THE AGONISTIC BEHAVIOUR OF THE VELVET SWIMMING CRAB, *LIOCARCINUS PUBER* (L.) (BRACHYURA, PORTUNIDAE)

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CONTENTS

SUMMARY

The velvet swimming crab, *Liocarcinus puber* (L.), is common in shallow, rocky sublittoral areas on the Atlantic coasts of Europe. In Britain, the commercial importance of *L. puber* has increased in the last 10 years, following the collapse of the Spanish fishery for this species. *L. puber* has traditionally been regarded as an "aggressive" crab, mainly due to its rapid defensive reaction to humans, but little is known of its intraspecific agonistic behaviour. The aims of the work in this thesis were: to describe the intraspecific agonistic behaviour of *L. puber* in relation to the size of interacting crabs; to investigate the initiation, outcome and content of agonistic interactions in competition for different resources; to estimate the energetic cost of agonistic interactions; to gauge the importance of this behaviour in natural populations and to determine whether behaviour observed in the laboratory is representative of that in the field; and to assess the influence of agonistic behaviour on the capture efficiency of creels. The agonistic behaviour of *L. puber* has been compared with predictions from game theory.

The agonistic displays of *L. puber* were similar to those described for other portunids, particularly the congeneric, *L. depurator*. The relative size of interacting crabs had a major influence on the content, duration and outcome of interactions. However, the smaller crab was as likely to initiate interactions as the larger crab, except when there was a large size difference, when all interactions were initiated and won by the larger crab. As the size difference decreased, the proportion of interactions won by the smaller crab approached 50% and interactions became longer, involving more potentially injurious behaviour. There was little apparent effect of absolute size on interactions, other than a slight reduction in interaction duration with increasing crab size.

The effects of resource value on agonistic behaviour have been investigated in the context of competition for food and mates. Over 5 days of food deprivation, interactions became more intense, involving a greater proportion of potentially injurious behaviour. After 12 days however, there was either only a slight further increase, or a reduction in intensity when the odour of food was absent or present, respectively. The increasing costliness of interactions during the initial period of deprivation accords with the predictions of game theory. Possible reasons for the

relative reduction in intensity after further food deprivation are discussed.

Males compete vigorously for sexually receptive females in the laboratory and there was indirect evidence that this occurs in the natural situation. Laboratory observations indicated that competition between males for females involves a high risk of injury and that males could successfully defend females against larger males. This result was reflected in studies of agonistic interactions between males exposed to the odour of sexually receptive females. In that situation, smaller males were as likely to win as their larger opponents, in contrast to the advantage that larger crabs usually have. Exposing males to the odour of receptive females prolonged interactions, but exposing them to the odour of conspecifics of either sex resulted in more potentially injurious behaviour.

The energetic cost of agonistic interactions has been investigated by using the scaphognathite rate as an indicator of the oxygen consumption of interacting crabs. There was no significant anaerobic metabolism during agonistic behaviour. Extremely high and variable respiratory rates were recorded during agonistic interactions. The maximum scaphognathite rates recorded were related to the degree of escalation. Estimation of the energetic cost of interactions took account of the protracted recovery period. The magnitude of this estimate was related to the content and duration of the interaction for losers, but not winners, although there was no significant difference between losers and winners in this measure. This study also highlighted differences in behaviour between winners and losers following interactions, in the laboratory at least.

Field observations by diving indicated that *L. puber* are inactive for much of the time. Males were more abundant and more active than females, suggesting that the majority of intraspecific encounters in the field are between males. Both diving and underwater television studies indicated that *L. puber* are largely nocturnal, but no activity was observed exclusively at night. In their natural environment, *L. puber* compete agonistically for food, space and probably also mates. Agonistic interactions observed in the field were qualitatively similar to those in the laboratory. The small number of interactions observed during daylight were the most intense recorded in the field.

22% of the study population were missing at least one limb. The incidence of injury was related to the size, but not the sex of crabs. Such injuries reduce the correlation between agonistic ability and size.

There was also an indication that injured crabs were less able to mate. A study of the influence of agonistic behaviour on the capture efficiency of creels was hampered by a low abundance of *L. puber*, due to intense commercial exploitation. In this situation, agonistic behaviour did not significantly reduce the capture rate of the trap, or increase the rate of escapement. Diminishing capture rate was associated with a declining number of crabs attracted to the creel. Further studies are required to determine the importance of interactions within the creel.

The results of these studies are discussed in relation to the ecology and commercial exploitation of *L. puber* and in relation to predictions of game theory.

1. INTRODUCTION

The success of an organism in survival and reproduction largely depends on its ability to acquire certain key resources. The exact nature of these resources may vary between and within species, but some types of resource are required universally across large groups of organisms. For example, all heterotrophic, sexual animals need food and mates to survive and reproduce. Within one species, individuals have similar resource requirements, but these may vary with age, gender, or other individual characteristics. For example, mates are an unimportant resource for immature individuals - for these, food and protection from life-threatening phenomena are of utmost importance.

Resources are often of restricted spatial distribution. Individuals must therefore live in proximity to conspecifics and compete with them for those resources that are in limited supply. Some resources occur as discrete entities that may be possessed and defended. In such circumstances, contest competition may develop, whereby individuals attempt to exclude others from the contested resource. Such intraspecific contest competition is frequently manifested as agonisitic behaviour (Huntingford and Turner, 1987). The term "agonistic behaviour" refers to the range of acts that may be used during interactions between individuals that result in one gaining immediate or future access to a resource at the expense of other individuals. Agonistic behaviour includes acts designed to injure an opponent, as well as non-injurious displays, defensive acts and retreat. Intraspecific agonistic interactions vary widely in intensity between and within species, from situations where one individual simply avoids another, through contests that are resolved by non-contact display, to fights that result in fatal injuries. This range of intensity is found in the agonistic behaviour of crustaceans (Schöne, 1968; Hyatt, 1983). Crustaceans have been observed to compete agonistically for food, mates, space and various forms of shelter (Dingle, 1983).

When a resource is contested by agonistic behaviour, the form and outcome of such competition affects utilisation of the resource by the population. The manner of utilisation of a resource affects its quantity and quality, which in turn influence the individuals utilising it. For example, dominant male American lobsters, *Homarus americanus*, evict other males from shelters near to their own, although they need only one shelter in which to mate (Karnofsky *et al.*, 1989a,b). Males are therefore

dispersed more widely and subordinates may occupy sub-optimal shelters. Agonistic behaviour, therefore, affects and is affected by the ecological and social environment in which it occurs.

