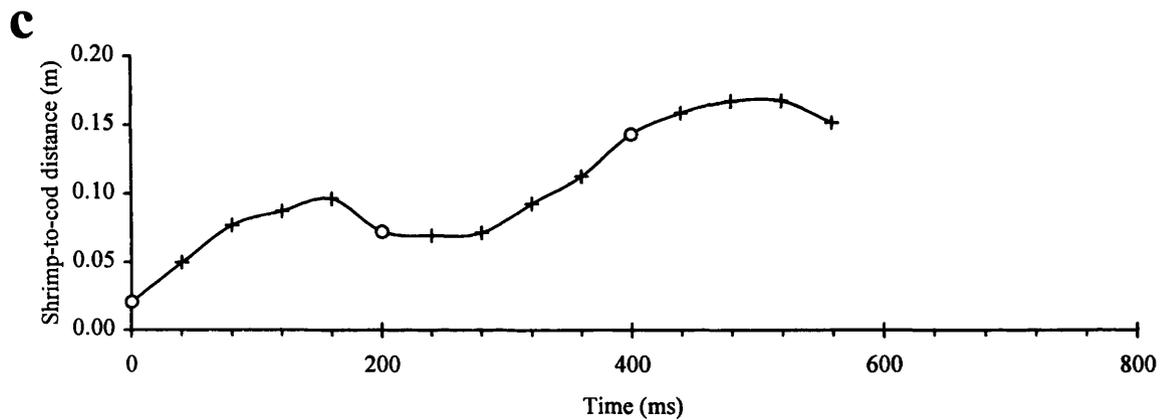
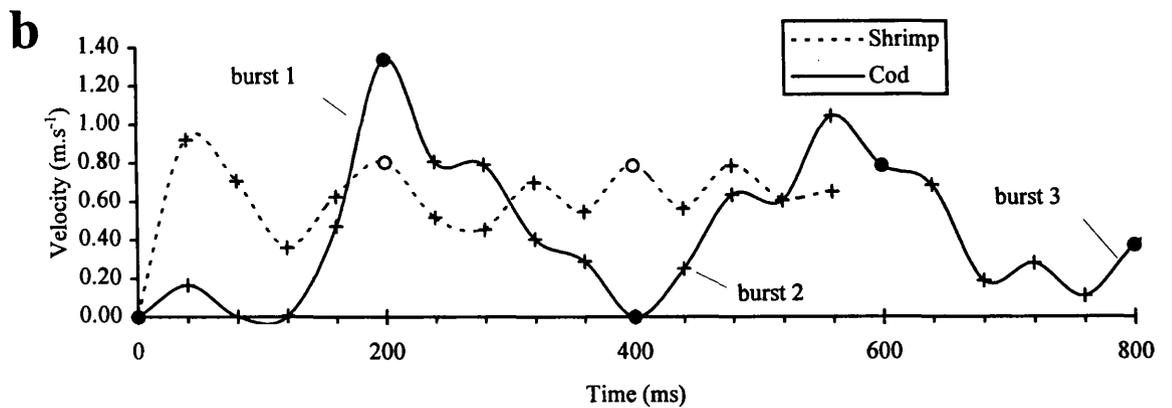
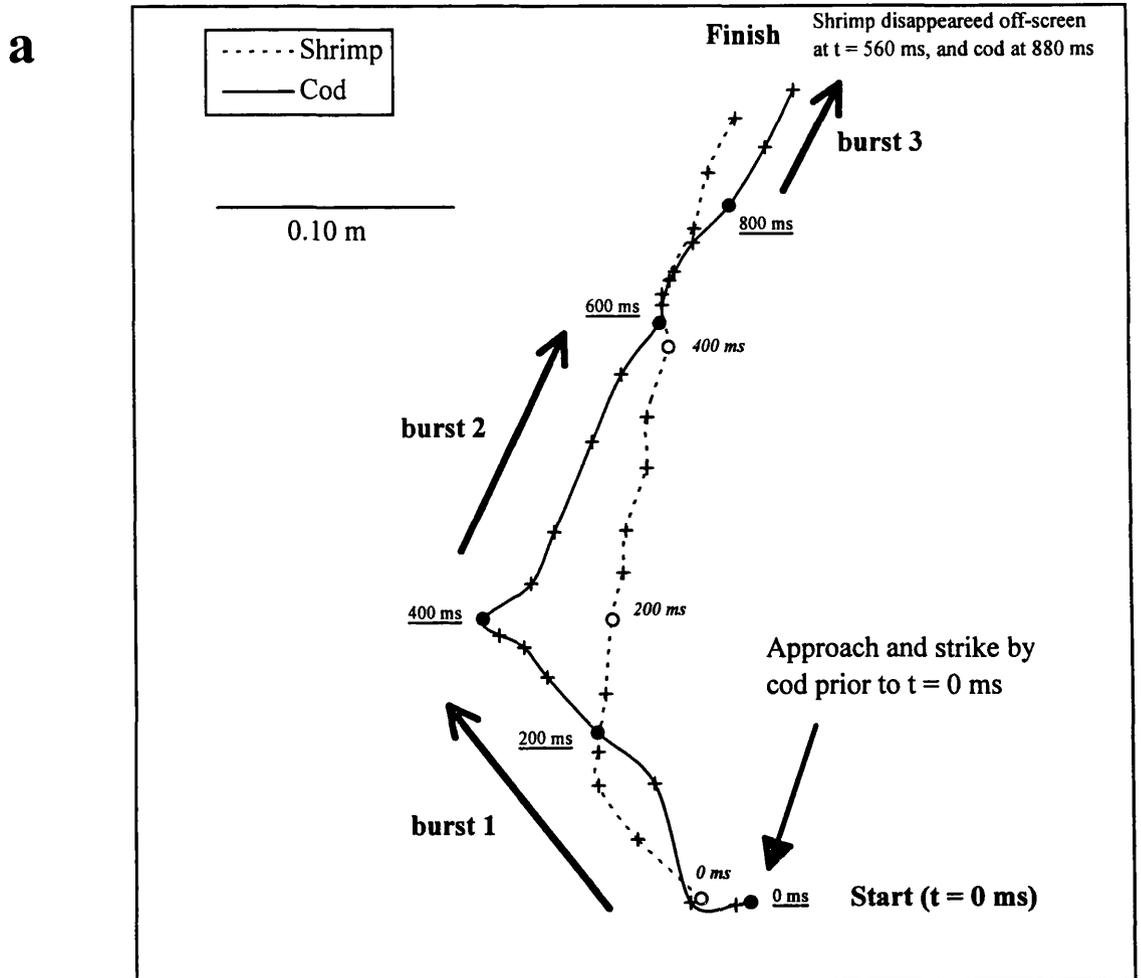
Frequency of pursuit durations between cod and (a) 14 mm shrimps, (b) 20 mm shrimps, (c) 30 mm shrimps, (d) 38 mm shrimps. Where no pursuit occurred, a time of zero was assigned. Underlined values indicate medians.

Fig. 4.13 Trajectories of a cod and shrimp during a pursuit, plots of escape and pursuit velocities, and plot of shrimp-to-cod distance

(a) An example (traced from a video recording) of the trajectories followed by a 20 mm shrimp being pursued by a 102 mm cod during Experiment 2. The lines are fitted through points digitised from the position every 40 ms of the shrimp's centre of mass and the leading edge of the cod. Numbers adjacent to the circles indicate the time elapsed at that point since the beginning of the sequence (*italic numbers* & empty circles = shrimp, underlined numbers & filled circles = cod). The shrimp was stationary on the substratum at $t = 0$ ms, but was tail flipping thereafter, and changed direction abruptly after escaping for a distance of approximately 6.5 cm. Open arrows indicate the direction of each burst phase by the pursuing cod. The trajectory of the cod intersected the escape path of shrimp at $t = 200$ ms and 600 ms.

(b) Velocity against time of the shrimp and cod during the pursuit shown in (a). Open and filled circles (shrimp and cod respectively) correlate with the concurrent points in the trajectory plot.

(c) Shrimp-to-cod distance against time during the pursuit shown in (a). Empty circles correlate with the concurrent shrimp and cod positions in the trajectory plot.



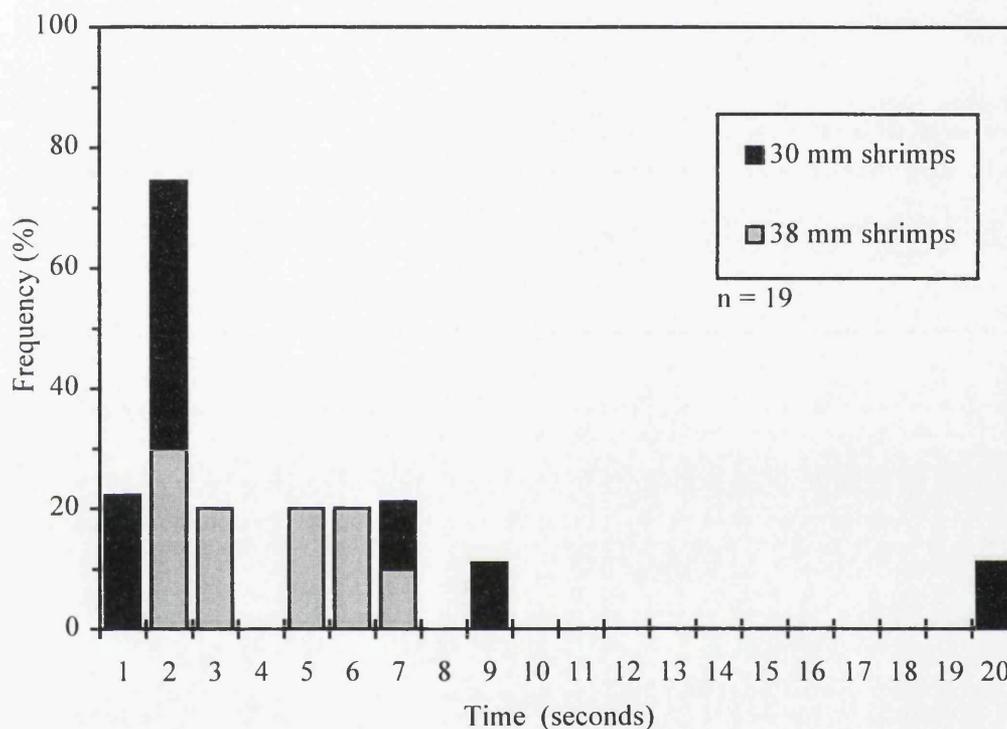


Fig. 4.14 Time taken by *Crangon crangon* to rebury at the end of an escape from a cod

Time taken by *C. crangon* (30 and 38 mm) to completely rebury themselves after landing on sediment at the end of a tail flip escape response in Experiment 2. Black = values for 30 mm shrimps; Grey = values for 38 mm shrimps. The values from each shrimp lengths are not significantly different from one another (Mann-Whitney test, $p = 0.487$).

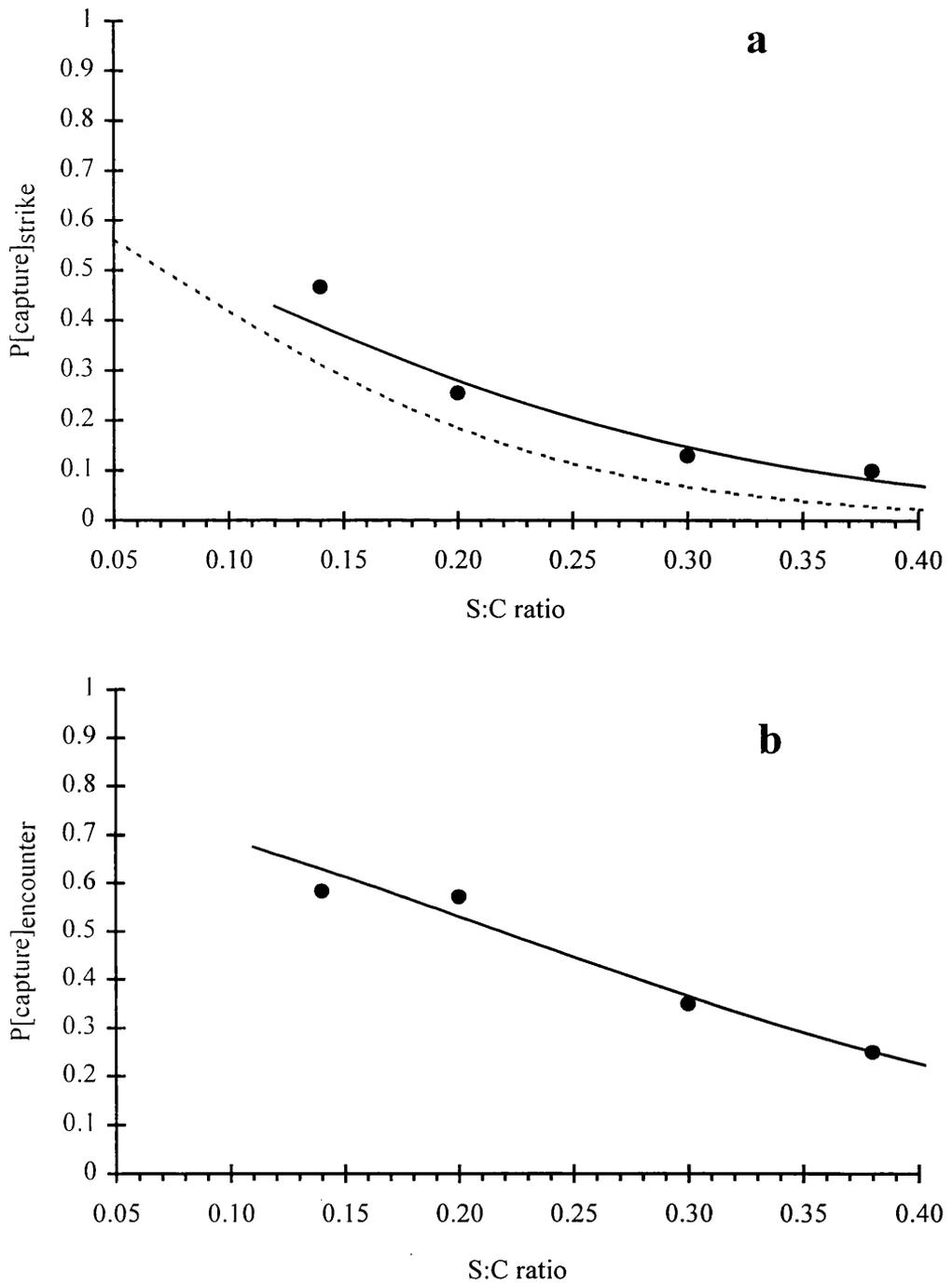


Fig. 4.15 Probability of shrimps being caught per strike and per encounter during Experiment 2

Probability of different lengths of shrimps being caught (a) per feeding strike ($n = 166$ strikes), and (b) per encounter ($n = 73$ encounters) by 100 mm cod feeding in an arena with a sediment substratum (Experiment 2). Filled circles represent mean values for different S:C ratio categories. Solid fitted lines are derived from logistic regressions (equations 4.9 and 4.10 respectively; $p = 0.001$ and 0.034). The dashed line in (a) has been included for comparison, and represents $P[\text{capture}]_{\text{approach}}$ for cod feeding in Experiment 1 (derived from equation 4.1).

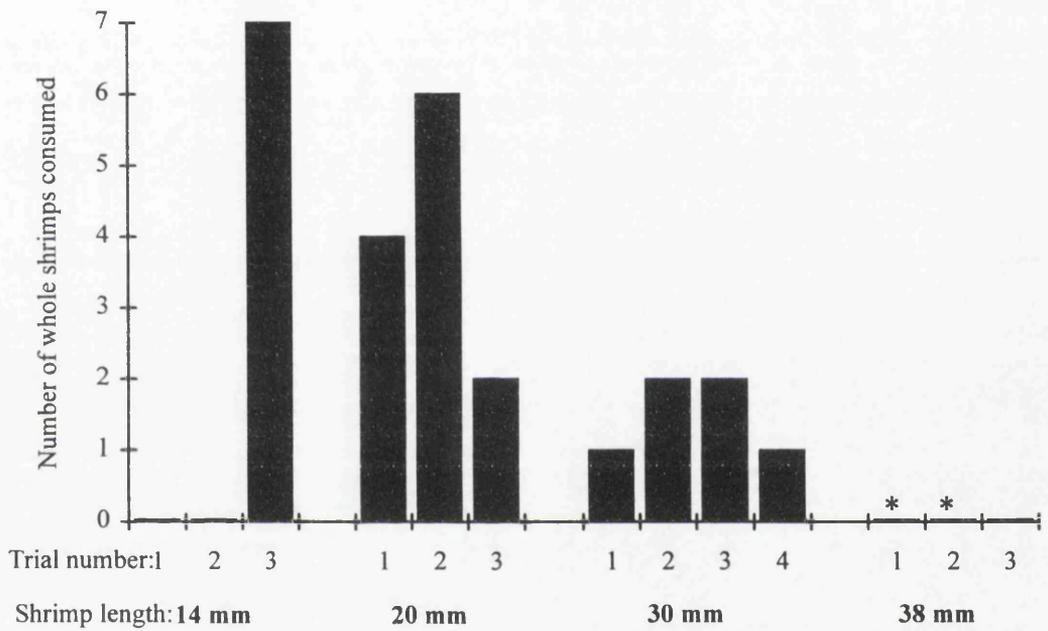


Fig. 4.16 Number of shrimps consumed within 2 hours by cod during Experiment 2

Number of shrimps consumed during each 2 hour trial by cod (100-103 mm) in Experiment 2 (visible light + sediment). Asterisks indicate cod which consumed just appendages of shrimps rather than whole shrimps.