As agonistic behaviour is used to compete for resources that enhance the probability of survival and reproduction, the success of individual animals in agonistic interactions influences their lifetime reproductive output, or fitness (Davies and Krebs, 1978). Agonistic interactions may lead to a potential increase in fitness through resource acquisition, but there may also be an associated decrement to fitness. Agonistic behaviour, in common with any activity, involves expenditure of time and energy, but may also result in injury or death, either directly through attack by an opponent, or indirectly through increased exposure to predators, for example. The net change in an individual's fitness is therefore the result of these "costs" and "benefits". Furthermore, since the outcome of an agonistic interaction depends on the behaviour of both interactants, the influence of agonistic behaviour on the fitness of an individual depends on the behaviour of other individuals in the population (Archer, 1987).

Many behavioural phenotypes are, at least partially, genetically determined (Hay, 1985). Genetically determined phenotypes that influence individual fitness are potentially subject to evolutionary change through natural selection (Sheppard, 1979). Natural selection results in organisms with collections of traits that promote individual fitness. It might be expected, therefore, that agonistic behaviour would evolve so that animals optimize their access to resources that can be contested in this way, subject to constraints imposed by their morphology and physiology and by their social and ecological environment.

Consideration of the costs and benefits of agonistic behaviour led Maynard Smith and Price (1973) to use game theory to develop an explanation for the non-injurious resolution of agonistic interactions in species that were capable of damaging each other. Previous explanations relied on the rationale of group selection, that escalated aggression would be detrimental to the species (e.g. Lorenz, 1966). Game theory was originally developed by economists to analyze human decisions in situations involving a conflict of interests. When applied to animal behaviour, an analogy is drawn between human choice of optimum strategy and natural selection acting on genetically determined behavioural phenotypes. Competition for resources is viewed as a game, in which individual animals are players adopting particular strategies. A

strategy is a specification of what an animal will do in particular circumstances and results in a pay-off in terms of fitness, that is related to the probability of acquiring the resource and the costs of competing for it (Maynard Smith, 1982). Central to the application of game theory to the evolution of animal behaviour is the concept of an "evolutionarily stable strategy" or ESS (Maynard Smith and Price, 1973). An ESS is a strategy, which when adopted by the majority of a population, has a higher average pay-off when played against itself and other strategies than the pay-off to any other strategy played against it. The gene pool of a population in which most individuals adopt such a strategy is therefore postulated to be uninvadable by a genotype specifying another strategy within the available set of strategies.

Using simplistic models of animal contests, Maynard Smith and Price (1973) illustrated how individual selection could result in evolutionary stability for strategies that prescribed that, under certain circumstances, individuals should withdraw from their opponents without risking injury. They also predicted that where the value of the resource was less than the cost of injury, "pure strategies" that specified only one mode of contest behaviour would not be evolutionarily stable, whereas "mixed strategies" could be. A mixed strategy prescribes the probabilities with which two or more pure strategies are played in a population. Subsequent theoretical studies have developed game theory models of contest behaviour to take account of asymmetries between contestants (Parker, 1974; Maynard Smith and Parker, 1976; Hammerstein and Parker, 1982; Leimar and Enquist, 1984; Enquist and Leimar, 1987), contests over resources of different value (Bishop *et al.*, 1978; Hammerstein and Parker, 1982; Enquist and Leimar, 1987), contests between relatives (Maynard Smith, 1982) and agonistic behaviour in sexual populations (Maynard Smith, 1982). "Asymmetries" between opponents may be related to differences in fighting ability (e.g. size) or differences in resource value assessment (Parker, 1974). Differences between opponents that are unrelated to fighting ability or resource value assessment (uncorrelated asymmetries) may also be used to settle contests without escalation (Maynard Smith and Parker, 1976; Hammerstein and Parker, 1982).

Game theory generates testable predictions based on individual selection and these predictions have been supported by some empirical studies (Maynard Smith, 1982; Enquist and Leimar, 1987). However, the game theory approach is not without problems. Although the behaviour of animals can be compared with predicted behaviour, it is often difficult to determine the effects on fitness of a particular

behavioural strategy. Variation in behaviour may not be genetically determined. For example, learning is one means of non-genetically determined behavioural variability. Although natural selection is thought to be the major agent of evolutionary change, in some circumstances, behavioural phenotypes may become prevalent in a population by other means, such as genetic drift (Gould and Lewontin, 1979). The early game theory models were based on the assumptions that populations were asexual and infinite. Models of sexual populations indicate that in some circumstances evolutionarily stable strategies do not exist (Maynard Smith, 1982), while there has been recent disagreement about the potential existence of ESS's in finite populations (Vickery, 1987; Maynard Smith, 1988; Vickery, 1988). Even if the behavioural phenotypes prevalent in populations do tend towards evolutionary stability, any evolutionary perturbation will result in a prevalence of unstable phenotypes during an approach to stability. Despite these considerations, game theory provides a theoretical framework within which questions about agonistic behaviour can be formulated and investigated (Maynard Smith, 1982).

In this thesis, predictions from game theory have been used to structure an investigation of the agonistic behaviour of the velvet swimming crab, *Liocarcinus puber*. *L. puber* is a marine brachyuran, most commonly found on hard substrata in the shallow sublittoral zone, (Allen, 1967; Ingle, 1980), although the species has been recorded from a depth of 80 m in the Firth of Clyde (Allen, 1967). Other common names for this species are: velvet crab, velvet fiddler, lady crab, Kerry witch (Ingle, 1980); in France, crâbe à laine (Bell, 1853) and in Spain, nécora (González Gurriarán, 1978). The sexes are distinguishable by abdominal morphology. Males have a narrow, tapering abdomen, which has two pairs of pleopods, modified as accessory copulatory organs. The abdomen of females is wide and rounded, with four pairs of pleopods, developed for carrying eggs. There is sexual dimorphism in overall size and in the relative size of the chelipeds, males being larger in both respects.

The portunids found in British waters have been subject to taxonomic revision in recent years (Ingle, 1980) and it has been suggested that *Liocarcinus puber* be assigned to a seperate genus, *Necora* (Holthuis, 1987).

L. puber has a typical brachyuran reproductive cycle (González Gurriarán, 1985). Prior to copulation, there is a period of pre-copulatory attendance by the male, when the female is held, dorsal side uppermost, against the sternal surface of the male by his ambulatory pereiopods (walking legs). Copulation takes place immediately after

the female moults. During copulation, the sternal surfaces of the two crabs are closely apposed, with the abdomens extended, the female's overlapping the male's. The male's accessory copulatory organs are inserted into genital openings on the female's cephalothorax and are used to transfer spermatophores from muscular projections of the vas deferens to the spermathecae of the female. There is usually a period of post-copulatory attendance by the male. Following copulation, fluids secreted with the spermatophores harden to form a "sperm plug" in the spermathecae, extending to the genital openings of the female. The female's ovaries develop after this and eggs are fertilised at spawning, when they are extruded onto the pleopods, where they remain until hatching. Females may spawn more than once between copulations and may moult between spawnings (González Gurriarán, 1985; Choy, 1988; Norman, 1989). The eggs hatch 1 to 3 months after spawning, depending on water temperature. The larvae are released into the plankton, where they develop through 5 zoeal stages to the megalopa, the final planktonic stage (Rice and Ingle, 1975). After moulting from the megalopa to the first crab instar, the crab settles from the plankton. Planktonic development is temperature dependent, but Rice and Ingle (1975) found that at 15°C, *L. puber* reached the first crab instar 46-56 days after hatching. Crabs reach maturity about 1 year after settlement and may live for 5 years.

Direct observations and gut content analyses have shown *L. puber* to feed on algae, principally laminarians (Choy, 1986; Norman and Jones, 1990), polychaetes (Choy, 1986), gastropods (Ebling *et al.*, 1964; Muntz *et al.*, 1965; Choy, 1986), bivalves (Kitching *et al.*, 1958; Ebling *et al.*, 1964; Muntz *et al.*, 1965; Romero *et al.*, 1982; Choy, 1986), barnacles (Choy, 1986), small crabs (Romero *et al.*, 1982), including juvenile *L. puber* (Choy, 1986), sea urchins (Muntz *et al.*, 1965) and piscine carrion (Choy, 1986).

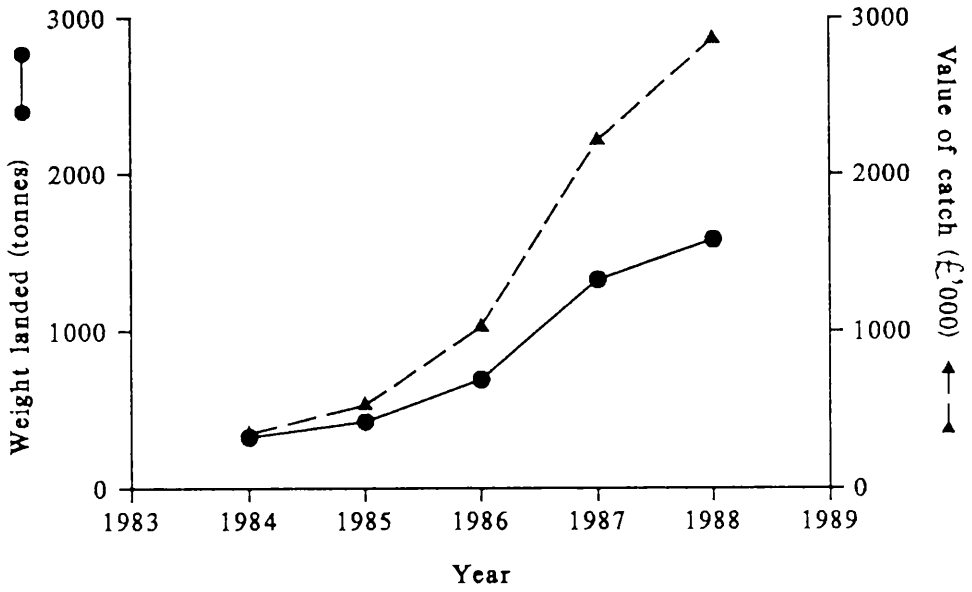
Fishermen traditionally regarded *L. puber* as a pest species, because they filled traps set for lobsters and edible crabs and stripped the bait. This suggests that they are abundant in some localities (MacMullen, 1983). However, underwater observations indicate that they do not often occur in large densities (Muntz *et al.*, 1965). Occasional, localised fluctuations in numbers indicate that some populations may be highly mobile (Bell, 1853). Norman (1989) found that there was much movement into and out of his littoral study site, with crabs showing little site attachment. Large catches of *L. puber* in creels may be due to attraction of crabs from a wide area.

L. puber was previously caught in abundance on the Atlantic coast of Spain, particularly in rías (flooded river valleys) where mussels are cultured on rafts (Romero *et al.*, 1982). However, intense, unregulated fishing led to the collapse of that fishery. In the last ten years, in response to demand in continental Europe, a fishery has developed for this species in Britain, based largely on the west coast of Scotland (Figure 1.1). Most *L. puber* are landed at Stornoway, Oban and Campbeltown (Department of Agriculture and Fisheries for Scotland, 1989). The main markets for these crabs are in Spain, Portugal and France, where crabs are sold live, at a price that is influenced by their condition (MacMullen, 1983).

L. puber has often been referred to as a highly "aggressive" species (Bell, 1853; White, 1857; Campbell, 1976), but this description seems to be based wholly on its rapid defensive reaction of spreading the chelipeds and striking and grasping humans that attempt to handle them. This is presumably an anti-predator response. Despite frequent references to "aggression", there are no detailed, published accounts of intraspecific agonistic behaviour in this species. *L. puber* is a predator of sublittoral and intertidal invertebrates and may be important in controlling the populations of some of these species (Kitching *et al.*, 1959; Ebling *et al.*, 1964; Muntz *et al.*, 1965; Choy, 1986; Norman, 1989). Information about the nature of resource competition in *L. puber* is important for a better understanding of the ecology of that species and of the structure of the communities it may influence. From an applied perspective, agonistic behaviour leads to size selectivity in catches and a reduction in efficiency of commercial traps for other crustaceans (Miller, 1978,1979; Brown, 1982; Bjordal, 1986; Robertson, 1989; Smith and Jamieson, 1989). It is therefore important to know if agonistic behaviour affects the performance of creels set for *L. puber*. Agonistic behaviour between *L. puber* during holding and transport can also result in damage that reduces their market price (MacMullen, 1983). Excessively damaged crabs are rejected at the market. An understanding of this behaviour may lead to improvements in traps and methods of holding and transport.