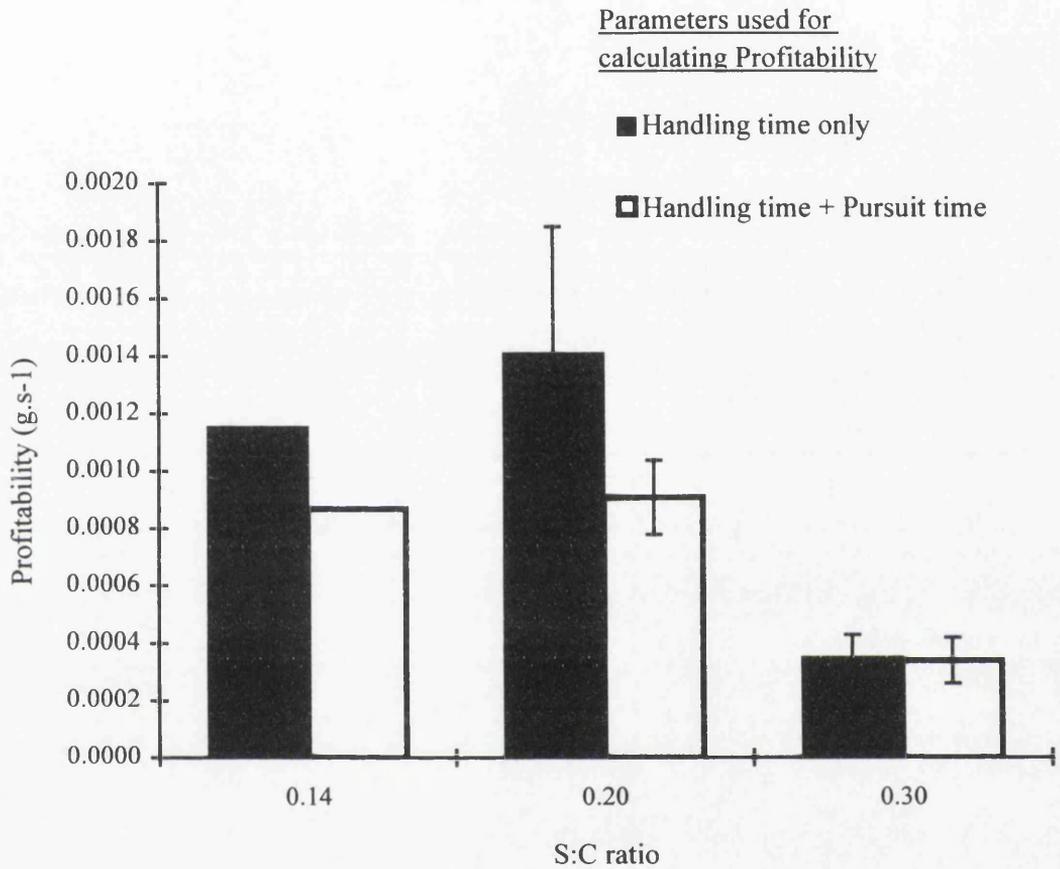


Fig. 4.17 Effect of pursuit times upon the profitability of shrimps

Effect of pursuit time upon the estimated profitability of *Crangon crangon* to 100 mm cod when feeding on shrimps of different lengths in Experiment 2. Profitability was calculated using handling time alone (black), and handling time + pursuit time (white) (see equation 4.11). Error bars represent the standard error of the mean. For S:C = 0.14, $n = 1$ cod consuming 7 shrimps (total dry weight consumed = 0.04 g.); for S:C = 0.20, $n = 3$ cod, each consuming 2 shrimps (total d.w. consumed each = 0.04 g.); for S:C = 0.30, $n = 4$ cod, each consuming 1 shrimp (total d.w. consumed each = 0.07 g.)

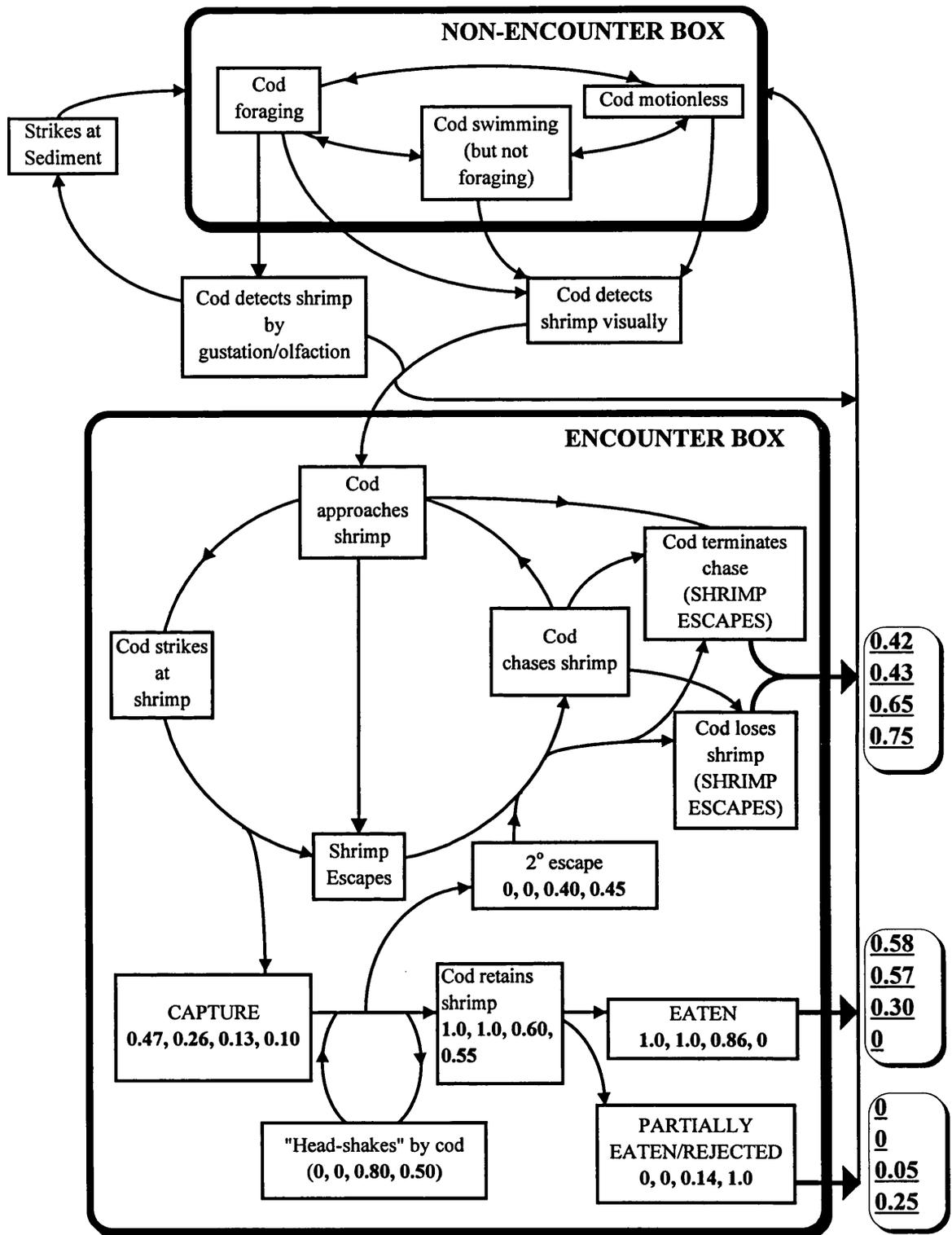


Fig. 4.18 Predator-prey cycle of cod feeding upon *Crangon crangon*

Predator-prey interactions for juvenile cod feeding upon *C. crangon* in Experiment 2 (low light, sand substratum, large arena). Numbers in activity boxes refer to the probability of the event occurring, given that the previous event has occurred, for shrimps of 14, 20, 30 and 38 mm respectively. Underlined numbers on the right of the Encounter box refer to the probability of a certain outcome per encounter.

Chapter 5

Field studies of predator-prey interactions between *Crangon crangon* and juvenile cod

5.1

INTRODUCTION

5.1.1 Aims of the study

In this chapter, an analysis has been performed of the prey items found in the stomachs of juvenile cod (*Gadus morhua*) caught at Tralee Beach, a shallow sandy bay on the west coast of Scotland. This was conducted in order to determine the shrimp:cod (S:C) length ratio of *Crangon crangon* consumed *in situ* by juvenile cod. These data have been compared with the results from Chapter 4, in which predator-prey interactions between juvenile cod feeding upon *C. crangon* were studied in the laboratory over a range of S:C length combinations.

The benthic community at Tralee Beach offers cod a variety of prey types and sizes to feed upon. For those cod feeding upon *Crangon crangon*, the frequency distribution of the S:C ratios of shrimps found in their stomachs has been compared with the 'optimal' S:C ratio, determined on the basis of handling time alone, in the laboratory (section 4.3.1.vi). The optimal S:C ratio *in situ* will depend upon a wider range of factors other than just handling time, such as encounter rate and capture success. Assuming that the probability of capturing a shrimp declines as the S:C ratio increases (sections 4.3.1.ii & 4.3.2.vi), one expectation is that the S:C ratio of shrimps caught *in situ* will be smaller than that predicted by the optimal S:C based upon handling time alone, unless shrimps of a lower S:C ratio are not available to the cod.

5.1.2 Description of study site

Tralee Beach is situated in Ardmucknish Bay in the Firth of Lorn on the west coast of Scotland (56° 31' N, 5° 29' W; Fig. 5.1). The beach is approximately 1 km long, and is exposed to south-westerly winds, although the fetch is quite small. It slopes gradually from low water mark to a depth of 10 m, and then drops off rapidly to a depth of 30 m or more. Below low water mark, the substratum consists predominantly of well-sorted fine sand with a component of silt and clay that increases with distance from the shore. Above low water mark, the sand increases in grain size, becomes less well sorted from west to east, and has a very low silt/clay content.

The intertidal macrofauna of the beach is relatively poor in species and biomass compared with other Scottish beaches ranked as moderately exposed by McIntyre (1970), or exposed by Eleftheriou & Nicholson (1975). Polychaetes and crustaceans are the dominant

intertidal macrofauna, and biomass is generally less than 1.5 g dry weight m⁻², although this value rises to 12 g.m⁻² near low water. Species diversity and biomass increase sub-tidally (Gregory, 1988).

The beach serves as a nursery and feeding area for up to 43 species of fish, and 16 species of macrocrustacea. The number of species, number of individuals, and biomass of both groups are greatest from spring to autumn, after which predation and emigration into deeper water result in their decline. *Crangon crangon* is the dominant epibenthic crustacean species, comprising more than 90 % of numbers in trawl samples, and occurs at all times of the year. Juvenile cod (mainly 0-group, but also some 1-group) are the most common of the Gadidae species occurring at the beach (a total of 4 species were recorded between 1986 and 1989; Gibson *et al.*, 1993). 0-group cod start to appear at Tralee Beach in May-June as they change from a pelagic larval phase to a demersal lifestyle (Gibson *et al.*, 1995). They remain at Tralee until late summer or autumn, with a small number staying as late as January. Whilst there, the cod undergo diurnal migrations from subtidal waters during the day, into intertidal regions at night-time (Burrows *et al.*, 1994).

5.2

MATERIALS & METHODS

5.2.1 Collection of samples

Cod and shrimps were collected on eight separate dates during 1993. These were 3 June, 17 June, 2 July, 20 July, 3 August, 31 August, 13 September and 23 November. The sea water temperature during this period varied from 13.8°C (3 August) to 8.3°C (23 November). Samples were collected within 3 hours after dusk, coinciding with times of spring low tide. On each occasion, 3 beach seine net samples (4 on 23 November) and 1 trawl sample were taken.

The beach seine net was 36 m long and 1.8 m deep, and was constructed of a 8 mm mesh in the central portion. The upper edge of the net was fitted with floats, and the lower edge with lead weights. For each sample, the net was set parallel to the shore (*c.* 50 m from the water's edge) in a depth of 2 m or less, and then hauled onto the beach by ropes attached to each end of the net. Gibson *et al.* (1993), using the same net at the same location, estimated the area of sea bed swept by each beach seine haul to be 1160 m². Cod which were trapped in the net were anaesthetised in a dilute solution of benzocaine (50 mg.l⁻¹), and then preserved in formalin (*c.* 10 %).

Trawl samples were collected using a 2 m beam trawl fitted with a main net of 15 mm stretched mesh, and a cod end of 3 mm stretched mesh. The net was towed behind a small boat in an off-shore direction from the water's edge to a depth of 5 m. The distance covered during each trawl was measured with a cyclometer attached to the trawl frame, and this was calibrated at Tralee Beach. Trawl distances varied from 160 to 220 m, and these measurements were used to estimate the area swept by the net (trawl area = trawl distance x net width). The contents of the net were preserved in formalin (c. 10 %).

5.2.2 Analysis of samples

The stomach contents of juvenile cod caught in the beach seine samples, and the length distribution of *Crangon crangon* caught in the trawl samples, were analysed in the laboratory.

Between 1 and 4 beach seine hauls were analysed from each of the seven collection dates, and this was dependent upon the number of cod that were caught on each occasion. For each haul analysed, all of the cod that were caught within it were examined, except on 31 August, when a sub-sample of 20 were examined. For these cod, the total length was measured (tip of snout to tip of tail), and the stomach contents were examined under a binocular microscope. Stomach fullness was estimated on a scale of 0-10 (0 = empty , 10 = full). Food items from each stomach were identified into categories (*Crangon crangon*, mysids, amphipods, cumaceans, isopods, polychaetes, bivalves, fish, miscellaneous), and the percent volume represented by each food type was estimated by eye. The total length (tip of rostrum to tip of telson) of each *C. crangon* found in the stomachs was either measured (to the nearest millimetre) with a pair of callipers, or estimated by measuring one of the various undigested body parts with a calibrated eyepiece graticule fitted to the microscope. The body parts that were measured, and the regression equations used for converting body part length into total shrimp length, are detailed in the **Appendix 1**.

Trawl samples were only analysed for the hauls made on 20 July, 31 August and 23 November due to the length of time required to sort these samples. Shrimps caught in the trawl net were sorted from the rest of the trawl sample, and the total length of each shrimp was measured to the nearest millimetre with a pair of callipers.

5.3

RESULTS

5.3.1 Population structure of *Gadus morhua* and *Crangon crangon* at Tralee Beach

The length-frequency distribution of the cod population at Tralee Beach between 3 June and 23 November 1993 is shown in Fig. 5.2. The mean number of cod per haul rose from 5 on 3 June (1 haul), to 140 (s.d. = 12.7, n = 2 hauls) on 20 July, and then gradually fell again to 8 (s.d. = 3.6, n = 4 hauls) on 23 November (see Table 5.1). These values correspond to densities of approximately 0.4, 12.1 and 0.7 individuals per 100 m⁻² respectively. During this period, the cod length category (5 mm bins) with the highest frequency increased from 40 to 95 mm.

The length frequency distribution (1 mm bins) of *Crangon crangon* at Tralee Beach is shown in Fig. 5.3. These data show that, on 20 July, shrimps of all lengths between 7-55 mm were present, with two main peaks at 19 and 38 mm. On 31st August, very few shrimps of less than 30 mm in length were caught. The length class with the highest abundance was 49 mm, and the largest shrimps were 61 mm. On 23 November, all length categories of shrimps between 9 and 41 mm were represented, with a few larger individuals up to 67 mm, and peaks in frequencies occurred at 17 mm and 30 mm.

The density of shrimps on each occasion, as determined by the number of shrimps caught per area swept by the trawl, was approximately 81, 66 and 41 individuals per 100 m⁻² respectively.

Due to the mesh size of the trawl, the numbers of small shrimps are probably considerably underestimated (this is further discussed under section 5.4.2). However, the results do verify that shrimps of nearly all lengths consumable by the cod population at Tralee Beach were available in June and November (i.e. S:C ratio < 0.36, based on Chapter 4). During August, fewer small shrimps were available in the trawl, but it is unclear whether this represents the real situation at the beach. The majority of cod feeding on *Crangon crangon* at this time were found to contain shrimps of 10 mm or less in their stomachs, indicating that recently settled shrimps were in fact available, and suggesting that net efficiency was probably the main reason for their absence from the trawl data.

5.3.2 Numbers and lengths of *Crangon crangon* eaten by *Gadus morhua*

Table 5.1 summarises the occurrence of *Crangon crangon* in the stomachs of cod at Tralee Beach. Cod fed upon *C. crangon* on all sampling dates between 3 June and 23 November, but the proportion feeding on them was usually less than 40 %, despite the fact that nearly all of the cod examined (> 98 %) contained food in their stomachs (mean stomach fullness on each occasion was between 4.9 and 6.7). For all samples combined, 19.6 % (n = 677) of stomachs contained *C. crangon*, and there was no evidence that this frequency changed with cod length (Chi-square test, $\chi^2 = 5.531$, d.f. = 5, p = 0.355; see Fig. 5.4). For those cod feeding on *C. crangon*, the proportion of the stomach content-volume attributable to this species was extremely variable within a single sample date, but mean values ranged between 10 and 60 %. The mean numbers of shrimps per stomach for those cod feeding upon *C. crangon* was between 1.14 and 1.55. Therefore, *C. crangon* is not a particularly prominent component of the cod diet at Tralee Beach. Amphipods were the most common food item in the cod stomachs on all sampling dates, both in terms of frequency of occurrence and the proportion of stomach volume they occupied, and mysids were also very prominent in the diet of cod of all sizes. The majority of other food items included harpacticoids copepods, cumaceans, isopods, polychaete worms and flatfish (plaice and dab).

The S:C ratio of *Crangon crangon* which were consumed whole by cod varied between 0.04 and 0.39. The percent occurrence of different S:C ratios was examined separately in cod < 80 mm (n = 153 feeding upon *C. crangon*), and cod > 80 mm (n = 41 feeding upon *C. crangon*) (Fig. 5.5). For the smaller cod (< 80 mm), shrimps falling within the S:C ratio category of 0.10 (bin width = 0.05) were eaten in greatest numbers (38 % of all shrimps consumed), and this was consistent between different field sampling dates. Therefore, the distribution of S:C ratios found *in situ* was biased towards shrimps smaller than those predicted by their handling time profitability determined in the laboratory (sections 4.3.1.vi), and this difference was significant (Chi-square test, $\chi^2 = 117$, d.f. = 7, p < 0.0001). For larger cod (> 80 mm), the peak S:C ratio category of shrimps which were consumed was 0.20 (29 % of all shrimps consumed), closely followed by 0.15 (27 %), and for these fish there was no significant difference between the S:C ratio distribution *in situ* and that predicted by the shrimp's handling time profitability ($\chi^2 = 3.84$, d.f. = 4, p > 0.25).

In addition to the cod which consumed whole individuals of *Crangon crangon*, a small number of cod (n = 9/677, or 1.3 % of all cod examined) were found to contain just a single

appendage (either a claw or a pleopod) of *C. crangon* in their stomach. By measuring the appendage, it was possible to estimate the length of the shrimp from which it was derived (using the relationships shown in Appendix 1). The resulting S:C ratios from these data ranged between 0.21 and 0.84, and 5 of the 9 appendages originated from shrimps with an S:C ratio > 0.40, indicating that they came from shrimps which the cod would not have been able to consume whole.