The aims of the work presented in this thesis were: to describe the intraspecific agonistic behaviour of *L. puber* in relation to the size of interacting crabs, to investigate possible changes in this behaviour in competition for different resources, to estimate the energetic cost of agonistic interactions and to gauge the importance of this behaviour in natural populations. The agonistic behaviour of *L. puber* is described in relation to variation in the size of interacting crabs in chapter 2. Chapters

Figure 1.1 The quantity and value of *L. puber* landed in Scotland in the years 1984 to 1988. Landings of this species were first recorded separately from "other shellfish" in 1984. Taking account of inflation, the value per tonne increased in each of these years.



Data from Department of Agriculture and Fisheries for Scotland (1989)

3 and 4 report the results of investigations of the effects of resource value on this behaviour. The resources investigated are food (chapter 3) and mates (chapter 4). A study of the energetic consequences of agonistic behaviour is described in chapter 5 and field observations of this behaviour are presented in chapter 6. In chapter 7, the preceding results are discussed in relation to the ecology and commercial exploitation of *L. puber* and in relation to predictions from game theory.

2. THE AGONISTIC DISPLAYS OF *LIOCARCINUS PUBER* AND THE EFFECTS OF PARTICIPANT SIZE ON AGONISTIC INTERACTIONS

2.1 INTRODUCTION

In crustaceans, as in many animals, aggressive displays result in an increase in the apparent size of the displayer and in presentation of potential weapons to an opponent (Schöne, 1968; Dingle, 1983). The conspicuous nature of these displays contrasts with the normally cryptic habits of crustaceans and this aspect of their behaviour has therefore attracted considerable attention. Early studies of crustacean agonistic behaviour were descriptive and some attempted to elucidate the evolution of this behaviour by comparing the displays of related species (Schöne, 1968). Later studies examined the factors that influence agonistic behaviour by experimental manipulation and others investigated the communicative properties of agonistic acts (Hyatt, 1983). More recently, crustaceans have been considered suitable subjects with which to test the predictions of evolutionary game theory (Hyatt *et al.*, 1979; Knowlton and Keller, 1982; Glass and Huntingford, 1988; Gardner and Morris, 1989; Adams and Caldwell, 1990).

The weapons displayed in the agonistic behaviour of many species of Crustacea have apparently evolved primarily for food gathering - for example the chelipeds of decapods and the modified raptorial appendages of stomatopods (Dingle, 1983). There is often modification of these appendages which seems to increase their efficacy in agonistic or sexual displays. In some cases, these modifications are morphological, such as the snapping chela of the Alpheidae (Ritzmann, 1973) or the enlarged chela of male ocypodid fiddler crabs (Crane, 1975), while in others conspicuous colouration of the display appendages is an integral part of the visual stimulus transmitted by the display (Dingle, 1983). To the human observer, crustacean agonistic displays are visually striking, but non-visual stimuli may also be important. Chemical cues have been implicated in the social behaviour of the crayfish, *Procambarus clarkii* (Ameyaw-Akumfi and Hazlett, 1975) and the stomatopod, *Gonodactylus festae* (Caldwell, 1979), acoustic cues are important in the nocturnal displays of fiddler crabs, *Uca* spp. (Salmon and Astaides, 1968) and tactile cues are important in the agonistic behaviour of the snapping shrimp, *Alpheus heterochelis* (Schein, 1975) and

the crayfish, *Orconectes rusticus* (Bruski and Dunham, 1987). Jachowski (1974) suggested that the strong respiratory currents produced by the blue crab, *Callinectes sapidus*, during agonistic interactions might act as a physical stimulus or as a carrier of pheromones. Barron and Hazlett (1989) have reported that the hermit crabs *Calcinus spp.* and *Clibanarius zebra* also produce strong respiratory currents during agonistic interactions, which apparently influence the outcome of contests.

The morphology of brachyurans constrains the number of possible body positions which can be used in aggressive displays. Consequently, there are broad similarities in the aggressive displays of a range of brachyuran families (Schöne, 1968). These displays usually involve elevation of the cephalothorax from the substratum by extension of the ambulatory pereiopods and upward tilting of the anterior margin. The chelipeds are often displayed by raising, extending and abducting them so that they are directed at an angle of up to 90° to the midline of the cephalothorax (Schöne, 1968). Other cheliped displays are known for some semi-terrestrial crabs. In some species of grapsid, the chelipeds are presented in a shield-like position in front of the cephalothorax and various types of cheliped movement are involved in the agonistic interactions of these crabs (Schöne, 1968; Warner, 1970; Abele *et al.*, 1986). A complex agonistic and sexual behavioural repertoire is associated with the extreme sexual dimorphism of ocypodid fiddler crabs (Crane, 1975).

Among the Portunidae, intraspecific agonistic behaviour has been described in *Carcinus maenas* (Schöne, 1968; Jensen, 1972), *Callinectes sapidus* (Jachowski, 1974) and *Liocarcinus depurator* (Glass and Huntingford, 1988). Jachowski (1974) described cheliped extending, cheliped shielding and a variety of cheliped movements directed at the other crab. Similar behaviours were described for *Liocarcinus depurator*, although shielding was not noted (Glass and Huntingford, 1988). In addition, cheliped extension in that species is sometimes accompanied by extreme extension of the ambulatory pereiopods and beating of the swimming legs (5th pereiopods). In both of these species, agonistic interactions varied from brief approach/retreat encounters to physical combat involving striking and grasping with the chelae. Schöne (1968) referred to the latter type of interaction as "a wild fight".

The most widely reported modifier of agonistic interactions in crustaceans is the relative size of the opponents: larger animals usually defeat smaller ones (Hyatt, 1983). Although there are numerous references to the importance of participant size in determining the content and outcome of interactions, there have been few

quantitative studies of these effects. Hazlett (1968) found that in agonistic interactions between hermit crabs, *Clibanarius vittatus*, the larger animal usually won and the probability of winning for the larger crab increased with the size difference between opponents. However, hermit crab agonistic interactions are frequently related to gastropod shell acquisition, when the effects on the interaction of the relative size of the opponents and the suitability of their shells to each other are difficult to separate (Dowds and Elwood, 1985). Caldwell and Dingle (1979) found that a size difference of as little as 10% influenced the outcome of contests between stomatopods (*Gonodactylus bredini*). Animals that were less than 70% of the length of their opponent did not win any encounters. That study also indicated that smaller contestants attempted to bluff their antagonists into retreat by performing exaggerated displays, although ultimately, they avoided their opponents.

Similar results were reported by Glass and Huntingford (1988) for *Liocarcinus depurator*. Crabs only defeated individuals larger than themselves when the size difference between them was small. Interactions between size-matched pairs were of longer duration than those between mis-matched pairs, but there were no obvious differences in the types of acts in interactions between crabs of various size differentials. Unexpectedly, crabs seemed equally likely to initiate interactions with individuals larger or smaller than themselves.

There are also few data on the effects of contestant absolute size on agonistic interactions. Hazlett (1975) found that absolute size had no influence on the distance separating antagonists when aggressive acts were performed in the hermit crabs *Clibanarius tricolor* and *C. antillensis*. Dingle (1983) reported that the proportion of non-contact to contact acts between size matched individuals did not vary with absolute size in *Gonodactylus viridis*, *G. spinulosus* or *G. oerstedii*, but this proportion was negatively correlated with absolute size in *G. chiragra*, *G. bredini* and *G. festae*. In a field study of *Pachygrapsus crassipes*, intense interactions were only observed between small individuals (Abele *et al.*, 1986). Agonistic interactions involving large *Liocarcinus depurator* tended to be longer than others, although there was no obvious relationship between absolute size and the behavioural composition of these encounters (Glass and Huntingford, 1988).

In those species utilising the chelipeds as weapons during physical combat, the size of these appendages might be expected to be a good predictor of agonistic ability. In many species there is indirect evidence that cheliped size is important, as

males have larger chelipeds than females and are agonistically superior (Hyatt, 1983). Chela size correlates well with probability of agonistic success in the American lobster, *Homarus americanus* (Scrivener, 1971; O'Neill and Cobb, 1979), while Berzins and Caldwell (1983) found that loss of the raptorial appendages adversely affected the agonistic ability of *Gonodactylus bredini*.

Potentially or actually injurious behaviour occurs in a variety of crustaceans, particularly when the size difference between opponents is small (Dingle, 1983). As these interactions usually begin with non-contact display, there must be some process of escalation from low to high intensity acts, but this process appears not to have been analyzed in detail in crustaceans. There have been several analyses of the sequence of acts during crustacean agonistic interactions (reviewed by Hyatt, 1983), but these have focused on the communicative properties of aggressive acts and on how these properties change during a contest. Caldwell and Dingle (1983) recognised "weak", "moderate" and "strong" displays in the stomatopod *Gonodactylus viridis*. They noted that although there was a tendency for weak displays to be followed by moderate and then strong ones, a variety of tactics was used.

The aim of the work reported in this chapter was to describe the agonistic behaviour of *Liocarcinus puber* and to investigate the effects of the relative and absolute size of participants on the initiation, content, duration and outcome of agonistic interactions. This information is a prerequisite to the study of other influences on the agonistic behaviour of *L. puber*.

2.2 MATERIALS AND METHODS

2.2.1 Collection and maintenance of crabs

Male *Liocarcinus puber* were collected by SCUBA divers throughout the year from shallow, sublittoral, rocky areas in the Firth of Clyde. Crabs were collected only if their exoskeleton was hard, if they had no excessive epifaunal growth and if they were not missing or regenerating any appendages. They were transported individually in polythene boxes to Glasgow, where they were transferred to individual polypropylene tanks (30 x 16 x 20 cm). The floor of these holding tanks had a covering of aquarium gravel and a halved section of PVC drain pipe (length ≈ 12 cm) was supplied as a shelter. The water was aerated using a compressed air supply and "air stones". These tanks were designed to maintain the crabs in sensory isolation from each other. Visual isolation was achieved by screening adjacent tanks from each other with grey PVC sheet (2 mm thick). Olfactory isolation was attempted by supplying the tanks separately with sea water (10-14°C, 30-32‰). As the supply was from a recirculating system with a capacity of 22,500 l, any chemicals produced by the crabs would be greatly diluted. However, as the nature and concentrations of chemicals produced and the olfactory sensitivity of *L. puber* were not known, chemical isolation could not be guaranteed. Constant illumination was supplied by fluorescent tubes.

Crabs were fed chopped fish or mussels 2-3 times per week. They were maintained in these conditions for at least one week prior to behavioural observations. During that period the carapace width - excluding the lateral spines - and the lengths of each cheliped were measured.

2.2.2 Observations of agonistic behaviour

In order to standardise the hunger of crabs, they were not fed for 24 hours before observations. Two crabs were transferred from their holding tanks to an observation tank, where they were separated by an opaque, vertical, removable partition to allow them a settling period of 15 minutes in continued isolation. The observation tank was made of either 1 cm thick acrylic (tank dimensions: 68 x 43 x 39 cm) or 0.5 cm thick glass (tank dimensions: 80 x 43 x 39 cm), both having an arena of 64 x 42 cm and a substratum of aquarium gravel about 2 cm deep. Three sides of the tank were

clad with grey PVC sheet (2 mm thick): observations were made through the front. The tank was illuminated by an 18 watt fluorescent bulb, the intensity of which was reduced with tracing paper. Light intensity measured with a quantum light recorder (meter - SKP 200, sensor SKP 215 0487 783, Skye Instruments Ltd.) was 1.82 - 2.52 $\mu E.m^{-2}.s^{-1}$ at the surface and 0.98 - 1.54 $\mu E.m^{-2}.s^{-1}$ at the bottom). The tank was supplied with sea water from the recirculating system. It was screened from visual disturbance by opaque polythene sheeting, with a small opening (18 x 9 cm) through which observations were made. A pulley allowed the partition to be actuated from outside the screen, thereby causing minimal disturbance to the crabs.

After the 15 minute settling period the partition was raised and subsequent behaviour of the crabs was recorded, either using a BBC-B microcomputer (Acorn Computers Limited, Cambridge) programmed as an event recorder, or using one of two video systems:

System 1: camera - Panasonic WV-1460/B; recorder - Panasonic NV-333 or Panasonic AG-6200 (Matsushita Electric Industrial Co., Ltd, Japan).

System 2: camera - National WV-1350 (Matsushita Electric Industrial Co. Ltd.) with Cosmicar ES, C6Z1218M2ES 12.5 - 75 mm f1:1.8 auto-iris zoom lens (Asahi Precision Co. Ltd, Tokyo, Japan); remote control for camera - Molynx Terrier pan and tilt unit (Molynx Ltd., Newport, Gwent) with Shawley control box (Robert Shawley & Co. Ltd.); recorder - Panasonic NV-333.

When one crab retreated in response to the other three times in succession, it was deemed to have been defeated, observations were terminated and the crabs were returned to their holding tanks.

After completion of observations, the crabs were held for a further two weeks to ensure that none was in Proecdysis (Stevenson, 1985). None moulted in this period.