5.4

DISCUSSION

5.4.1 Comparison of the cod diet at Tralee Beach with other cod populations

Due to the considerable commercial importance of cod, a large literature on their diet has accumulated over recent decades (e.g. Nagabhushanam, 1965; Rae, 1967; Daan, 1973; Robb & Hislop, 1980; Pihl, 1982; Hawkins *et al.*, 1985; Daan *et al.*, 1990; Mattson, 1990; Costa & Elliott, 1991). However, the majority of information concerns adult cod, and comparatively little information exists on the diet of 0-group cod.

Crangon crangon have been reported to occur in the diet of 0-group cod in the Forth Estuary on the east coast of Scotland (Crossan, 1985; Costa & Elliott, 1991; McLusky, pers. comm., University of Stirling), the Humber Estuary on the east coast of England (Marshall & Elliott, pers. comm., Hull University), and the Severn Estuary on the south coast of Wales (Bamber, pers. comm., Fawley Aquatic Research Laboratories Ltd.). In the Forth and Severn Estuaries, *C. crangon* are dominant food items in the stomachs of cod (approximately 90 % of the diet in the Forth). By contrast, *C. crangon* is comparatively scarce in cod caught in the Humber, constituting approximately 40 % of the diet. *C. crangon* form an even lower proportion of the diet than this at Tralee Beach. Differences in the abundance of *C. crangon*, and the relative density with respect to other prey species, are probably the main reasons for these geographical variations.

5.4.2 Predator-prey relationships between cod and *Crangon crangon* at Tralee Beach

In order to evaluate whether predators are selecting (either actively, or passively) prey of a certain type or length, it is essential to know the relative availability of each prey item to the predator. In this respect, the field work at Tralee Beach was hampered by difficulties in measuring the availability of *Crangon crangon* of different lengths. This was partly due to the

selectivity of the sampling gear, which would have captured shrimps of different lengths on a size-dependent basis. The values determined for the density of shrimps represent absolute minima, since only a fraction of shrimps in the trawl's path would have actually entered it; others would either have passed under the net, or escaped from the mouth of the trawl. Furthermore, this probably would have occurred in a size-dependent manner, with larger shrimps escaping from the trawl more successfully than small ones. Once caught, the efficiency of the net in retaining shrimps is also likely to have varied in a size dependent manner. Van Lissa (1977) estimated that the retention of a 5 x 5 mm mesh fitted to a 2 m beam trawl was 27 % for *C. crangon* between 5-10 mm, 53 % between 10-15 mm, 96 % between 15-20 mm, and 100 % for larger shrimps. The trawl net used at Tralee Beach had a cod-end mesh of 3 x 3 mm, and assuming an isometric relationship between mesh size and shrimp retention, shrimps with a length of less than 12 mm would be have been lost in varying degrees, and larger shrimps would have been lost from the outer portion of the net (15 x 15 mm mesh). The habitat conditions at the time of sampling also have a large influence upon the retention of the net, because on certain dates macroalgae from the seabed clogged the trawl mesh. This may have resulted in higher retention of small shrimps, but it also makes it extremely difficult and time-consuming to locate small shrimps within the debris trapped within the net, possibly causing their numbers to be underestimated. Problems with weed retention in the trawl prevented a more extensive survey of the shrimp population within the available time.

Nevertheless, small shrimps (S:C ratio 0.05-0.36) are likely to have been available to the cod throughout the survey period. *Crangon crangon* larvae are present in the plankton through the summer months, and recruitment continues through spring, summer and autumn (see section 1.2). Therefore, the smallest shrimp length classes, although rare in the trawl surveys, are probably the most abundant during most of the summer and autumn.

The maximum length of whole shrimps consumed by cod at Tralee Beach (S:C = 0.34) agrees well with that observed in the laboratory (S:C = 0.36, section 4.3.1.i), except for one 61 mm cod which managed to consume a shrimp with an S:C ratio of 0.39 on 2 July (*cf.* section 4.3.2.vii, in which shrimps with an S:C = 0.38 were never consumed in the laboratory). One possible explanation for this may be that this shrimp was in a post moult condition when it was caught, thereby making it easier to swallow due its soft exoskeleton. Stein (1977) found that the handling time required by smallmouth bass (*Micropterus dolomieu*) to consume a recently

moulted crayfish (*Orconectes propinquus*) was only 10 % of that required to consume an intermoult crayfish of a similar size. *Crangon crangon* undergo approximately 30 moults if they live to maturity, but moult frequency is dependent upon temperature and shrimp age. At temperatures similar to those found at Tralee Beach, small shrimps (5-30 mm) probably undergo a moult every 5-20 days, and this often occurs at night time (based upon data in Tiews, 1970). As a consequence of this, post-moult shrimps will be available for cod to prey upon, and may be more vulnerable to predation than inter-moult shrimps.

For cod of less than 80 mm in length at Tralee, the peak S:C ratio category of shrimps in their stomach was 0.10 (58 % of *Crangon crangon* eaten). This was due to the dominance of newly recruited shrimps (5-10 mm) in their diet. In the laboratory, shrimps were consumed with optimal profitability at an S:C ratio of between 0.15 and 0.20 (sections 4.3.1.vi & 4.3.2.ix). Therefore, *in situ*, small cod fed mainly upon sub-optimal shrimps (with regard to handling time). There are a variety of reasons why this might be. One may be that if search times for the prey that are included in the cod's diet are long compared to handling time (observations made in section 4.3.2 support this), then, according to the predictions made by OFT, the cod's diet should broaden to include less profitable items (Begon *et al.* 1986, p. 318). If this extends to include newly recruited shrimps with an S:C ratio of 0.10, these may become more prevalent in the diet than larger shrimps due to their higher relative abundance at Tralee (i.e. they are encountered more frequently). In addition, higher capture success of small shrimps compared to larger ones (sections 4.3.1.ii & 4.3.2.vi) will also increase the relative profitability of shrimps with an S:C ratio less than 0.15, because it effectively increases the time and energy expenditure required to successfully locate (i.e. capture) larger shrimps. The effect of capture success may be even more relevant when feeding in the dark because cod are unable to pursue shrimps if they escape the cod's first strike (section 4.3.3.ii). On most sampling dates there was moonlight when the samples were collected (no information is available on the illumination threshold limits at which cod are able to visually track and pursue prey), and a proportion of the food items in the stomach may well have been caught before dusk. In addition, pursuit times increase with S:C ratio. Small cod, being more vulnerable to predation than large cod, may be less willing to engage in a pursuit because it may make them more conspicuous to larger predators (e.g. 1+ group whiting, *Merlangius merlangus*, which were also caught in the seine hauls), and the effect of this would also be to bias the diet towards smaller shrimps.

In cod exceeding 80 mm, the peak S:C ratio category was 0.20 (29 % of all food items eaten), closely followed by 0.15 (27 %). Therefore, larger cod do not concentrate their feeding upon newly recruited shrimps (i.e. 5-10 mm), and feed instead upon slightly larger shrimps which have a higher profitability in terms of handling time. This may reflect a reduction in the density of small shrimps during the latter part of the sampling period (when cod > 80 mm were more abundant). Another possible explanation may be that, even if newly recruited shrimps are very abundant, their relative profitability compared to greater S:C ratios decreases as cod become larger. This is because, although handling time remains approximately the same for a shrimp of a given S:C ratio, the weight (i.e. energy content) of shrimps increases exponentially with shrimp length (Kils, 1982). Therefore, the advantage of being able to quickly locate abundant supplies of small newly recruited shrimps diminishes with increasing cod length as the relative profitability of larger shrimps increases.

Overall, the importance of *Crangon crangon* in the diet of cod at Tralee Beach is relatively minor compared to other food items, in particular amphipods and mysids. This is probably due to a combination of factors, including the relative abundance of different prey types, and the comparative effectiveness of their anti-predation defences against foraging cod. With regard to the escape response of *C. crangon*, even in the confined conditions in the laboratory, 40 % or more of encounters with cod resulted in shrimps with an S:C ratio of between 0.14 and 0.38 successfully escaping an encounter (section 4.3.2.vi). Kaiser *et al.* (1992a) suggested that the tail flip escape response of the mysid *Neomysis integer* was responsible for their low occurrence in the diet of small 15-spined sticklebacks (*Spinachia spinachia*), and that instead, small sticklebacks prey mostly upon the non-elusive amphipod *Gammarus locusta*. However, when feeding on mysids, large sticklebacks have a greater capture success than small sticklebacks, and this enables them to increase the proportion of mysids in their diet.

Mysids were an important component in the diets of both small and large cod at Tralee Beach, despite the elusiveness of these prey. Small cod may have greater success than small sticklebacks in capturing mysids, because sticklebacks feed by suction, whereas cod have a mechanism intermediate between suction and ram feeding (Mattson, 1990; Norton, 1991). Data from Rademacher & Kils (1996) indicate, for 10 mm individuals, that the tail flip velocity of the mysid *Neomysis integer* is approximately the same as that of a 10 mm *Crangon crangon*, but 25 mm individuals of *Praunus flexuosus* (Neil & Ansell, 1995) appear to be

slower than similarly sized *C. crangon*. The ease with which mysids can be located by cod compared with *C. crangon* may also be influential in the inclusion of the former in the diet of cod. Mysids are relatively cryptic, but they do not bury within the substratum; some species (e.g. *P. flexuosus*) remain stationary on the sediment surface for considerable amounts of time, whilst others (e.g. *N. integer*) may congregate in swarms within 1 m of the substratum (Mauchline, 1980 - p. 237; O'Brien & Ritz, 1988), and this may make them easier to locate than buried *C. crangon*. It would be interesting to compare the search times and capture success of cod feeding upon *C. crangon* with those for mysids of comparable sizes.

Table 5.1 Summary of cod numbers and stomach contents from Tralee Beach between 2 June and 23 November 1993

* A sub-sample of 20 cod were analysed from a single beach seine haul taken on 31 August. n.d. = not determined.

Sample dates during 1993	Number of beach seine samples analysed	Total number of cod caught	Mean number of cod per beach seine haul (\pm s.d.)	Length category of cod (nearest 5 mm) with the highest frequency	Mean stomach fullness of all cod examined	% of cod with whole <i>C. crangon</i> in their stomach	For cod which ate <i>C. crangon</i> , mean number of shrimps in stomach (\pm s.d.)	For cod which ate <i>C. crangon</i> , mean % of stomach volume comprising shrimps (\pm s.d.)
3 June	1	5	5.0 (\pm 0.0)	40 mm	5.8	40 %	n.d.	30 % (\pm 14)
17 June	3	26	8.7 (\pm 3.5)	50 mm	5.3	62 %	n.d.	33 % (\pm 24)
2 July	2	144	72.0 (\pm 11.3)	55 mm	5.5	33 %	1.37 (\pm 0.97)	48 % (\pm 32)
20 July	2	280	140 (\pm 12.7)	60 mm	5.6	9 %	1.33 (\pm 0.80)	51 % (\pm 35)
3 August	2	122	61.0 (\pm 31.1)	65 mm	6.7	17 %	1.14 (\pm 0.36)	35 % (\pm 32)
31 August*	1	(20)*	n.d.	n.d.	n.d.	30 %	1.50 (\pm 0.55)	n.d.
13 September	1	46	46.0 (\pm 0.0)	75 mm	5.5	22 %	1.50 (\pm 1.58)	10 % (\pm 11)
23 November	4	34	9.3 (\pm 3.4)	95 mm	4.9	33 %	1.55 (\pm 0.93)	60 % (\pm 30)

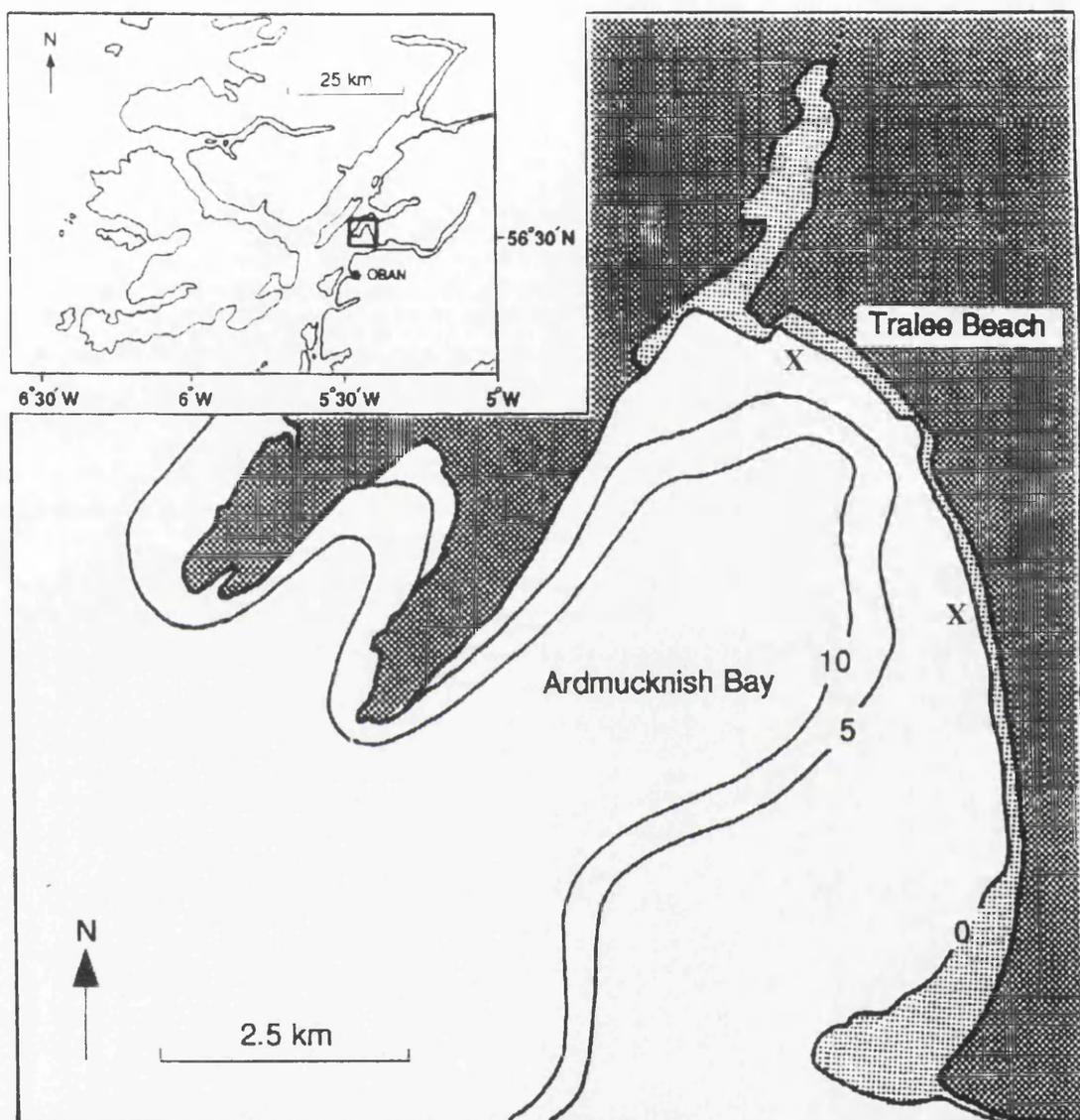


Fig. 5.1 Map of Tralee Beach, the site at which field samples were collected

Map of Tralee Beach, the site at which field samples were collected. Cod and shrimps were collected from areas between the two 'X' marks.

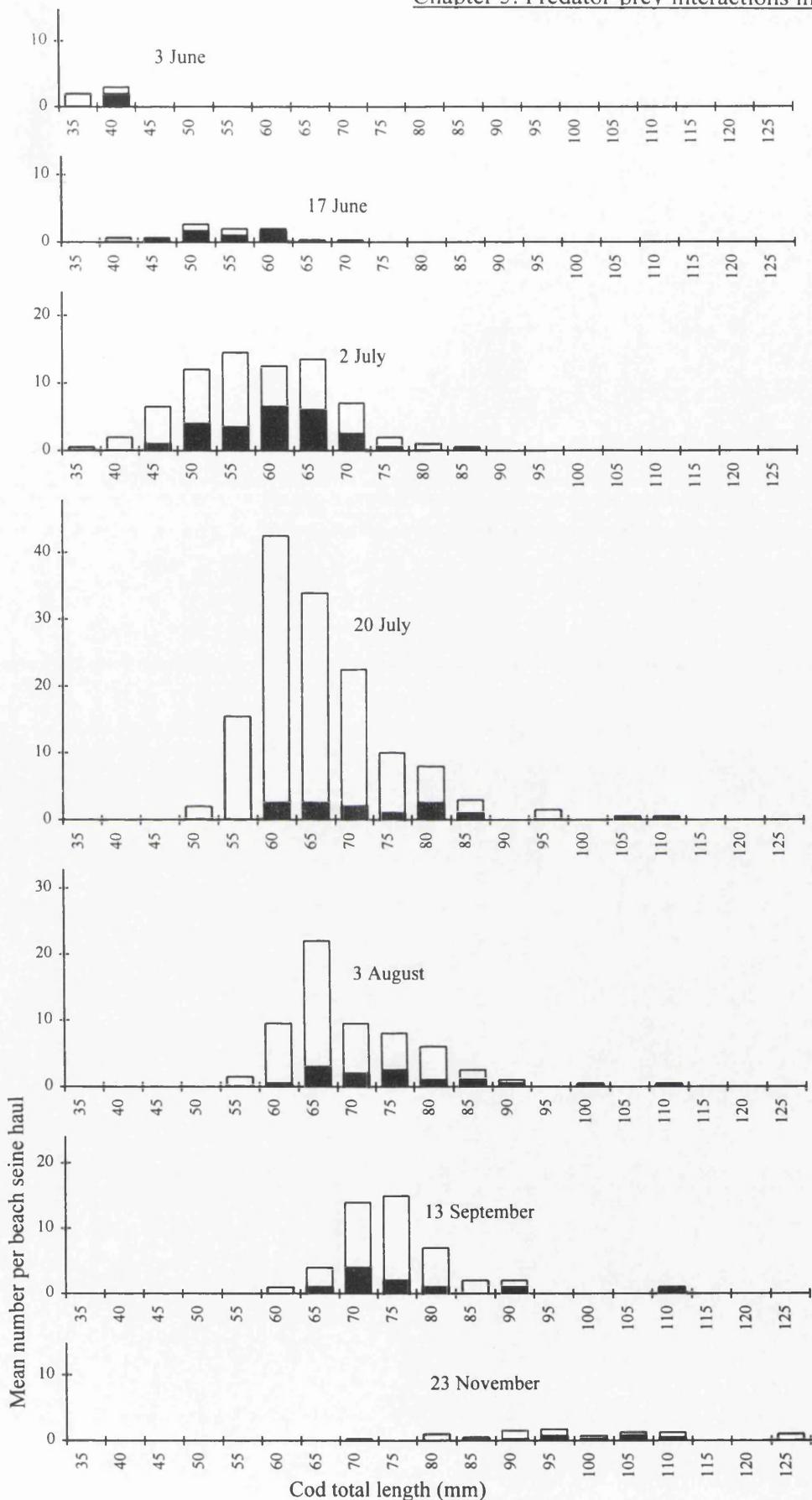


Fig. 5.2 Length-frequency distribution of cod at Tralee Beach during 1993

Mean numbers of cod per beach seine haul at Tralee Beach for each 5 mm length category between 3 June and 23 November 1993 (no cod were caught during mid-May). Black areas represent cod with *C. crangon* in their stomach, and white areas represent those without.