2.2.3 Statistical methods

The effects of participant size on the agonistic behaviour of male *L. puber* have been investigated in 105 interactions. The relative size of interactants has been

quantified by the ratio of the carapace width of the smaller crab to that of the larger (referred to as the size ratio). Interactions have been grouped into the following size ratio classes: 0.59-0.69, 0.70-0.79, 0.80-0.89, 0.90-1.00. The number of interactions in each of these categories was 13, 6, 25 and 61 respectively.

Comparisons of observed frequencies with hypothetical values were made using two-tailed exact binomial probabilities. Comparisons of two observed frequencies were made with the Log Likelihood Ratio Test with William's correction (Sokal and Rohlf, 1981). Where sample sizes permitted, frequencies were compared using the normal approximation to the binomial distribution (Bailey, 1981). Means have been compared by analysis of variance (ANOVA, Sokal and Rohlf, 1981) followed by Ramsey's revision of Ryan's Q Test with Kramer's modification for unequal sample sizes (Day and Quinn, 1989).

2.3 RESULTS

2.3.1 Description of agonistic behaviour in *Liocarcinus puber*

Male *L. puber* engaged in agonistic interactions in the observation tank when they encountered each other as a result of the movement of one or both crabs. Interactions were composed of recognisable acts, although there was variability in the exact positioning of the cephalothorax and limbs in their execution. For future reference, these acts have been defined as follows:

1. **Stand** - the crab was stationary with the chelipeds partially flexed and directed medially and ventrally. All legs were in contact with the substratum and supported the cephalothorax above the substratum.

2. **Crouch** - the crab was stationary with the chelipeds fully flexed and apposed to the pterygistomial region. The cephalothorax rested on the substratum with the dorsoventral plane approximately parallel to it. This posture appeared to minimise the apparent size of the crab.

3. **Move towards** - the crab moved slowly, sideways towards the other crab. The chelipeds were flexed and were usually held close to the pterygistomial region.

4. **Move away** - the crab moved away from the other crab in a similar manner to 3.

5. **Extended chelipeds, swimming legs down** - the chelipeds were extended, raised and abducted. The chelae were usually at least partially open. The cephalothorax was tilted with the anterior margin raised. The 5th pereiopods (swimming legs) were not raised and usually contacted the substratum. The effect of this was to increase the apparent size of the animal and to present potential weapons (the chelae) to an opponent. A modification of this display, in which the cephalothorax is inclined vertically or tilted backwards with the sternum exposed, is used in response to human disturbance from above and is presumably an anti-predator response.

6. **Extended chelipeds, swimming legs raised** - similar to 5., but the cephalothorax was raised from the substratum and the 5th pereiopods were extended and raised above the carapace. This display always occurred when the crabs were facing each other in close proximity. In this position they sometimes pushed against each other and gripped each other's chelae. The chelae were usually fully open, unless gripping the opponent's chelae.

7. **Extended chelipeds, swimming legs beating** - as for 6. but with the cephalothorax raised, apparently to its full extent. The 5th pereiopods beat in swimming-type movements. This activity appeared to be used to generate force during pushing bouts.

8. **Approach in display** - the crab moved towards the other frontally (cf. 3) while adopting an extended cheliped display. This behaviour could start at any distance from the other crab within the confines of the tank, but most frequently occurred within about five carapace lengths.

9. **Retreat in display** - the crab moved away from the other rapidly, usually by swimming, with the cheliped nearer the opponent held extended with the chela open. This behaviour always began within about five carapace lengths of the other crab.

10. **Retreat without display** - the crab moved away from the other rapidly, often by swimming, with both chelipeds flexed.

11. **Strike** - the crab struck its opponent with the distal ends of the chelae by a rapid adduction of both chelipeds from an extended cheliped display. On some occasions one cheliped was used. Strikes were performed with the chelae closed or open. If the chelae were open, a grasp (*q.v.*) sometimes followed contact with the opponent.

12. **Grasp** - the crab gripped the opponent with one or both chelae. The walking legs of opponents were the usual target of successful grasps. This act could result in crushing of the gripped limb, but grasps were rarely observed in this study.

2.3.2 Initiation and resolution of agonistic interactions

After the settling period, crabs remained stationary or moved about the observation tank. For ease of explanation the two crabs have been designated crab 1 and crab 2. At the start of agonistic interactionsthree situations could be identified:

1. Crab 1 moved towards crab 2 which was stationary. Crab 1 adopted an extended cheliped display as it approached. Crab 2 either retreated or also adopted an extended cheliped display. In this case it seems clear that crab 1 was the initiator.

2. Crab 1 moved towards crab 2 which was stationary. Neither crab displayed and crab 2 moved away as the distance between them decreased. In this case crab 1 was designated the initiator.

3. Crab 1 moved towards crab 2 which was stationary. During this approach, crab 1 did not display, but as it neared crab 2, the latter adopted an extended cheliped display. In this situation it is not clear if crab 1 had:

   (i) detected crab 2 and was attempting to displace it without display,

   (ii) detected crab 2 and was about to display when crab 2 displayed first,

   (iii) detected crab 2 but was not engaging in agonistic behaviour,

   (iv) not detected crab 2.

   In situations (i) and (ii) crab 1 would have initiated the interaction, while in situations (iii) and (iv), crab 2 would have been the initiator. However these situations were indistinguishable to the human observer. For the present study, therefore, the initiator has been designated as the first crab to adopt an extended cheliped display; or in non-display interactions, the crab whose approach caused the retreat of the other.

These designations allow precise definition of the beginning of an interaction for measuring the duration. However, for the reasons given above, in some circumstances they may inaccurately reflect the relative agonistic motivation of the two crabs.

One crab eventually elicited repeated retreats from its opponent. However, in some interactions a crab which initially retreated, subsequently caused its opponent to retreat consistently. The winner was therefore defined as the crab which elicited three or more retreats from its opponent without any further offensive behaviour from the latter. The duration of the interaction was taken as the time from initiation to the first of repeated retreats by the loser.

2.3.3 The effects of relative size on initiation and outcome

In the size ratio category representing unevenly matched crabs (size ratio = 0.59-0.69), all 13 interactions were initiated by the larger crab - a proportion significantly greater than 50% (exact Binomial probability, P = 0.0002). The proportion of interactions initiated by the smaller crab in each of the other categories was not significantly different from 50% (Figure 2.1).

The larger of the two crabs won significantly more than 50% of the interactions in all size ratio categories, although the proportion won by the smaller crab increased towards 50% as the size difference between interactants decreased (Figure 2.2).