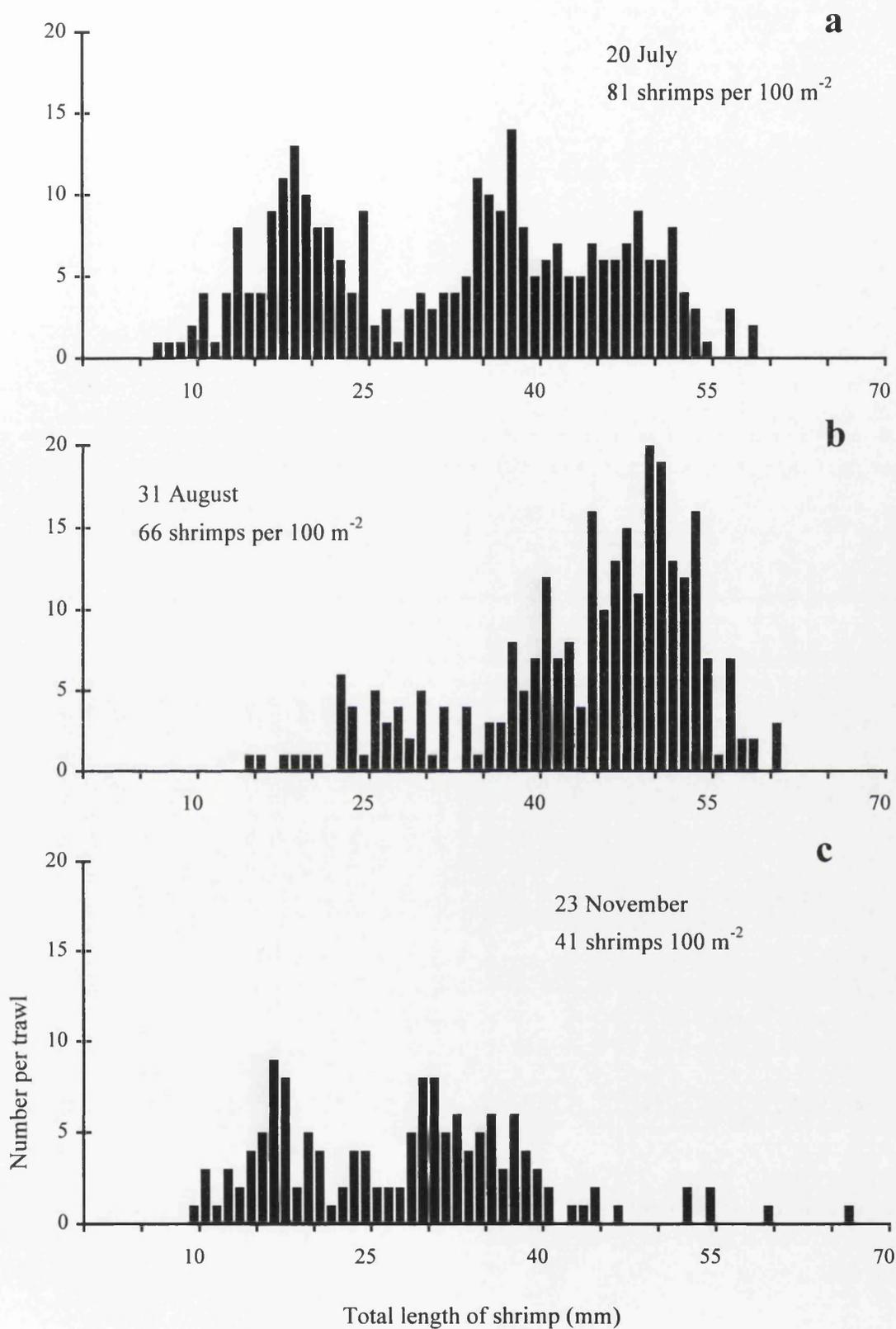


Fig. 5.3 Length-frequency distribution of *Crangon crangon* at Tralee Beach

Length-frequency distribution (1 mm length categories) of *C. crangon* from trawl samples at Tralee beach on (a) 20 July, (b) 31 August, and (c) 23 November 1993.

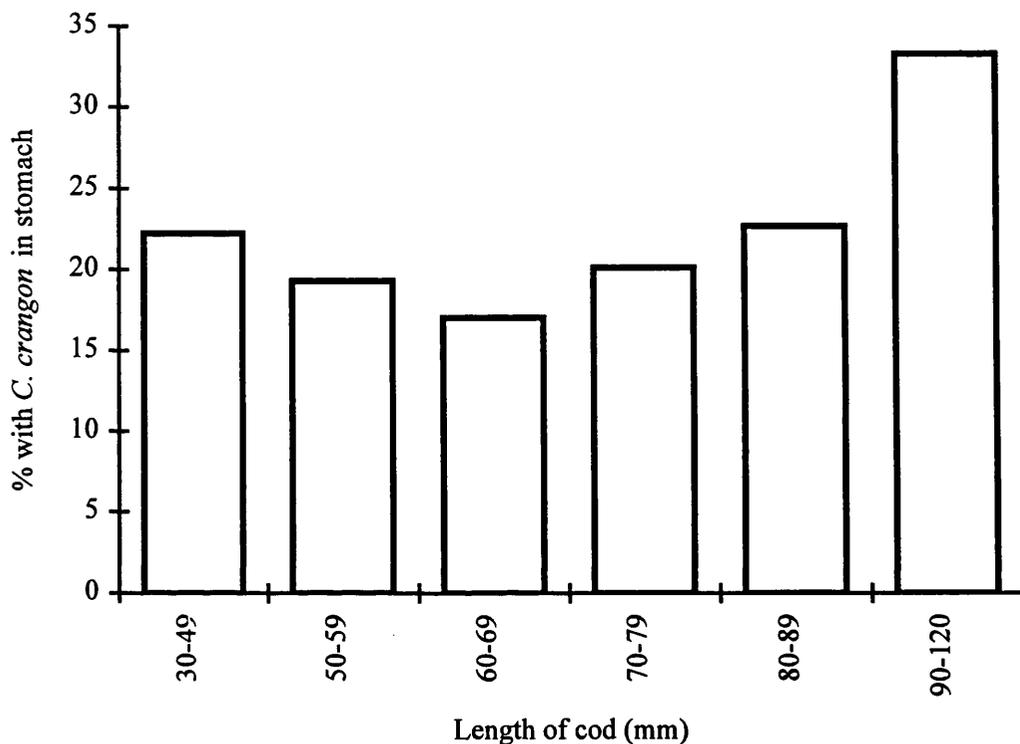


Fig. 5.4 Percent occurrence of *Crangon crangon* in the stomachs of cod of different lengths at Tralee Beach

Percentage occurrence of *C. crangon* in the stomachs of cod of different lengths at Tralee Beach. Note that the length categories are not equal due to grouping of data in a manner amenable to Chi-square analysis. The percent occurrence for all the data combined was 19.6 %, and there was no significant difference between any of the length categories ($\chi^2 = 5.531$, d.f. = 5, $p = 0.355$).

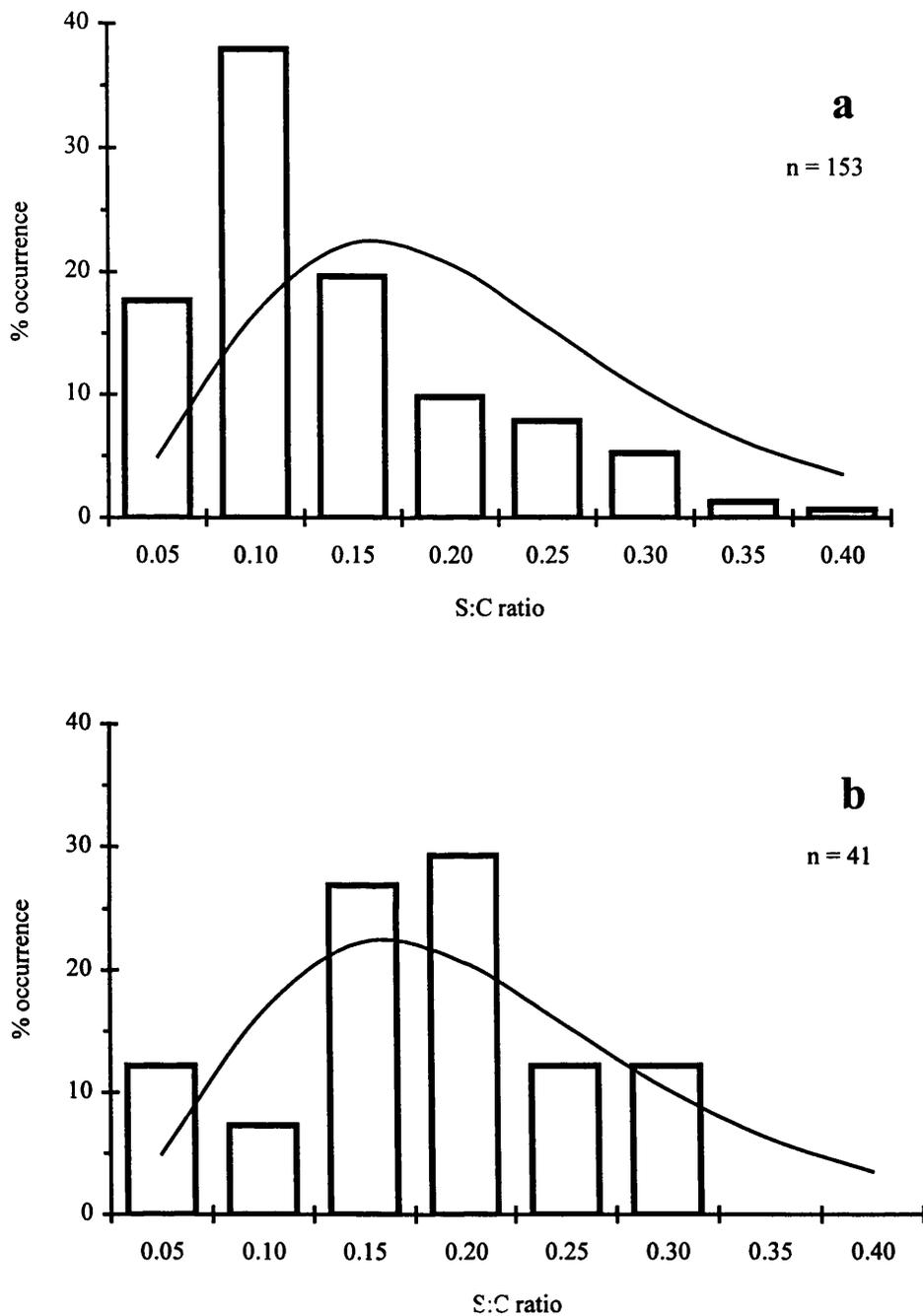


Fig. 5.5 Percent occurrence of S:C ratios for shrimps that were consumed whole by cod at Tralee Beach

Percent occurrence of S:C ratios for the shrimps that were consumed whole by cod at Tralee Beach. The fitted lines represent the predicted values, assuming a direct relationship with handling time profitability (derived from **section 4.3.1.vi**) (a) Cod < 80 mm in length. The observed values differ significantly from the predicted values (Chi-square test, $\chi^2 = 117$, d.f. = 7, $p < 0.0001$). (b) Cod > 80 mm in length. The observed values do not differ significantly from the predicted values (Chi-square = 3.84, d.f. = 4, $p > 0.25$).

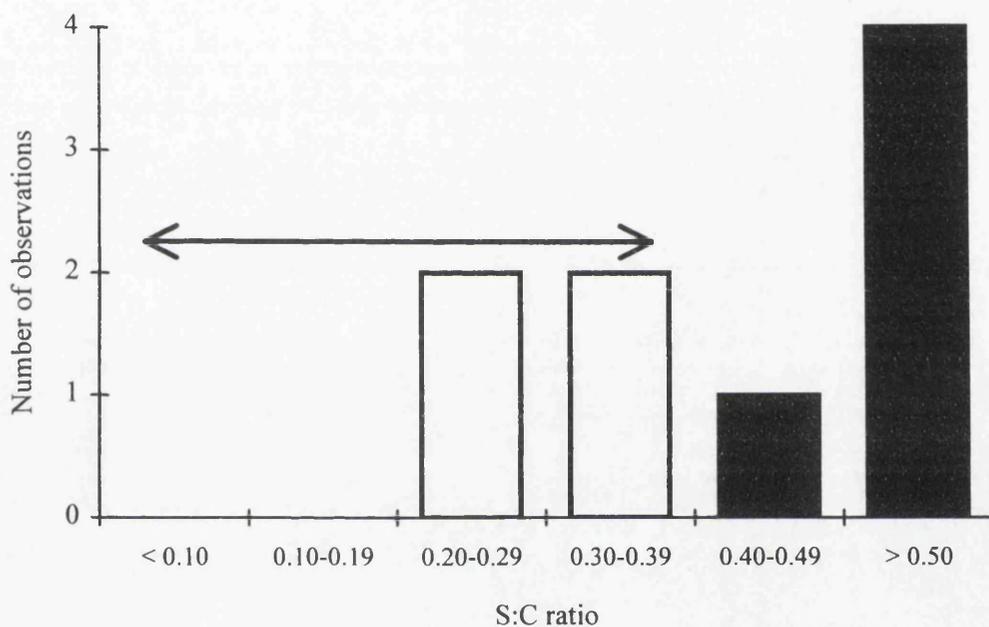


Fig. 5.6 S:C ratios of shrimps from which only an appendage was consumed

S:C ratios of shrimps from which only an appendage was consumed by cod at Tralee Beach (9 cod out of a total of 677 that were examined). The double headed arrow indicates the range over which cod are able to consume shrimps whole; white bars = appendages from shrimps within this range, black bars = appendages from shrimps outside this range.

Chapter 6
Conclusions and Prospects

This investigation has used high speed and conventional video techniques to describe the tail flip escape behaviour of the brown shrimp *Crangon crangon*. These have enabled a variety of aspects to be examined, including the mechanism of tail flip swimming, the size-dependent nature of the escape kinematics, the escape strategies employed by shrimps whilst tail flipping, and the size-dependent success of tail flip escapes from a natural predator, the cod *Gadus morhua*. Results from laboratory experiments have also been compared with *in situ* predation on *C. crangon* by juvenile cod on the west coast of Scotland. Therefore, a broad range of inter-related features of tail flip swimming have been integrated that link aspects from the individual level to the population level.

The majority of investigations on tail flip swimming to date have concentrated on relatively large crustaceans; tail flip swimming in smaller decapod shrimps has only been examined in detail by two other authors hitherto (Daniel & Meyhöfer, 1989; Smith, 1993). Therefore, this investigation has addressed an area in which current knowledge is comparatively lacking, and has revealed several novel aspects of tail flip swimming in decapod crustaceans.

Escapes by *Crangon crangon* have been found to consist of either a single tail flip, or a series of tail flips which together constitute an escape swimming bout. The first tail flip of an escape translates a shrimp either vertically or laterally, and this is dependent upon whether the shrimp rotates about its longitudinal axis during the initial flexion stages of an escape (Chapter 2; Arnott *et al.* 1994, 1995; Neil & Ansell, 1994). If the first tail flip is vertical, *C. crangon* usually performs a roll during the following re-extension phase instead, causing the shrimp to swim on its side during the second and subsequent tail flips of an escape, regardless of the first tail flip mode. This mechanism is in direct contrast to the tail flip behaviour which has been described for other types of decapods, which instead tend to tail flip in an upright body position (e.g. Wine & Krasne, 1972; Webb, 1979; Jacklyn & Ritz, 1986; Newland *et al.*, 1992b). The tail flip mechanism in *C. crangon* is more akin to that of mysid shrimps, which also direct the initial tail flip of an escape laterally by performing a body rotation during the flexion phase (Kaiser & Hughes, 1992; Kaiser *et al.* 1992a; Neil & Ansell, 1995). This raises the question of how *C. crangon* and mysids control their body orientation during tail flips. Crustaceans possess statocyst-controlled self-righting responses which, in large crustaceans,

maintain an animal in an upright body orientation both whilst it is stationary, and whilst it is tail flipping (Newland & Neil, 1990b). In *C. crangon* and mysids, however, the normal upright control response when at rest must be over-ridden during an escape response, but the neuronal control of this temporary phase-shift during an escape remains to be determined. Furthermore, the neuronal processes which bring about the body rotation to the shrimps left or right at the beginning of an escape deserve further attention, and in particular, it needs to be confirmed whether laterally directed escapes can be mediated by giant fibre pathways. If so, *C. crangon* would provide an interesting subject for further study, because it presents new challenges in understanding the underlying processes of 'command neurones', of which the crayfish giant fibre mediated tail flip response is often quoted as a classical example (Kupfermann & Weiss, 1978).

A further similarity between the tail flip swimming of *Crangon crangon* and mysids occurs in the use of the antennal scales for providing thrust during the flexion phase of each tail flip (**Chapter 2**). Previously, it was assumed that virtually all the thrust during tail flips in decapod crustaceans is provided by the movement of the expanded uropods (tail fan) through the water (Webb, 1979), and by 'squeeze forces' generated as the abdomen meets the cephalothorax at the end of body flexion (Daniel & Meyhöfer, 1989). However, in *C. crangon*, the antennal scales expand to form a propulsive head fan during tail flips, and removal of these results in a 35 % decline in the mean tail flip velocity (**section 2.3.6.iii**; Arnott *et al.*, 1997). The use of the head fan for generating thrust can be linked to the comparatively symmetrical (jackknife) flexion mechanism of *C. crangon*, in which the majority of body flexion occurs in the anterior region of the abdomen, whilst the posterior-most region remains extended. This creates movement of both the head fan and the tail fan through the water to enable both surfaces to generate thrust, and it is likely that squeeze forces also become enhanced by this means of tail flipping.

When the tail flip mechanism of *Crangon crangon* (**Chapter 2**) is considered in conjunction with the assumed optimal path of an escape (**Chapter 3**), the influence of the shrimp's habitat upon these two inseparable processes becomes apparent. *C. crangon* escapes from predators by swimming predominantly in the horizontal plane, and it has been argued that this increases the shrimp's probability of survival by keeping it close to the substratum, since the sediment acts as a refuge from predators. However, the jackknife body flexion mode of tail flipping, while maximising velocity, also tends to translate a shrimp vertically when an

upright body orientation is maintained, thereby removing the shrimp from the substratum. The apparent incompatibility between jackknife tail flipping and escaping horizontally is resolved by *C. crangon* rotating onto one side whilst tail flipping, since this provides a simple solution which accommodates both strategies.

The steering of tail flips by *Crangon crangon* during an escape swimming bout requires further investigation in order to determine the mechanisms by which shrimps control the direction in which tail flips occur. Steering in the horizontal plane is achieved primarily by altering the angle of pitch between one tail flip and the next whilst the shrimp is swimming on its side (section 2.3.3.ii). Various actions which may be responsible for bringing this about have been suggested: these include movement of the pleopods during body re-extension, 'rudder-like' use of the antennal scales, and plasticity in the temporal sequence in which the abdominal muscles contract during tail flips. Conclusive evidence for any of these mechanisms is so far lacking though.

An investigation into the escape trajectories of *Crangon crangon* (Chapter 3) has given an insight into potential 'escape rules' that determine the direction of an escape. The escape rules during the initial stages of an escape appear to operate within anatomical constraints which prevent *C. crangon* from escaping in certain directions. These anatomical constraints determine the 'escape envelopes' available to each side of a shrimp when a laterally directed first tail flip occurs (section 3.3.5), but a further limitation is imposed by the direction from which a predator attacks, since a behavioural choice by the shrimp not to escape at angles too close to the attacker results in an 'exclusion envelope' (section 3.3.7). The interaction of these rules for any given attack-escape angle can be represented by a graphic overlay of the escape and exclusion envelopes (section 3.4.5).

Within these limitations, unpredictable (protean) elements of shrimp escapes with respect to attack direction have also been quantified (section 3.4.7). Protean behaviour during escape from predators has been reported to have an important influence on escape success in a wide variety of animal species, but most accounts of protean behaviour are qualitative or subjective rather than quantitative (Driver & Humphries, 1988). This short-coming has been addressed in a number of recent studies on fish (Domenici & Blake, 1993), amphibians (Boothby & Roberts, 1995; Brown & Taylor, 1995) and lizards (Martín & López, 1996), but the data presented in Chapter 3 provides the first of its kind for animals which use a tail flip mode of escape. The use of circular statistics is particularly useful in such investigations,

because it reveals protean properties of escape trajectories which may otherwise be missed using linear statistics, as demonstrated by Domenici & Blake (1993). Comparison of escape strategies across such a broad range of animal groups should be encouraged, since it provides useful information on common adaptive features which have co-evolved under different sets of circumstances, but also highlights possible causes of divergent escape strategies.

Elements of unpredictability which have been quantified include the proportion of escapes which are directed to the ipsilateral or contralateral side of an attack during the first tail flip of an escape, the proportion of escapes which include a sudden change of direction at the end of the first tail flip, the proportion of escapes which are directed either away from, or behind the stimulus direction, and the angular distribution of those escapes which are directed away from an attack. All of these elements have an inherent unpredictability, and the degree of this may vary depending upon the attack direction. However, although protean behaviour is commonly believed to result in greater escape success, quantifying the effectiveness of the unpredictability itself has not been attempted in this or any other study, perhaps because of the experimental difficulties which arise in measuring such a parameter.

One means of overcoming experimental difficulties in the study of escape behaviour is to use computer modelling techniques. This approach has been employed by Weihs & Webb (1984), who used a simple step-by-step representation of kinematics and detection processes to investigate optimal avoidance tactics in predator-prey interactions. Although such types of models are useful, they are unrepresentative of natural interactions in which the principal processes are event-driven and may be probabilistic or imprecise. Furthermore, purely deterministic models do not accommodate the variability of data which often arises from experimental observations. Recent developments in rule-based algorithms (Yager & Filev, 1994) appear to offer scope for the development of more realistic models of predator-prey interactions. These methods enable experimental knowledge of behavioural patterns and formal mathematical descriptions of the constituent processes to be combined interactively. These can be used to test hypotheses on causal mechanisms and new behavioural rules, and in addition to generating a more refined model of the dynamics of natural predator-prey problems, this approach offers the potential for improved assessment of the outcome of encounters and a greater understanding of the underlying mechanism involved. Furthermore, similarities between evasion problems faced by animals, and evasion problems confronted in non-biological systems such as aeronautical aerial combat (Baron *et al.*, 1970), offer the

opportunity for a multi-disciplinary approach to modelling such systems. The use of 'fuzzy modelling' techniques have been used to this effect by Anderson (1995) as an initial step to modelling the evasion data presented in **Chapter 3**.

Analysis of the kinematic parameters during tail flips has revealed that body length significantly influences mean velocity, maximum velocity and maximum acceleration of tail flips. All three parameters increase as juvenile shrimps increase in length, but peak at a body length of between 50-60 mm, after which performance starts to decline. This probably occurs because unequal scaling relationships exist between the length of the shrimp's body, the cross-sectional area of the abdominal flexor muscles, the thrust forces produced during flexion, and the balance of rotational *versus* translational thrust (Daniel & Meyhöfer, 1989). This has important implications with regard to the vulnerability of shrimps to predators, because escape velocity is likely to have a strong influence upon the probability of being caught in the event of an attack by a predator (Howland, 1974; Webb, 1976). In **Chapter 4**, it has been shown that, for a predatory cod of given body length, small *Crangon crangon* are more likely to be captured per strike than large *C. crangon*, and on average, cod will have to pursue large shrimps for a longer period before being able to capture them. For fish feeding upon *C. crangon*, this will have an important effect upon the net energetic value to them of shrimps of different lengths. Couched in terms of Optimal Foraging Theory (OFT), the escape response of shrimps will reduce their profitability because fish will have to search for longer periods in order to successfully locate a shrimp (i.e. capture it), and may have to engage in energetically costly behaviour (i.e. pursuits) in order to achieve a capture. If all prey species of all sizes are ranked in order of their profitability to a particular predator, escape behaviour has the effect of lowering the rank of *C. crangon* with respect to other non-elusive prey species, as well as lowering the profitability of large shrimps with respect to small ones. Depending upon the range of prey items available, this may lead to the exclusion of *C. crangon* from the diet of certain species unless their abundance is particularly high (Stephens & Krebs, 1986). This may explain the relatively low proportion of shrimps found in the stomachs of juvenile cod at Tralee Beach on the west coast of Scotland (**Chapter 5**).

However, predation experiments were conducted only on shrimps of a limited length range between 6-38 mm; over this range, tail flip velocity rises as a positive function of shrimp length. It is possible that predators large enough to consume shrimps greater than this will have a higher capture success for shrimps of a given shrimp:cod (S:C) length ratio, because

tail flip performance no longer continues to improve with shrimps above a length of 50-60 mm. Furthermore, no experiments were conducted on 'berried' shrimps (i.e. female shrimps > c.45 mm in length with eggs attached to their pleopods). These shrimps may also be more vulnerable to predation than non-berried shrimps, because the eggs are likely to hinder tail flips due to (i) the additional mass of the eggs, and (ii) interruption of the water flow pattern by the eggs between the cephalothorax and abdomen during tail flips, causing a decline in squeeze force. Further work on this aspect is required in order to confirm this supposition.

A final important aspect that deserves attention is the interactive effect of light upon the success of escape responses in *Crangon crangon*. In section 4.3.3.ii, data are presented which suggest that, in the dark, shrimps have a much greater probability of escape from cod than in the light because cod are unable to engage in a pursuit. Moore & Moore (1976a) also reported that flounder (*Platichthys flesus*) had a lower capture success of *C. crangon* in turbid rather than clear water conditions. In their natural habitat, the ability of predators to capture elusive prey such as shrimps will therefore be subject to continual change according to features such as the predator's visual threshold, water depth, the time of day, the phase (i.e. brightness) of the moon, the degree of cloud cover, and water turbidity. Therefore, the profitability of shrimps to a particular predator will be dynamic rather than static in nature. This supports the view of Hart & Gill (1993), who advocate the use of dynamic foraging models for predicting prey choice by fish.

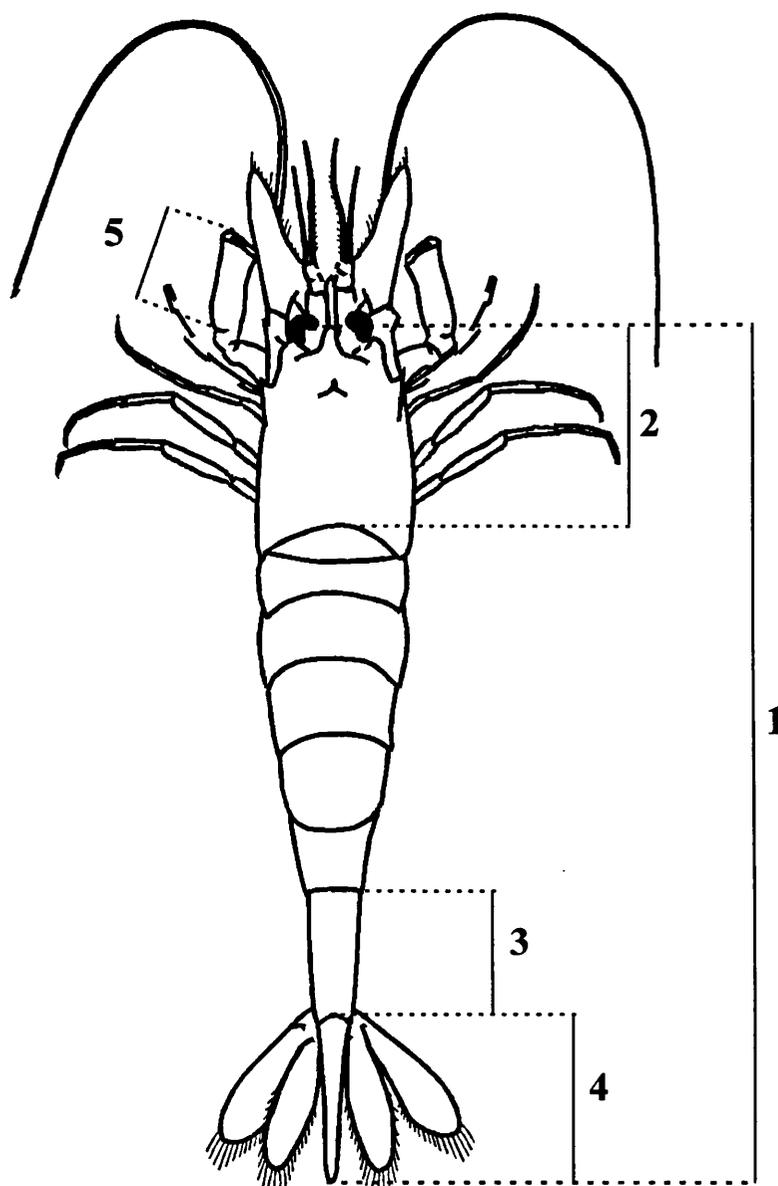
Appendix 1

Appendix 1

Body measurements used in Chapter 5 for estimating the total length of *Crangon crangon* found in the stomachs of juvenile cod.

Conversion factors were derived by taking measurements from shrimps of between 5 and 60 mm caught in trawl samples at Tralee Beach, or caught by hand in Dunstaffnage Bay. Measurements were made using a binocular microscope with a calibrated eyepiece graticule, or in the case of large shrimps, with a pair of callipers. The dimensions of all body parts which were measured increased as a linear function of total body length.

Fig. A1
Body parts of *Crangon crangon* which were measured



Body parts measured (all measurements are in millimetres), and relationship between body part length and total shrimp length. Numbers in bold refer to numbers in Fig. A1.

(1) Total shrimp length (rostrum tip to telson tip).

(2) Carapace length.

$$\text{Total length} = 3.91(\text{carapace length}) + 0.76 \quad r^2 = 0.994$$

(3) Sixth abdominal segment.

$$\text{Total length} = 7.13(\text{6th seg. length}) - 0.915 \quad r^2 = 0.995$$

(4) Telson length.

$$\text{Total length} = 5.54(\text{telson length}) + 0.32 \quad r^2 = 0.983$$

(5) Claw length (there was no significant difference between left and right claw lengths)

Claw length was not routinely used to estimate the length of shrimps which had been eaten whole, because there was a possibility that shrimps were regenerating a previously shed claw. In cases where a cod had eaten only the claw of a shrimp, however, the relationship was used to estimate the length of the shrimp from which the claw was probably derived.

$$\text{Total length} = 1.33(\text{claw length}) + 8.33 \quad r^2 = 0.99$$

References

REFERENCES

- Abdullah, R. & Shukor, N.A.A. 1993. Isozyme variation between 2 closely related species, *Crangon crangon* (L.) and *Crangon allmanni* Kinahan (Decapoda, Caridea). *Crustaceana*. **64**: 114-121.
- Al-Adhub, A.H.Y. & Naylor, E. 1975. Emergence rhythms and tidal migrations of the brown shrimp, *Crangon crangon* (L.). *J. mar. biol. Ass. U.K.* **55**: 801-810.
- Alexander, R. McN. 1970. Mechanics of the feeding action of various teleost fishes. *J. Zool., Lond.* **162**, 145-156.
- Allen, J.A. 1960. On the biology of *Crangon allmani* Kinahan in Northumberland waters. *J. mar. biol. Ass. U.K.* **39**: 481-508.
- Allen, J.A. 1967. *Crustacea: Euphausiacea and Decapoda*. The Fauna of the Clyde Sea Area Series. Scottish Marine Biological Association.
- Anderson, J. 1995. Rule-based mathematical models of predator/prey interactions. *Glasgow University Aerospace Engineering Internal Report. No. 9524*.
- Ansell, A.D. & Gibson, R.N. 1993. The effect of sand and light on predation of juvenile plaice (*Pleuronectes platessa*) by fishes and crustaceans. *J. Fish Biol.* **43**: 837-845.
- Ansell, A.D. & Neil, D.M. 1991. Analysis of escape swimming in the mysid *Praunus flexuosus* by using high-speed video recording. *J. mar. biol. Ass. U.K.* **71**: 731.
- Arnott, S.A., Ansell, A.D. & Neil, D.M. 1994. Escape behaviour of the brown shrimp, *Crangon crangon*, in response to predation by juvenile cod. *J. mar. biol. Ass. U.K.* **74** (3): p. 724.
- Arnott, S.A., Neil, D.M. & Ansell, A.D. 1995. Escape trajectories of the brown shrimp, *Crangon crangon*, in response to visual stimuli presented by natural and artificial predators. In: *Nervous Systems & Behaviour: Proceedings of the 4th International Congress of Neuroethology* (eds. M. Burrows, T. Matheson, P.L. Newland & H. Schuppe). p. 466. Stuttgart: Thieme Medical Publishers. Inc.
- Arnott, S.A., Neil, D.M. & Ansell, A.D. 1997. Functions of the antennal scales during tail flip escape swimming in the brown shrimp, *Crangon crangon*. (Meeting abstract in press) *Estuarine Coastal Shelf Sci.*
- Atema, J. 1988. Distribution of chemical stimuli. In: *The Biology of Crustacea: Structure and Function*. Vol. 3: (eds. D.C. Sandeman & H.L. Atwood). pp. 369-398. New York: Academic Press.

- Atwood, H.L. 1973. An attempt to account for the diversity of crustacean muscles. *Am. Zool.* 13: 357-378.
- Bailey, K.M. & Houde, E.D. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Adv. Mar. Biol.* 25: 1-83.
- Bamber, R. N. & Henderson, P.A. 1994. Seasonality of caridean decapod and mysid distributions and movements within the Severn Estuary and Bristol Channel. *Biol. J. Linn. Soc.* 51: 83-91.
- Barnes, R.D. 1987. Invertebrate Zoology (5th edition.). USA: CBS College Publishing.
- Baron, S., Chu, K.-C., Ho, Y.-C. & Kleinman, D.L. 1970. A new approach to aerial combat games. *NASA CR-1626*.
- Batchelor, G.K. 1967. *An Introduction to Fluid Dynamics*. London: Cambridge University Press.
- Batschelet, E. 1981. *Circular statistics in Biology*. London: Academic Press Inc.
- Batty, R.S., Blaxter, J.H.S. & Richard, J.M. 1990. Light intensity and the feeding behaviour of herring, *Clupea harengus*. *Mar. Biol.* 107: 383-388.
- Beddow, T., van Leeuwen, J. & Johnston, I.A. 1995. Swimming kinematics of fast starts are altered by temperature acclimation in the marine fish *Myoxocephalus scorpius*. *J. exp. Biol.* 198: 203-208.
- Begon, M., Harper, J.L. & Townsend, C.R. 1986. *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications.
- Behrendt, A. 1987. Don't let eels steal your stock. *Fish Farmer*. (Sept/Oct). 50-51.
- Bellman, K.L. & Krasne, F.B. 1983. Adaptive complexity of interactions between feeding and escape in crayfish. *Science*. 221: 779-781.
- Berghahn, R. 1996. Episodic mass invasions of juvenile gadoids into the Wadden Sea and their consequences for the population dynamics of brown shrimp (*Crangon crangon*). *Marine Ecology*. 17: 251-260.
- Berghahn, R., Wiese, K. & Lüdemann, K. 1995. Physical and physiological-aspects of gear efficiency in North Sea brown shrimp fisheries. *Helgolander wiss. Meeresunters. Mar. Invest.* 49, (1-4): 507-518.
- Beukema, J.J. 1992. Dynamics of juvenile shrimp *Crangon crangon* in a tidal-flat nursery of the Wadden Sea after mild and cold winters. *Mar. Ecol. Prog. Ser.* 83: 157-165.