Both larger and smaller crabs were more successful when they initiated than when they responded (Table 2.1; G_{adj} = 5.221, df = 1, P<0.025). Larger crabs won 86.9% of the interactions they initiated, compared with 68.2% of the interactions in which they were the responder. Smaller crabs won 31.8% of the interactions they initiated, compared with 13.1% of those in which they were the responder. By definition, the initiator won interactions with unilateral aggression. However, in the 72 interactions with display by both crabs, there was no association between initiating and winning (G_{adj} = 0.021, df = 1, P>0.90). Of these interactions, larger crabs won 77.1% of those that they initiated compared with 75.7% when responding. Smaller crabs won 24.3% of bilateral display interactions they initiated, compared with 22.9% when responding.

2.3.4 The content and duration of agonistic interactions

Interactions could be classified with respect to their behavioural content, according to the degree of involvement of the two crabs and the potential for injury.

Figure 2.1 The percentage of interactions initiated by the smaller crab in different size ratio categories. Size ratio is the ratio of the carapace width of the smaller crab to that of the larger.

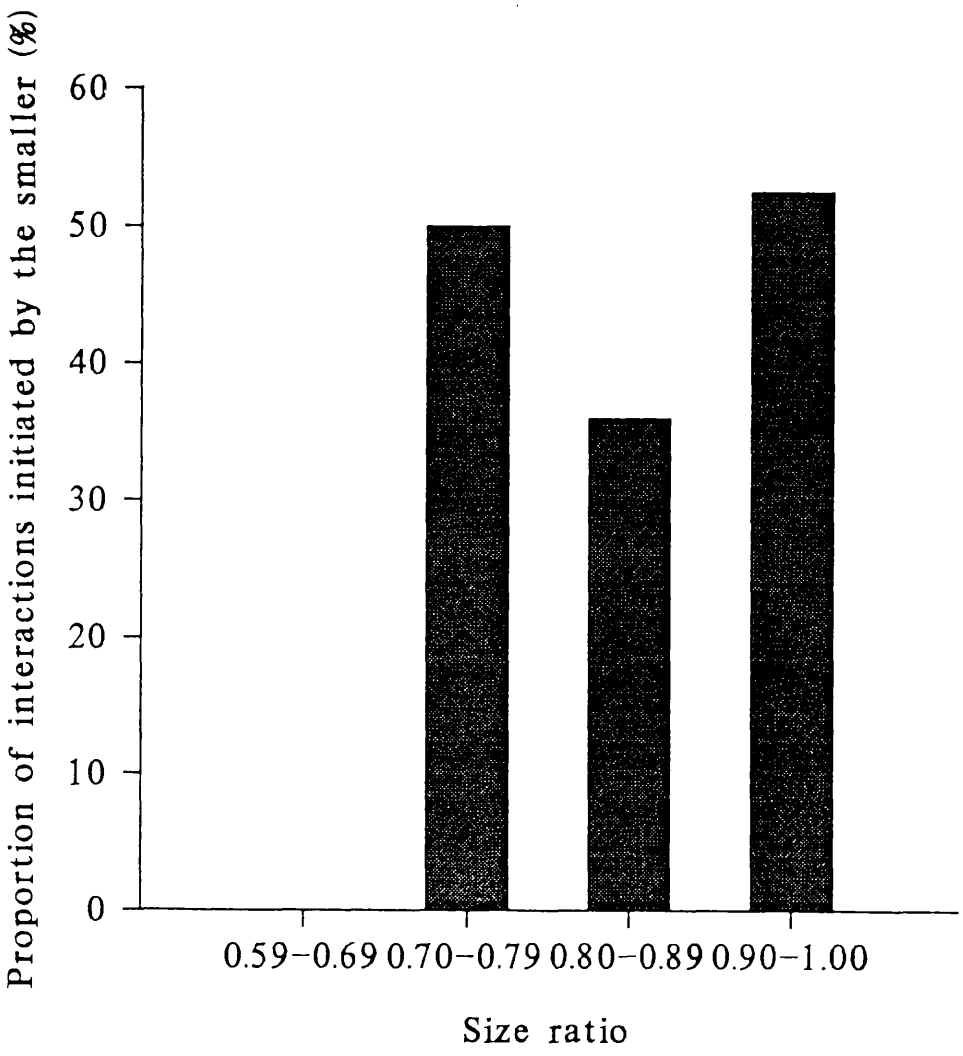


Figure 2.2 The percentage of interactions won by the smaller crab in different size ratio categories. Size ratio is the ratio of the carapace width of the smaller crab to that of the larger.