- Blake, M.A. & Hart, P.J.B. 1995. The vulnerability of juvenile signal crayfish to perch and eel predation. *Freshwater Biol.* **33**: 233-244.
- Blaxter, J.H.S. & Batty, R.S. 1990. Herring behaviour in the light and dark. In: *Light and Life in the Sea* (eds. P.J. Herring, A.K. Campbell, M. Whitfield & L. Maddock). pp. 209-220. Cambridge: Cambridge University Press.
- Blaxter, J.H.S. 1970. Light & Fishes. In: *Marine Ecology*, Vol. 1: Environmental Factors (Part 1) (ed. O. Kinne). pp. 213-320. London: Wiley-Interscience.
- Boddeke, R. 1966. Sexual cycle and growth of brown shrimp (*Crangon crangon*). *ICES C.M.* 1966/M. **6**: 1-2.
- Boddeke, R. 1975. Autumn migration and vertical distribution of the brown shrimp *Crangon crangon* (L.) in relation to environmental conditions. In: *Proceedings of the 9th European Marine Biological Symposium* (ed. H. Barnes). pp. 483-494. Aberdeen: Aberdeen University Press.
- Boddeke, R. 1976. The seasonal migration of the brown shrimp *Crangon crangon*. *Neth. J. Sea Res.* **10**: 103-130.
- Boddeke, R. 1982. The occurrence of winter and summer eggs in the brown shrimp (*Crangon crangon*) and the pattern of recruitment. *Neth. J. Sea Res.* **16**: 151-162.
- Boddeke, R., Bosschieter, J.R. & Goudswaard, P.C. 1988. Mating, sperm transfer and sex change in *Crangon crangon* (Decapoda, Natantia). *Am. Zool.* **28**: 109A.
- Bone, Q. & Trueman, E.R. 1983. Jet propulsion in salps (Tunicata: Thaliacea). *J. Zool. Lond.* **201**: 481-506.
- Boothby, K.M. & Roberts, A. 1995. Effects of site tactile stimulation on the escape swimming responses of hatching *Xenopus laevis* embryos. *J. Zool. Lond.* **235**: 113-125.
- Borremans, C. & Redant, F. 1983. *In vitro* experiments on the predation by the swimming crab, *Macropipus holsatus*, on brown shrimps, *Crangon crangon*. International Council for the Exploration of the Sea Shellfish Committee, C.M. 1983/K:19. 7 pp.
- Brawn, V.M. 1969. Feeding behaviour of cod (*Gadus morhua*). *J. Fish. Res. Bd. Can.* **26**: 583-596.
- Breithaupt, T. Schmitz, B. & Tautz, J. 1995. Hydrodynamic orientation of crayfish (*Procambarus clarkii*) to swimming fish prey. *J. comp. Physiol. A.* **177**: 481-491.
- Breithaupt, T. & Tautz, J. 1990. The sensitivity of crayfish mechanoreceptors to hydrodynamic and acoustic stimuli. In: *Frontiers in Crustacean Neurobiology*.

- Advances in Life Sciences (eds. K. Wiese, W-D. Krenz, J. Tautz, H. Reichert & B. Mulloney). pp. 114-120. Basel: Birkhäuser Verlag.
- Broekema, M.M.M. 1942.** Seasonal movements and the osmotic behaviour of shrimp *Crangon crangon* L. *Arch. néerl. Zool.* **6**: 1-100.
- Brown, R.M. & Taylor, D.H. 1995.** Compensatory escape mode trade-offs between swimming performance and manoeuvring behaviour through larval ontogeny of the wood frog *Rana sylvatica*. *Copeia*: 1-7.
- Bullock, T.H. 1984.** Comparative neuroethology of startle, rapid escape, and giant fiber-mediated responses. In: *Neural Mechanisms of Startle Behavior* (ed. R.C. Eaton). pp. 1-13. New York: Plenum Publishing Corporation.
- Bulnheim, H.P. & Schwenzer, D.E. 1993.** Population genetic-studies on *Crangon crangon* and *Crangon allmanni* (Crustacea, Decapods) from European coastal areas. *Zool. Jhrb. abt. Allg. Zool. Physiol. Tiere.* **97**: 327-347.
- Burrows, M.T., Gibson, R.N., Robb, L. & Comely, C.A. 1994.** Temporal patterns of movement in juvenile flatfishes and their predators - underwater television observations. *J. exp. mar. Biol. Ecol.* **177**: 251-268.
- Burton, M. 1969.** *Animal Partnerships*. London, Warne.
- Buskey, E.J. 1994.** Factors affecting feeding selectivity of visual predators on the copepod *Acartia tonsa*: locomotion, visibility and escape responses. *Hydrobiologia.* **293**: 447-453.
- Camhi, J.F. & Tom, W. 1978.** Escape behaviour of the cockroach *Periplaneta americana*. I. Turning response to wind puffs. *J. comp. Physiol. A.* **128**: 193-201.
- Carr, W.E.S. 1982.** Chemical stimulation of feeding behaviour. In: *Chemoreception in Fishes* (ed. T.J. Hara). Amsterdam: Elsevier.
- Cattaert, D., Clarac, F. & Neil, D.M. 1988.** Anatomical and physiological organisation of the swimmeret system of the spiny lobster *Jasus lalandii* as adaptive components of the tail flick. *J. comp. Physiol. A.* **162**: 187-200.
- Cattrijsse, A., Makwaia, E.S., Dankwa, H.R., Hamerlynck, O. & Hemminga, M.A. 1994.** Nekton communities of an intertidal creek of a European estuarine brackish marsh. *Mar. Ecol. Prog. Ser.* **109**: 195-208.
- Caudri, L.W.D. 1937.** Einfluss der Temperatur and des Salzehalts auf die Sterblichkeit von Garnelen (*Crangon crangon* L.). *Arch. néerl. Zool. T.* **3**: 179-196.

- Chance, M.R.A. & Russell, W.M.S. 1959.** Protean displays: a form of allaesthetic behaviour. *Proc. zool. Soc. Lond.* **132**: 65-70.
- Chassard-Bouchaud, C. 1965.** L'adaptation chromatique les Natantia (Crustacés Décapodes). *Cah. Biol. Mar.* **6**: 469-576.
- Comer, C.M. & Dowd, J.P. 1987.** Escape turning behaviour of the cockroach. Changes in directionality induced by unilateral lesions of the abdominal nervous system. *J. comp. Physiol. A.* **160**: 571-583.
- Costa, M.J. & Elliott, M. 1991.** Fish usage and feeding in two industrialized estuaries - the Tagus, Portugal, and the Forth, Scotland. In: *19th Symposium of the Estuarine & Coastal Sciences Association - Estuaries and Coasts: Spatial and Temporal Intercomparisons* (eds. M. Elliott & J.P. Ducrottoy). pp. 289-297.
- Cromarty, S.I., Cobb, J.S. & Kass-Simon, G. 1991.** Behavioural analysis of the escape response in the juvenile lobster *Homarus americanus* over the molt cycle. *J. exp. Biol.* **158**: 565-581.
- Crossan, R. 1985.** Observations on the abundance, growth and feeding of whiting and cod in the Firth of Forth estuary. Unpub. Hons. thesis. University of Stirling.
- Croy, M.I. & Hughes, R.N. 1991a.** The influence of hunger on feeding behaviour and the acquisition of learned foraging skills by the fifteen-spined stickleback, *Spinachia spinachia* L. *Anim. Behav.* **41**: 161-170.
- Croy, M.I. & Hughes, R.N. 1991b.** Hierarchical response to prey stimuli and associated effects of hunger and foraging experience in the fifteen-spined stickleback, *Spinachia spinachia* L. *J. Fish Biol.* **38**: 599-607.
- Daan, N. 1973.** A quantitative analysis of the food intake of North Sea cod, (*Gadus morhua*). *Neth. J. Sea Res.* **6**: 479-517.
- Daan, N., Bromley, P.J., Hislop, J.R.G., & Nielsen, N.A. 1990.** Ecology of North Sea Fish. *Neth. J. Sea Res.* **26**: 343-386.
- Daniel & Meyhöfer, 1989.** Size limits in escape locomotion of caridean shrimp. *J. exp. Biol.* **143**: 245-265.
- Daniel, T., Jordan, C. & Grunbaum, D. 1992.** Hydrodynamics of swimming. In: *Advances in Comparative and Environmental Physiology, Vol. 11. Mechanics of Animal Locomotion* (ed. R. McN. Alexander). pp. 17-49. Berlin: Springer-Verlag.

- DeBlois, E.M. & Rose, G.A. 1995. Effect of foraging activity on the shoal structure of cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **52**: 2377-2387.
- Dekker, W. 1983. An application of the Andersen consumption model in estimating prey size preference of North Sea cod. *I.C.E.S. Demersal Fish Committee, C.M. 1983/G:63*.
- del Norte-Campos, A.G.C. & Temming, A. 1994. Daily activity, feeding and rations in gobies and brown shrimp in the northern Wadden Sea. *Mar. Ecol. Prog. Ser.* **115**: 41-53.
- Denny, M.W., Daniel, T.L. & Koehl, M.A.R. 1985. Mechanical limits to size in wave-swept organisms. *Ecol. Monogr.* **55**: 69-102.
- Dobson, A.P., Hudson, P.J. & Lyles, A.M. 1992. Macroparasites: Worms and Others. In: *Natural Enemies: The Population Biology of Predators, Parasites and Diseases* (ed. M.J. Crawley). pp. 329-374. Oxford: Blackwell Scientific Publications.
- Doflein, F. 1900. Die decapoden Krebse der arktischen Meere. *Fauna arct. Bd. 1*: 313-362.
- Domenici, P. & Blake, R.W. 1991. The kinematics and performance of the escape response in the angelfish (*Pterophyllum eimekei*). *J. exp. Biol.* **156**: 187-205.
- Domenici, P. & Blake, R.W. 1993. Escape trajectories in angelfish (*Pterophyllum eimekei*). *J. exp. Biol.* **177**: 253-272.
- Døving, K.B. & Selset, R. 1980. Behavior patterns in cod released by electrical stimulation of olfactory tract bundlets. *Science.* **207**: 559-560.
- Driver, P.M. & Humphries, D.A. 1988. *Protean Behaviour: The Biology of Unpredictability*. Oxford: Oxford University Press.
- Dumont, J.P.C. & Wine, J.J. 1987. The telson flexor neuromuscular system of the crayfish. III. The role of feedforward inhibition in shaping a stereotyped behaviour pattern. *J. exp. Biol.* **127**: 295-311.
- Edmunds, M. 1966. Protective mechanisms in the Eolidacea (Mollusca Nudibranchia). *J. Linn. Soc. Lond.* **46**: 27-71.
- Edmunds, M. 1974. *Defence in Animals*. Harlow: Longman.
- Edwards, D. H. 1995. The neural mechanisms of social dominance status in crustaceans. In: *Nervous Systems & Behaviour: Proceedings of the 4th International Congress of Neuroethology* (eds. M. Burrows, T. Matheson, P.L. Newland & H. Schuppe). p. 3. Stuttgart: Thieme Medical Publishers. Inc.
- Edwards, D.H. & Mulloney, B. 1987. Synaptic integration in excitatory and inhibitory crayfish motoneurons. *J. Neurophysiol.* **57**: 1425-1445.

- Edwards, R.R. & Steele, J.H. 1968. The ecology of 0-group plaice and common dabs at Loch Ewe. I. Population and food. *J. exp. mar. Biol. Ecol.* **2**: 215-238.
- Eleftheriou, A. & Nicholson, M.D. 1975. The effects of exposure on beach fauna. *Cah. Biol. mar.* (suppl.). **16**: 695-710.
- Ellington, C.P., 1984. The aerodynamics of hovering insect flight. VA vortex theory. *Phil. Trans. R. Soc. B.* **305**: 115-144.
- Ellis, T.R. 1994. Productivity and mortality of early life stages of flatfishes. Ph.D. Thesis. University of Liverpool, U.K.
- Elner, R.W. & Hughes, R.N. 1978. Energy maximisation in the diet of the shore crab, *Carcinus maenas*. *J. Anim. Ecol.* **47**: 103-116.
- Elshoud-Oldenhave, M.J.W. & Osse, J. 1976. Functional morphology of the feeding system of the ruff - *Gymnocephalus cernua* (L. 1758) - (Teleostei, Percidae). *J. Morph.* **150**: 399-422.
- Emlen, J.M. 1966. The role of time and energy in food preference. *Am. Nat.* **100**: 611-617.
- Endler, J.A. 1986. Defense against predators. In *Predator-prey relationships: perspectives and Approaches from the Study of Lower Vertebrates* (eds. M.E. Feder & G.V. Lauder). pp. 109-134. Chicago: University Chicago Press.
- Evans, S. & Tallmark, B. 1985. Niche separation within the mobile predator guild on marine shallow soft bottoms. *Mar. Ecol. Prog. Ser.* **23**: 279-286.
- Fernandez, H.R. 1973. Spectral sensitivity and visual pigments of the compound eye of the galatheid crab *Pleuroncodes planipes*. *Mar. Biol.* **20**: 148-153.
- Fuiman, L.E. & Magurran, A.E. 1994. Development of predator defences in fishes. *Rev. Fish Biol. Fish.* **4**: 145-183.
- Garvey, J.E., Stein, R.A. & Thomas, H.M. 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. *Ecology.* **75**: 532-547.
- Gee, J.M. 1987. The impact of epibenthic predation on estuarine intertidal harpacticoid copepod populations. *Mar. Biol.* **96**: 497-510.
- Ghidalia, W. 1985. Structural and biological aspects of pigments. In: *The Biology of Crustacea, Vol. 9. Integument, Pigments and Hormonal Processes* (eds. D. E. Bliss & L.H. Mantel). pp. 301-394. Orlando: Academic Press Inc.

- Gibson, R.N., Ansell, A.D. & Robb, L. 1993. Seasonal and annual variation in abundance and species composition of fish and macrocrustacean communities on a Scottish Beach. *Mar. Ecol. Prog. Ser.* **98** (1-2): 89-105.
- Gibson, R.N., Yin, M.C. & Robb, L. 1995. The behavioural basis of predator-prey size relationships between shrimps (*Crangon crangon*) and juvenile plaice. *J. mar. biol. Ass. U.K.* **75** (2): 337-349.
- Gill, A.B. & Hart, P.J.B. 1994. Feeding behaviour and prey choice of the threespine stickleback: the interacting effects of prey size, fish size and stomach fullness. *Anim. Behav.* **47**: 921-932.
- Gill, A.B. & Hart, P.J.B. 1996. How feeding performance and energy intake change with a small increase in the body size of the threespine stickleback. *J. Fish Biol.* **48**: 878-890.
- Gotto, R.V. 1969. *Marine Animals: Partnerships and Other Associations*. London, English Universities.
- Gregory, S.F. 1988. An investigation of the invertebrate macrofauna of a sandy beach near Oban, Argyll, with specific study of mouthpart components of *Bathyporeia pilosa* Lindstöm and *B. pelagica* (Bate) (Amphipoda: Haustoridae). BSc. (Hons) thesis, University of Stirling.
- Grimm, A.S. 1965. Osmotic and ionic regulation in the shrimps, *Crangon crangon* Fabricius and *Crangon allmani* Kinahan. PhD Thesis, University of Glasgow.
- Gruschczyk, B. & Kamp, G. 1990. The shift from glycogenolysis to glycogen resynthesis after escape swimming: studies on the abdominal muscle of the shrimp, *Crangon crangon*. *J. comp. Physiol B.* **159**: 753-760.
- Haefner, P.A. & Spaargaren, D.H. 1993. Interactions of ovary and hepatopancreas during the reproductive cycle of *Crangon crangon* (L.). I. Weight and volume relationships. *J. Crust. Biol.* **13**: 523-531.
- Hagerman, L. 1970. Locomotory activity patterns of *Crangon vulgaris* (Fabricius) (Crustacea: Natantia). *Ophelia*. **8**: 255-266.
- Hagerman, L. 1971. Osmoregulation and sodium balance in *Crangon vulgaris* (Fabricius) (Crustacea, Natantia) in varying salinities. *Ophelia*. **9**: 21-30.
- Hagerman, L. 1973. Ionic regulation in *Crangon vulgaris* (Fabr.) (Crustacea, Natantia) from brackish water. *Ophelia*. **12**: 151-157.

- Hagerman, L. 1978. Aspects of the osmotic and ionic regulation of the urine in *Crangon vulgaris* (Fabr.) (Crustacea: Natantia). *J. exp. mar. Biol. Ecol.* **32**: 7-14.
- Hambright, K.D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Trans. Am. Fish Soc.* **120**: 500-508.
- Hamerlynck, O. & Hostens, K. 1993. Growth, feeding, production, and consumption in 0-group bib (*Trisopterus luscus* L.) and whiting (*Merlangius merlangus* L.) in a shallow area of the south-west Netherlands. *ICES J. Mar. Sci.* **50**: 81-91.
- Hara, T.J. 1993. Chemoreception. In: *The Physiology of Fishes* (ed. D.H. Evans). pp. 191-218. Boca Raton: CRC Press.
- Harper, D.G. & Blake, R.W. 1989. On the error involved in high-speed film when used to evaluate maximum acceleration of fish. *Can. J. Zool.* **67**: 1929-1936.
- Harris, C.L. 1996. *Concepts in Zoology*, 2nd edition. New York: Harper Collins Publishers.
- Hart, P.J.B. 1993. Teleost foraging: facts and theories. In: *Behaviour of Teleost Fishes*, 2nd edition (ed. T.J. Pitcher). pp. 253-306. London: Chapman & Hall.
- Hart, P.J.B. & Gill, A.B. 1992. Constraints on prey size selection by the three-spined stickleback: energy requirements and the capacity and fullness of the gut. *J. Fish Biol.* **40**: 205-218.
- Hart, P.J.B. & Gill, A.B. 1993. Choosing prey size: a comparison of static and dynamic foraging models for predicting prey choice by fish. In: *Behavioural Ecology of Fishes*, Ettore Majorana International Life Sciences Series, Vol. II (eds. F.A. Huntingford & P. Torricelli). pp. 91-104. Chur: Harwood Academic Publishers.
- Hart, P.J.B. & Hamrin, S.F. 1990. The role of behaviour and morphology in the selection of prey by pike. In: *Behavioural Mechanisms of Food Selection*, NATO ASI series, Vol. G 20 (ed. R.N. Hughes). pp. 235-254. Berlin: Springer-Verlag.
- Hart, P.J.B. & Ison, S. 1991. The influence of prey size and abundance, and individual phenotype on prey choice by the three-spined stickleback, *Gasterosteus aculeatus* L. *J. Fish Biol.* **38**: 359-372.
- Hartsuyker, L. 1966. Daily tidal migrations of the shrimp *Crangon crangon*. *Neth. J. Sea Res.* **3** (1): 52-58.
- Hawkins, A.D., MacLennan, D.N., Urquhart, G.G. & Robb, C. 1974. Tracking cod *Gadus morhua* L. in a Scottish sea loch. *J. Fish Biol.* **6**: 225-236.

- Hawkins, A.D., Soofiani, N.M. & Smith, G.W. 1985. Growth and feeding in juvenile cod (*Gadus morhua* L.). *J. Cons. int. Explor. Mer.* **42**: 11-32.
- Heatwole, H. 1968. Relationship of escape behaviour and camouflage in anoline lizards. *Copeia*. 109-113.
- Heinisch, P. & Wiese, K. 1987. Sensitivity to movement and vibration of water in the North Sea shrimp *Crangon crangon*. *J. Crust. Biol.* **7**: 401-413.
- Henderson, P.A. & Holmes, R.H.A. 1987. On the population biology of the common shrimp *Crangon crangon* (L.) (Crustacea: Caridea) in the Severn Estuary and Bristol Channel. *J. mar. biol. Ass. U.K.* **67**, 825-847.
- Henderson, P.A. & Holmes, R.H.A. 1989. Whiting migration in the Bristol Channel: a predator-prey relationship. *J. Fish Biol.* **34**, 409-416.
- Henderson, P.A., Seaby, R. & Marsh, S.J. 1990. The population zoogeography of the common shrimp (*Crangon crangon*) in British waters. *J. mar. biol. Ass. U.K.* **70**, 89-97.
- Herrick, C. J. 1900. A contribution upon the cranial nerves of the codfish. *J. comp. Neurol.* **10**: 265-316.
- Herrick, C. J. 1907. A study of the vagal lobes and funicular nuclei of the brain of the codfish. *J. comp. Neurol.* **17**: 67-89.
- Hidaka, I. 1982. Taste receptor stimulation and feeding behaviour in the puffer. In: *Chemoreception in Fishes* (ed. T.J. Hara). Amsterdam: Elsevier.
- Holling, C.S. 1959. The components of predation as revealed by a study of small-mammal predation on the European sawfly. *Can. Ent.* **91**: 293-320.
- Holmes, R.A. & Gibson, R.N. 1986. Visual cues determining prey selection in the turbot, *Scophthalmus maximus*. *J. Fish Biol.* **29**: 49-58.
- Howland, H.C. 1974. Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *J. Theor. Biol.* **47**: 333-350.
- Hoyle, J.A. & Keast, A. 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). *Can. J. Zool.* **65**: 1972-1977.
- Hughes, R.N. 1980. Optimal foraging theory in the marine context. *Oceanogr. Mar. Biol. Ann. Rev.* **18**: 423-481.
- Hughes, R.N. 1993. Basic optimal diet theory. In: *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour* (ed. R.N. Hughes). pp. 1-9. Oxford: Blackwell Scientific Publications.

- Jacklyn, P.M. & D.A. Ritz. 1986. Hydrodynamics of swimming in scyllarid lobsters. *J. exp. mar. Biol. Ecol.* **101**: 85-99.
- Jansenn, G.M. & Kuipers, B.R. 1980. On tidal migration in the shrimp *Crangon crangon*. *Neth. J. Sea Res.* **14**: 339-348.
- Janssen, J. 1976. Feeding modes and prey size selection in the alewife (*Alosa pseudoharengus*). *J. Fish. Res. Bd. Can.* **33**: 1972-1975.
- Jensen, K.T. & Jensen, J.N. 1985. The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. *J. exp. mar. Biol. Ecol.* **89**: 157-174.
- Jobling, M. 1995. *Environmental Biology of Fishes*. London: Chapman & Hall.
- Johnson, G.E. 1924. Giant nerve fibres in crustaceans, with special reference to *Cambarus* and *Palaemonetes*. *J. comp. Neurol.* **36**: 323-373.
- Jones, K.A. 1992. Food search behaviour and the use of chemical lures in commercial and sports fishing. In: *Fish Chemoreception* (ed. T.J. Hara). London: Chapman & Hall.
- Jones, R. 1974. The rate of elimination of food from the stomachs of haddock *Melanogrammus aeglefinus*, cod *Gadus morhua* and whiting *Merlangius merlangus*. *J. Cons. int. Explor. Mer.* **35**: 225-243.
- Jönsson, B., Sundbäck, K., Nilsson, P., Nilsson, C., Swanberg, I.L. & Ekebom, J. 1993. Does the influence of the epibenthic predator *Crangon crangon* L. (brown shrimp) extend to the sediment microalgae and bacteria. *Neth. J. Sea Res.* **31**: 83-94.
- Kaiser, M.J. & Hughes, R.N. 1992. Factors affecting the behavioural mechanisms of diet selection in fishes. In: *Behavioural Ecology of Fishes*, Ettore Majorana International Life Sciences Series, Vol. II (eds. F.A. Huntingford & P. Torricelli). pp. 105-118. Chur: Harwood Academic Publishers.
- Kaiser, M.J., Gibson, R.N. & Hughes, R.N. 1992a. The effect of prey type on the predatory behaviour of the fifteen-spined stickleback, *Spinachia spinachia* (L.) *Anim. Behav.* **43**: 147-156.
- Kaiser, M.J., Westhead, A.P., Hughes, R.N. & Gibson, R.N. 1992b. Are digestive characteristics important contributors to the profitability of prey? *Oecologia.* **90**: 61-69.
- Kamp, G. 1989. Glycogenolysis during recovery from muscular work. *Biol. Chem. Hoppe-Seyler.* **370**: 565-573.

- Kamp, G. & Juretschke, H.P. 1987. An in vivo ^{31}P -NMR study of the possible regulation of glycogen phosphorylase *a* by phosphagen via phosphate in the abdominal muscle of the shrimp *Crangon crangon*. *Biochim. biophys. Acta.* **929**: 121-127.
- Kasapi, M.A., Domenici, P., Blake, R.W. & Harper, D. 1992. The kinematics and performance of escape responses of the knifefish *Xenomystus nigri*. *Can. J. Zool.* **71** (1): 189-195.
- Kils, U. 1982. The swimming behaviour, swimming performance and energy balance of the Antarctic krill, *Euphausia superba*. *Biomass Sci. Ser.* **3**: 1-121.
- Kislalioglu, M. & Gibson, R.N. 1976a. Prey 'handling time' and its importance in food selection by the 15-spined stickleback, *Spinachia spinachia* (L.). *J. exp. mar. Biol. Ecol.* **25**: 151-158.
- Kislalioglu, M. & Gibson, R.N. 1976b. Some factors governing prey selection by the 15-spined stickleback, *Spinachia spinachia* (L.). *J. exp. mar. Biol. Ecol.* **25**: 159-169.
- Kovach, W.L. 1994. *Oriana for Windows, ver. 1.0*. Kovach Computing Services, Pentraeth, Wales, U.K.
- Krasne, F. 1965. Escape from recurring tactile stimulation in *Branchiomma vesiculosum*. *J. exp. Biol.* **42**: 307-322.
- Krasne, F. & Wine, J.J. 1975. Extrinsic modulation of crayfish escape behaviour. *J. exp. Biol.* **63**: 433-450.
- Krasne, F. & Wine, J.J. 1984. The production of crayfish escape responses. In: *Comparative Neurobiology of Startle Responses and other Fast Escape Responses* (ed. R. Eaton). pp. 179-211. New York: Plenum Press.
- Krasne, F. & Wine, J.J. 1988. Evasion responses of the crayfish. In: *Aims and Methods in Neuroethology* (ed. D.M. Guthrie). pp. 10-45. Manchester: Manchester University Press.
- Krebs, J.R. & Davies, N.B. 1993. *An Introduction to Behavioural Ecology*, 3rd Edition. Oxford: Blackwell Scientific Publications.
- Kruuk, H. 1972. *The Spotted Hyaena*. Chicago: University of Chicago Press.
- Kuipers, B.R. & Dapper, R. 1981. Production of *Crangon crangon* in the tidal zone of the Dutch Wadden Sea. *Neth. J. Sea Res.* **15**: 33-53.
- Kuipers, B.R. & Dapper, R. 1984. Nursery function of Wadden Sea tidal flats for the brown shrimp *Crangon crangon*. *Mar. Ecol. Prog. Ser.* **17**: 171-181.

- Kupfermann, I. & Weiss, K.R. 1978. The command neuron concept. *Behav. Brain Sci.* 1: 3-39.
- Land, M. & Layne, J. 1995. The visual control of behaviour in fiddler crabs. II. Tracking control systems in courtship and defence. *J. comp. Physiol A.* 177: 91-103.
- Landeau, L. & Terborgh, J. 1986. Oddity and the 'confusion effect' in predation. *Anim. Behav.* 34: 1372-1380.
- Lang, F., Govind, C.K., Costello, W.J. & Greene, S.I. 1977. Developmental neuroethology: changes in escape and defensive behavior during growth of the lobster. *Science.* 197: 682-685.
- Langton, R.W. 1982. Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, and fifteen other northwest Atlantic finfish. *Fish. Bull. U.S.* 80: 745-759.
- Larimer, J.L., Eggleston, A.C., Masukawa, L.M. & Kennedy, D. 1971. The different connections and motor outputs of lateral and medial giant fibres in the crayfish. *J. exp. Biol.* 54: 391-402.
- Lauder, G.V. 1983. Functional and morphological bases of trophic specialization in sunfishes (Teleostei, Centrarchidae). *J. Morph.* 178: 1-21.
- Lauder, G.V. & Clark, B.D. 1984. Water flow patterns during prey capture by teleost fishes. *J. exp. Biol.* 113: 143-150.
- Lauder, G.V. & Norton, S.F. 1980. Asymmetrical muscle activity during feeding in the gar, *Lepisosteus oculatus*. *J. exp. Biol.* 84: 17-32.
- Lazzari, C. & Varjú, D. 1990. Visual lateral fixation and tracking in the haematophagous bug *Triatoma infestans*. *J. comp. Physiol A.* 167: 527-531.
- Le Mao, P. 1986. Feeding relationships between benthic infauna and the dominant benthic fish of the Rance estuary (France). *J. mar. biol. Ass. U.K.* 66: 391-401.
- Lebour, M.V. 1931. The larvae of the Plymouth Caridea. I. The larvae of the Crangonidae. II. The larvae of the Hippolytidae. *Proc. zool. Soc. Lond.* 1-9.
- Levi, R. & Camhi, J.M. 1996. Producing directed behaviour: muscle activity patterns of the cockroach escape response. *J. exp. Biol.* 199: 563-568.
- Liem, K.F. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am. Zool.* 20: 295-314.
- Lima, S.L. & Dill, L. 1990. Behavioral decisions made under the risk of predation: a review and prospects. *Can. J. Zool.* 68: 619-640.

- Lloyd, A.J. & Yonge, C.M. 1947. The biology of *Crangon vulgaris* L. in the Bristol Channel and Severn Estuary. *J. mar. biol. Ass. U.K.* 26: 626-661.
- MacArthur, R.H. & Pianka, E.R. 1966. On optimal use of a patchy environment. *Am. Nat.* 100: 603-609.
- Macer, C.T. 1967. The food web in Red Wharf Bay (North Wales) with particular reference to young plaice (*Pleuronectes platessa*). *Helgolander wiss. Meeresunters. Mar. Invest.* 15: 560-573.
- Mackie, A.M. 1982. Identification of the gustatory feeding stimulants. In: *Chemoreception in Fishes* (ed. T.J. Hara). Amsterdam: Elsevier.
- Mackney, P.A. & Hughes, R.N. 1996. Foraging behaviour and memory window in sticklebacks. *Behaviour.* 132: 1241-1253.
- McLusky, D.S., Hagerman, L. & Mitchell, P. 1982. Effect of salinity acclimation on osmoregulation in *Crangon crangon* and *Praunus flexuosus*. *Ophelia.* 21: 89-100.
- Malcolm, S.B. 1990. Mimicry: status of a classical evolutionary paradigm. *Trends Ecol. Evol.* 5: 57-62.
- Malcolm, S.B. 1992. Prey defence and predator foraging. In: *Natural Enemies: The Population Biology of Predators, Parasites and Diseases* (ed. M. J. Crawley). pp. 458-475. Oxford: Blackwell Scientific Publications.
- Martín, J. & López, P. 1995. Escape behaviour of juvenile *Psammodromus algirus* lizards: Constraints of or compensation for limitations in body size? *Behaviour.* 132: 181-192.
- Martín, J. & López, P. 1996. The escape response of juvenile *Psammodromus algirus* lizards. *J. comp. Psychol.* 110: 187-192.
- Marui, T. & Caprio, J. 1992. Teleost gustation. In: *Fish Chemoreception* (ed. T.J. Hara). pp. 171-198. London: Chapman & Hall.
- Mather, M.E. & Stein, R.A. 1993. Direct and indirect effects of fish predation on the replacement of a native crayfish by an invading congener. *Can. J. Fish. Aquat. Sci.* 50: 1279-1288.
- Mattson, S. 1990. Food and feeding habits of fish species over a soft sublittoral bottom in the Northeast Atlantic. 1. Cod (*Gadus morhua* L.) (Gadidae). *Sarsia.* 75 (3): 247-260.
- Mauchline, J. 1980. The biology of mysids. *Adv. Mar. Biol.* 18: 3-369.
- McIntyre, A.D. 1970. The range of biomass in intertidal sand, with specific reference to the bivalve *Tellina tenuis*. *J. mar. biol. Ass. U.K.* 50: 561-575.

- Metcalf, N.B., Huntingford, F.A. & Thorpe, J.E. 1987.** The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. *Anim. Behav.* **35**: 901-911.
- Microsoft Corporation. 1993.** *Excel version 5.0*. Microsoft Place, Wharfedale Road, Winnersh Triangle, Wokingham, Berks., UK.
- Minitab Inc. 1995.** *Minitab 10.51 Xtra for Windows*. 3081 Enterprise Drive, State College, PA, 16801-3008, USA.
- Mittenthal, J.E. & Wine, J.J. 1973.** Connectivity patterns of crayfish giant interneurons: visualisation of synaptic regions with cobalt dye. *Science*. **179**: 182-184.
- Modin, J. & Pihl, L. 1994.** Differences in growth and mortality of juvenile plaice, *Pleuronectes platessa* L., following normal and extremely high settlement. *Neth. J. Sea Res.* **32**: 331-341.
- Moore, J.W. & Moore, I.A. 1976a.** The basis of food selection in flounders, *Platichthys flesus* (L.), in the Severn Estuary. *J. Fish Biol.* **9**: 139-156.
- Moore, J.W. & Moore, I.A. 1976b.** The basis of food selection in some estuarine fishes. Eels, *Anguilla anguilla* (L.), whiting, *Merlangius merlangus* (L.), sprat, *Sprattus sprattus* (L.) and stickleback, *Gasterosteus aculeatus* L. *J. Fish Biol.* **9**: 375-390.
- Moore, P.A., Scholz, N. & Atema, J. 1991.** Chemical orientation of lobsters, *Homarus americanus*, in turbulent odour plumes. *J. Chem. Ecol.* **17**: 1293-1307.
- Moss, F. & Wiesenfeld, K. 1995.** The benefits of background noise. *Scient. Am.* **273**(2): 66-69.
- Moyse, J., Thorpe, J.P. & Al-Hamadani, E. 1982.** The status of *Littorina aestuarii* Jeffreys: an approach using morphology and biochemical genetics. *J. Chonch.* **31**: 7-15.
- NAC, 1989.** NAC, Kodak Ltd., Hemel Hamstead, Herts., UK.
- Nagabhushanam, A.K. 1965.** On the biology of the commoner gadoids in Manx waters. *J. mar. biol. Ass. U.K.* **45**: 615-657.
- Nalbach, H-O, 1990a.** Discontinuous turning reaction during escape in soldier crabs. *J. exp. Biol.* **148**: 483-487.
- Nalbach, H-O. 1990b.** Visually elicited escapes in crabs. In: *Frontiers in Crustacean Neurobiology* (eds. K. Wiese, W-D. Krenz, J. Tautz, H. Reichert & B. Mulloney). pp. 165-172. Basel: Birkhäuser Verlag.

- Neil, D.M. & Ansell, A.D. 1995. The orientation of tail-flip escape swimming in decapod and mysid crustaceans. *J. mar. biol. Ass. U.K.* **75**: 55-70.
- Newland, P.L. 1985. The control of escape behaviour in the Norway Lobster, *Nephrops norvegicus* (L.). PhD Thesis, University of Glasgow.
- Newland, P.L. & Chapman, C.J. 1989. The swimming and orientation behaviour of the Norway lobster, *Nephrops norvegicus* (L.) in relation to trawling. *Fisheries Res.* **8**: 63-80.
- Newland, P.L. & Neil, D.M. 1990a. The tail flip of the Norway lobster, *Nephrops norvegicus*: I. Giant fibre activation in relation to swimming trajectories. *J. comp. Physiol. A.* **166**: 517-527.
- Newland, P.L. & Neil, D.M. 1990b. The tail flip of the Norway lobster, *Nephrops norvegicus*: II. Dynamic righting reactions induced by body tilt. *J. comp. Physiol. A.* **166**: 517-527.
- Newland, P.L., Cattaert, D., Neil, D.M. & Clarac, F. 1992a. Steering reactions as adaptive components of the tail-flip in the spiny lobster, *Jasus lalandii*. *J. exp. Biol.*, **164**: 261-282.
- Newland, P.L., Neil, D.M. & Chapman, C.J. 1992b. Escape swimming in the Norway lobster, *Nephrops norvegicus*. *J. Crust. Biol.* **12**: 342-353.
- Norton, S.F. 1991. Capture success and diet of cottid fishes: the role of predator morphology and attack kinematics. *Ecology.* **72**: 1807-1819.
- Norton, S.F. 1995. A functional approach to ecomorphological patterns of feeding in cottid fishes. *Env. Biol. Fish.* **44**: 61-78.
- Nyberg, D.W. 1971. Prey capture in largemouth bass. *Am. Midl. Nat. Monogr.* **86**: 128-144.
- O'Brien, W.J. 1979. Predator-prey interactions of planktivorous fish and zooplankton. *Am. Scient.* **67**: 572-581.
- O'Brien, D.P. & Ritz, D.A. 1988. Escape responses of gregarious mysids (Crustacea: Mysidacea): towards a general classification of escape responses in aggregated crustaceans. *J. exp. mar. Biol. Ecol.* **116**: 257-272.
- O'Dor, R.K. 1988. The forces acting on swimming squid. *J. exp. Biol.* **137**. 421-442.
- Onnen, T. & Zebe, E. 1983. Energy metabolism in the tail muscles of the shrimp, *Crangon crangon*, during work and subsequent recovery. *Comp. Biochem. Physiol.* **74(A)** (4): 833-838.

- Ortmann, A. 1891. Die Dekapoden-Krebse des Strasburger Museums. II. *Zool. Jb., Abt. Syst.* 5: 693-750.
- Paul, D.H. 1990. Neural phylogeny - its use in studying neural circuits. In: *Frontiers in Crustacean Neurobiology* (eds. K. Wiese, W-D. Krenz, J. Tautz, H. Reichert & B. Mulloney). pp. 537-546. Basel: Birkhäuser Verlag.
- Pawson, M.G. 1977. Analysis of a natural chemical attractant for whiting *Merlangius merlangus* and cod *Gadus morhua* using a behavioural bioassay. *Comp. Biochem. Physiol.* 56A: 129-135.
- Pihl, L. 1982. Food intake of young cod and flounder in a shallow bay on the Swedish west coast. *Neth. J. Sea Res.* 15: 419-432.
- Pihl, L. 1985. Food selection and consumption of mobile epibenthic fauna in shallow marine areas. *Mar. Ecol. Prog. Ser.* 22: 169-179.
- Pihl, L. & Rosenberg, R. 1982. Production, abundance, and biomass of mobile epibenthic marine fauna in shallow waters, western Sweden. *J. exp. mar. Biol. Ecol.* 57: 273-301.
- Pihl, L. & Rosenberg, R. 1984. Food selection and consumption of the shrimp *Crangon crangon* in some shallow marine areas. *Mar. Ecol. Prog. Ser.* 15: 159-168.
- Pinn, E.H. & Ansell, A.D. 1993. The effect of particle size on the burying behaviour of the brown shrimp, *Crangon crangon*. *J. mar. biol. Ass. U.K.* 73: 365-377.
- Pitcher, T.J. & Parrish, J.K. 1993. Functions of shoaling behaviour in teleosts. In: *Behaviour of Teleost Fishes*, 2nd edition (ed. T.J. Pitcher). London: Chapman & Hall.
- Poolsanguan, B. & Uglow, R.F. 1974. Quantitative changes in blood sugar levels of *Crangon vulgaris*. *J. comp. Physiol.* 93: 1-6.
- Rademacher, K. & Kils, U. 1996. Predator-prey dynamics of 15-spined stickleback *Spinachia spinachia* and the mysid *Neomysis integer*. *Arch. Fish. Mar. Res.* 43: 171-181.
- Rae, B.B. 1967. The food of cod in the North Sea and on West of Scotland grounds. *Mar. Res.* (Department of Agriculture and Fisheries for Scotland, Aberdeen). No. 1. 68 pp.
- Raffaelli, D., Conacher, A., McLachlan, H. & Emes, C. 1989. The role of epibenthic crustacean predators in an estuarine food web. *Estuarine Coastal Shelf Sci.* 289: 149-160.
- Rand, D.M. & Lauder, G.V. 1981. Pry capture in the chain pickerel, *Esox niger*: correlations between feeding and locomotor activity. *Can. J. Zool.* 59: 1072-1078.

- Rao, K.R. 1985. Pigmentary effectors. In: *The Biology of Crustacea, Vol.9. Integument, Pigments and Hormonal Processes* (eds. D.E. Bliss & L.H. Mantel). pp. 395-462. New York: Academic Press Inc.
- Redant, F. 1980. Population dynamics of the brown shrimp *Crangon crangon* L. in the Belgian coastal waters: II-Predation, Mortality. *I.C.E.S., CM.* 1980/K:33.
- Reichert, H. 1988. Control of sequences of movements in crayfish escape behaviour. *Experimentia.* 44: 395-401.
- Reichert, H. & Wine, J.J. 1983. Co-ordination of lateral giant and non-giant systems in crayfish escape behaviour. *J. comp. Physiol. A.* 153: 3-15.
- Richards, S.J. & Bull, C.M. 1990. Size-limited predation on tadpoles of three Australian frogs. *Copeia*, 1990: 1041-1046.
- Robb, A.P. & Hislop, J.R.G. 1980. The food of five gadoid species during the pelagic 0-group phase in the northern North Sea. *J. Fish Biol.* 16: 199-217.
- Roberts, A., Krasne, F. B., Hagiwara, G., Wine, J.J. & Kramer, A.P. 1982. Segmental giant: evidence for a driver neuron interposed between command and motor neurons in the crayfish escape system. *J. Neurophysiol.* 47: 761-781.
- Robin, J.P. & Marchand, J. 1986. Preliminary observations on the feeding activity of fishes during tidal and diel cycles in the Loire Estuary: The bib *Trisopterus luscus* L. 1758. *Mar. Ecol.* 7 (2): 181-189.
- Robinson, M.H. 1969. The defensive behaviour of some orthopteroid insects from Panama. *Trans. R. ent. Soc. Lond.* 121: 281-303.
- Roeder, K.D. & Treat, A.E. 1961. The detection and evasion of bats by moths. *Am. Scient.* 49: 135-148.
- Roeder, K.D. 1962. The behaviour of free-flying moths in the presence of artificial ultrasonic pulses. *Anim. Behav.* 10: 300-304.
- Salvat, B. 1962. Faune des sédiments meubles intertidaux du bassin d'Arcachon. Systématique et écologie. *Cah. Biol. mar.* 3: 219-244.
- Sars, G.O. 1890. Bidrag til kundsskaben om Decapodernes Forvandlug. III. Fam. Crangonidae. *Arch. Math. Natur.* 14 132-195.
- Satchell, G.H., 1991. *Physiology and Form of Fish Circulation*. Cambridge: Cambridge University Press.

- Schuijf, A. 1975. Directional hearing in the cod under approximate free field conditions. *J. comp. Physiol.* **98**: 307-332.
- Semlitsch, R.D. 1990. Effects of body size, sibship, and tail injury on the susceptibility of tadpoles to dragon fly predation. *Can. J. Zool.* **68**: 1027-1030.
- Sih, A. 1993. Effects of ecological interactions on forager diets: competition, predation risk, parasitism and prey behaviour. In: *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour* (ed. R.N. Hughes). pp. 182-211. Oxford: Blackwell Scientific Publications.
- Sillar, K.T. & Heitler, W.J. 1985. The neural basis of escape swimming behaviour in the squat lobster *Galathea strigosa*. I. Absence of cord giant axons and anatomy of motor neurones involved in swimming. *J. exp. Biol.* **117**: 251-269.
- Singh-Renton, S. & Bromley, P.J. 1996. Effects of temperature, prey type and prey size on gastric evacuation in small cod and whiting. *Journal of Fish Biology.* **49**: 702-713.
- Smaldon, G. 1979. *British coastal shrimp and prawns. Keys and notes for the identification of the species* (Synopsis of the British Fauna, no. 15: Linnean Society). London.
- Smith, K.H. 1993. A study of the escape behaviour of the brown shrimp, *Crangon crangon* (L.). M.Sc. thesis, University of Glasgow, Scotland.
- Soofiani, N.M. & Hawkins, A.D. 1982. Energetic costs at different levels of feeding in juvenile cod, *Gadus morhua*. *J. Fish. Biol.* **21**: 577-592.
- Spaargaren, D.H. 1971. Aspects of the osmotic regulation in the shrimps *Crangon crangon* and *Crangon allmanni*. *Neth. J. Sea Res.* **5**(3): 275-335.
- Spaargaren, D.H. 1975. Energy relations in the ion regulation in three crustacean species. *Comp. Biochem. Physiol.* **51A**: 543-548.
- Spaargaren, D.H. 1980. The significance of seawater viscosity for the tidal transport of common shrimps, *Crangon crangon* L. *Ophelia.* **19**(2): 145-153.
- Spanier, E., Weihs, D. & Almog-Shtayer, G. 1991. Swimming of the Mediterranean slipper lobster. *J. exp. mar. Biol. Ecol.* **145**, pp. 15-31.
- SPSS Inc. 1993. *SPSS 5.0.2*. SPSS Inc., 444 N. Michigan Avenue, Chicago, Illinois, 60611.
- Srygley, R.B. 1994. Locomotor mimicry in butterflies? The associations of positions of centre of mass among groups of mimetic, unprofitable prey. *Phil. Trans. R. Soc. B.* **343**: 145-155.

- Stein, R.A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology*. **58**: 1237-1253.
- Stephens, D.W. & Krebs, J.R. 1986. *Foraging Theory*. Princeton: Princeton University Press.
- Takahata, M & Wine, J.J. 1987. A local interneurone which receives differential input from the medial and lateral giant axons. *J. exp. Biol.* **129**: 385-389.
- Tadeka, M. & Takii, K. 1992. Gustation and nutrition in fishes: application to aquaculture. In: *Fish Chemoreception* (ed. T.J. Hara). London: Chapman & Hall.
- Tallmark, B. & Evans, S. 1986. Substrate related differences in antipredator behaviour of two gobiid fish species and the brown shrimp, and their adaptive value. *Mar. Ecol. Prog. Ser.* **29**: 217-222.
- Tautz & Saundeman, 1980. The detection of water borne vibration by sensory hairs on the chelae of the crayfish. *J. exp. Biol.* **88**: 351-356.
- Taylor, R.C., 1968. Water vibration reception: A neurophysiological study in unrestrained crayfish. *Comp. Biochem. Physiol.* **27**: 795-805.
- Thetmeyer, H. & Kils, U. 1995. To see and not be seen: the visibility of predator and prey with respect to feeding behaviour. *Mar. Ecol. Prog. Ser.* **126**: 1-8.
- Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). *Meddr. Danm. Fisk.-og Havunders.* **4**(1): 1-523.
- Tiews, K. 1965. Lichtung des Norseegarnelenbestandes (*Crangon crangon* L.) durch Wegfrass. *Arch. FischWiss.* **16** (2): 169-181.
- Tiews, K. 1970. Synopsis of biological data on the common shrimp *Crangon crangon* (Linnaeus, 1758). *FAO Fisheries Report.* **57** (4): 1167-1224.
- Tiews, K. 1978. The predator-prey relationship between fish populations and the stock of brown shrimp (*Crangon crangon* L.) in German coastal waters. *Rapp. P.-v. Réun. Cons. int. Explor. Mer.* **172**: 250-258.
- Ugolini, A. & Pezzani, A. 1993. Learning of escape direction in *Idotea baltica*. *Mar. Behav. Physiol.* **22**: 183-192.
- Ursin, E. 1973. On prey size preference of cod and dab. *Meddr. Danm. Fisk.-og Havunders.* **7**: 85-98.

- van de Veer, H.W. & Bergman, M.J.N. 1987. Predation by crustaceans on a newly settled 0-group plaice *Pleuronectes platessa* population in the western Wadden Sea. *Mar. Ecol. Prog. Ser.* **35**: 203-215.
- van Donk, E & de Wilde, P.A.W.J. 1981. Oxygen consumption and motile activity of the brown shrimp *Crangon crangon* related to temperature and body size. *Neth. J. Sea Res.* **15**(1): 54-64.
- van Leeuwen, J.L. & Muller, M. 1983. The recording and interpretation of pressures in prey sucking fish. *Neth. J. Zool.* **33**: 425-475.
- van Lissa, J.H.L. 1977. Aantallen, voedselopname, groei en produktie van de garnaal (*Crangon crangon* L.) in een getijdengebied, alsmede de voedselopname en groei onder laboratoriumomstandigheden. *Intern Verslagen Nederlands Instituut voor Onderzoek der Zee, Texel.* 1977-10: 1-101.
- Vermeij, G.J. 1982. Unsuccessful predation and evolution. *Am. Nat.* **120**: 701-720.
- Vermeij, G.J. 1987. *Evolution and Escalation: An Ecological History of Life*. Princeton: Princeton University Press.
- Vinyard, G.L. 1982. Variable kinematics of Sacramento perch (*Archoplites interruptus*) capturing evasive and non-evasive prey. *Can. J. Fish. Aquat. Sci.* **39**: 208-211.
- Wahle, R.A. 1992. Body-size antipredator mechanisms of the American lobster. *Oikos.* **65**: 52-60.
- Wainwright, P.C. 1986. Motor correlates of learning behaviour: feeding on novel prey by pumpkinseed sunfish (*Lepomis gibbosus*). *J. exp. Biol.* **126**: 237-247.
- Wainwright, P.C. & Lauder, G.V. 1988. Feeding biology of sunfishes: patterns of variation in the feeding mechanism. *Zool. J. Linn. Soc.* **88**: 217-228.
- Walther, F.R. 1969. Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Guenther 1884). *Behaviour.* **34**: 184-221.
- Wardle, C.S. 1975. Limit of fish swimming speed. *Nature.* **255**: 725-727.
- Wardle, C.S. 1993. Fish behaviour and fishing gear. In: *Behaviour of Teleost Fishes*, 2nd edition (ed. T.J. Pitcher). pp. 609-644. London: Chapman & Hall.
- Ware, D.M. 1973. Risk of epibenthic prey to predation by rainbow trout, (*Salmo gairdneri*). *J. Fish. Res. Bd. Can.* **30**: 787-797.
- Wassersug, R.J. & Sperry, D.G. 1977. The relationship of locomotion to differential predation on *Pseudacris triseriata* (Anura: Hylidae). *Ecology.* **58**: 830-839.

- Waterman, T.H. 1960. (ed.) *The Physiology of Crustacea, I-II*. Academic Press.
- Watson, J.T. & Ritzmann, R.E. 1994. The escape response versus the quiescent response of the American cockroach: behavioural choice mediated by physiological state. *Anim. Behav.* **48**: 476-478.
- Webb, J.K. & Shine, R. 1993. Prey-size selection, gape limitation and predator vulnerability in Australian blindsnakes (Typhlopidae). *Anim. Behav.* **45**: 1117-1126.
- Webb, P.W. 1976. The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri*, and a consideration of piscivorous predator-prey interactions. *J. exp. Biol.* **65**: 157-177.
- Webb, P.W. 1979. Mechanics of escape responses in crayfish (*Orconectes virilis*). *J. exp. Biol.* **79**: 245-263.
- Webb, P.W. 1982. Responses of northern anchovy, *Engraulis mordax*, larvae to predation by a biting planktivore, *Amphiprion percula*. *Fish. Bull.* **79** (4): 727-735.
- Webb, P.W. 1984. Chase response latencies of some teleostean piscivores. *Comp. Biochem. Physiol.* **79A** (1): 45-48.
- Webb, P.W. 1986. Effect of body form and response threshold on the vulnerability of 4 species of teleost prey attacked by largemouth bass (*Micropterus salmoides*). *Can. J. Fish. Aquat. Sci.* **43**: 763-771.
- Webb, P.W. & Skadsen, J.M. 1980. Strike tactics in *Esox*. *Can. J. Zool.* **58**: 1462-1469.
- Weber, R.E. & van Marrewijk, W.J.A. 1972. Free amino acids and isosmotic intracellular regulation in the brown shrimp *Crangon crangon*. *Life Sci.* **11**: 589-595.
- Weihs, D. & Webb, P.W. 1984. Optimal avoidance tactics in predator-prey interactions. *J. Theor. Biol.* **106**: 189-206.
- Werner, E.E. 1974. The fish size, prey size, handling time relation in several sunfish and some implications. *J. Fish. Res. Bd. Can.* **31**: 1531-1536.
- Werner, E.E., Mittlebach, G.G. & Hall, D.J. 1981. The role of foraging profitability and experience in habitat use by the bluegill sun fish. *Ecology.* **62**(1): 116-125.
- Wiese, K. 1976. Mechanoreceptors for near field water displacement in crayfish. *J. Neurophysiol.* **39**: 816-833.
- Wilbur, H.M., Morin, P.J. & Harris, R.N. 1989. Salamander predation and the structure of experimental communities: anuran responses. *Ecology.* **64**: 1423-1429.

- Williams, P.J. & Brown, J.A. 1992. Development changes in the escape response of larval winter flounder *Pleuronectes americanus* from hatch through metamorphosis. *Mar. Ecol. Prog. Ser.* **88**: 185-193.
- Wilson, L.J. & Paul, D.H. 1987. Tailflipping of *Munida quadrispina* (Galatheidae): conservation of behavior and underlying musculature with loss of anterior contralateral flexor motoneurons and motor giant. *J. comp. Physiol A.* **161**: 881-890.
- Wine, J.J. & Krasne, F.B. 1972. The organisation of escape behaviour in the crayfish. *J. exp. Biol.* **56**: 1-18.
- Wine, J.J. & Krasne, F.B. 1982. The cellular organization of crayfish escape behaviour. In: *The Biology of Crustacea: Neural Integration and Behaviour*, Vol. 4 (eds. D.C. Sandeman & H.L. Atwood). pp. 241-292. New York: Academic Press.
- Wine, J.J., 1984. The structural basis of an innate behaviour pattern. *J. exp. Biol.* **112**: 283-319.
- Wollebaek, A. 1908. Remarks on decapod crustaceans of the North Atlantic and the Norwegian fjords. I and II. *Bergens Mus. Arb.* (12), 74 pp.
- Woodbury, P.B. 1986. The geometry of predator avoidance by the blue crab, *Callinectes sapidus* Rathbun. *Anim. Behav.* **34**: 28-37.
- Yager, R.R. & Filev, D.P. 1994. *Essentials of Fuzzy Modelling and Control*. New York: Wiley.
- Ydenberg, R.C. & Dill, L.M. 1986. The economics of fleeing from predators. *Adv. Study Behav.* **16**: 229-249.
- Zar, J.H. 1984. *Biostatistical Analysis*. Upper Saddle River: Prentice-Hall Inc.