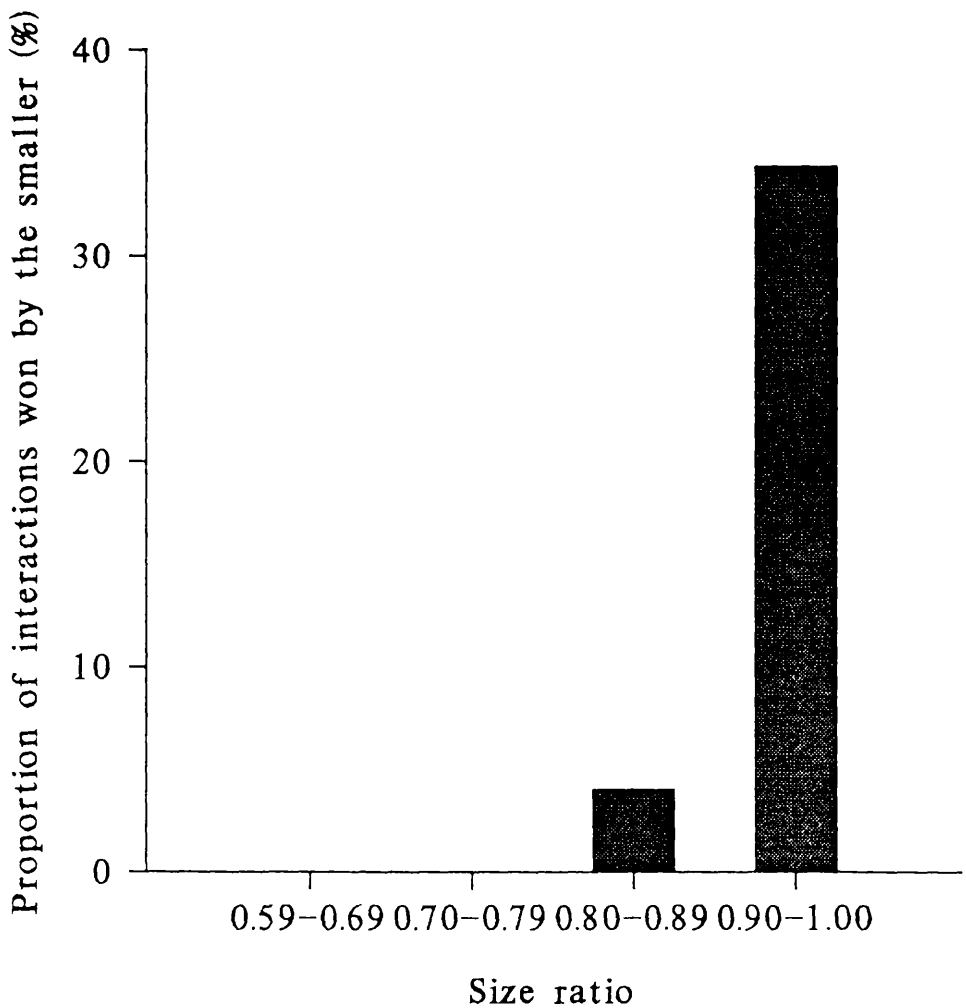


Table 2.1 Initiation and resolution of agonistic interactions between male Liocarcinus puber. Size ratio is the ratio of the smaller crab's carapace width to that of the larger. Contact interactions are those involving strikes or grasps with the chelae.

(a) Size ratio 0.59 - 0.69

Initiating crab	Winning crab				Totals
	Non-contact		Contact		
	Larger	Smaller	Larger	Smaller	
Larger	12	0	1	0	13
Smaller	0	0	0	0	0
Totals	12	0	1	0	13

(b) Size ratio 0.70 - 0.79

Initiating crab	Winning crab				Totals
	Non-contact		Contact		
	Larger	Smaller	Larger	Smaller	
Larger	3	0	0	0	3
Smaller	2	0	1	0	3
Totals	5	0	1	0	6

(c) Size ratio 0.80 - 0.89

Initiating crab	Winning crab				Totals
	Non-contact		Contact		
	Larger	Smaller	Larger	Smaller	
Larger	7	0	9	0	16
Smaller	5	0	3	1	9
Totals	12	0	12	1	25

Table 2.1 continued.

(d) Size ratio 0.90 - 1.00

Initiating crab	Winning crab				Totals
	Non-contact		Contact		
	Larger	Smaller	Larger	Smaller	
Larger	12	2	9	6	29
Smaller	9	6	10	7	32
Totals	21	8	19	13	61

These interaction types have been subjectively placed in order of increasing intensity as follows:

Type 1. The interaction ended after the approach of one crab elicited the retreat of the other. Neither crab displayed. (n = 12)

Type 2. One crab displayed and the other retreated without displaying. (n = 18)

Type 3. One crab displayed and struck the other, which retreated without displaying. (n = 3)

Type 4. Both crabs displayed. No strikes were performed by either crab. (n = 28)

Type 5. Both crabs displayed. One retreated after a single strike by its opponent. (n = 15)

Type 6. Both crabs displayed. One retreated after multiple strikes by its opponent. (n = 10)

Type 7. Both crabs displayed. One retreated after strikes by both crabs. (n = 19)

In some of the interactions involving physical combat, strikes or grasps were preceded by a progression from non-contact display to the crabs pushing against each other, to display with the 5th pereiopods raised and then beating, apparently to make the push more forceful. However, where this was the case, there was frequently a reversion to non-contact display before resolution of the interaction. In other cases, strikes or grasps were not preceded by this sequence of displays. In general, the interactions did not follow a pattern of gradual escalation, with resolution being immediately preceded by the most intense acts.

The relationship between the content of interactions and the size differential of the participants has been investigated by comparing the mean size ratios of interactants in different types of interaction. As most of the size ratios were between 0.70 and 1.00, they were arcsine transformed before analysis of variance (Sokal and Rohlf, 1981). This analysis indicated that there were significant differences between

the mean size ratios of crabs engaging in different types of interaction (Figure 2.3, $F_{(5,99)} = 9.72$, $P<0.001$; type 3 interactions were rare, so data from this type were pooled with those from type 2, which also represented unilateral display). *A posteriori* comparisons (Table 2.2) indicated that interactions between size-matched crabs tended to involve bilateral display (display by both crabs) and in some cases striking by one or both crabs (types 4 - 7). Interactions between crabs of disparate size involved predominantly unilateral aggression (types 1 - 3). The ordinal intensity of interactions was significantly correlated with the size ratio of the interactants (Spearman rank correlation coefficient, $r_s = 0.446$, df = 103, $P<0.001$). Interaction intensity tended to be greater when there was a small size differential between interactants.

The mean durations of interactions were correlated with their variances. Transformation to common logarithms alleviated this problem (Sokal and Rohlf, 1981). Analysis of variance of the transformed data indicated that there were significant differences between the mean durations of different types of interaction (Figure 2.4, $F_{(5,99)} = 15.74$, $P<0.001$, data from interaction type 3 were pooled with those from type 2). Interactions involving unilateral aggression (types 1 - 3) were shorter than those where both crabs displayed (types 4 - 7) (Table 2.3). The mean durations of interactions involving bilateral display and at least one strike were not significantly different from each other. Interactions with bilateral display and bilateral striking or grasping were longer than those with bilateral display and no strikes or grasps. The duration of interactions was correlated with their ordinal intensity ($r_s = 0.648$, df = 103, $P<0.001$).

Consistent with the relationships between interaction intensity and size ratio and between interaction intensity and duration, interaction duration was significantly correlated with the size ratio of the interactants (Figure 2.5, correlation between log transformed durations and arcsine transformed size ratios, $r = 0.381$, df = 103, $P<0.01$). Longer interactions occurred between more evenly size-matched crabs.

In the size ratio range in which smaller crabs were successful (0.80-1.00), there was no significant difference in the duration of interactions won by the smaller crab compared with those won by the larger (mean duration of interactions won by the smaller (with 95% confidence limits calculated from transformed data) = 72 (+84.6, -38.8) s, mean duration of interactions won by the larger = 54 (+30.6, -19.5) s, ANOVA of log transformed durations, $F_{(1,84)} = 0.42$, $P = 0.517$).

Figure 2.3 The mean size ratios of crabs involved in different types of interaction. See text for definitions of interaction types. Means and 95% confidence intervals were calculated from arcsin-transformed data, but are presented untransformed.

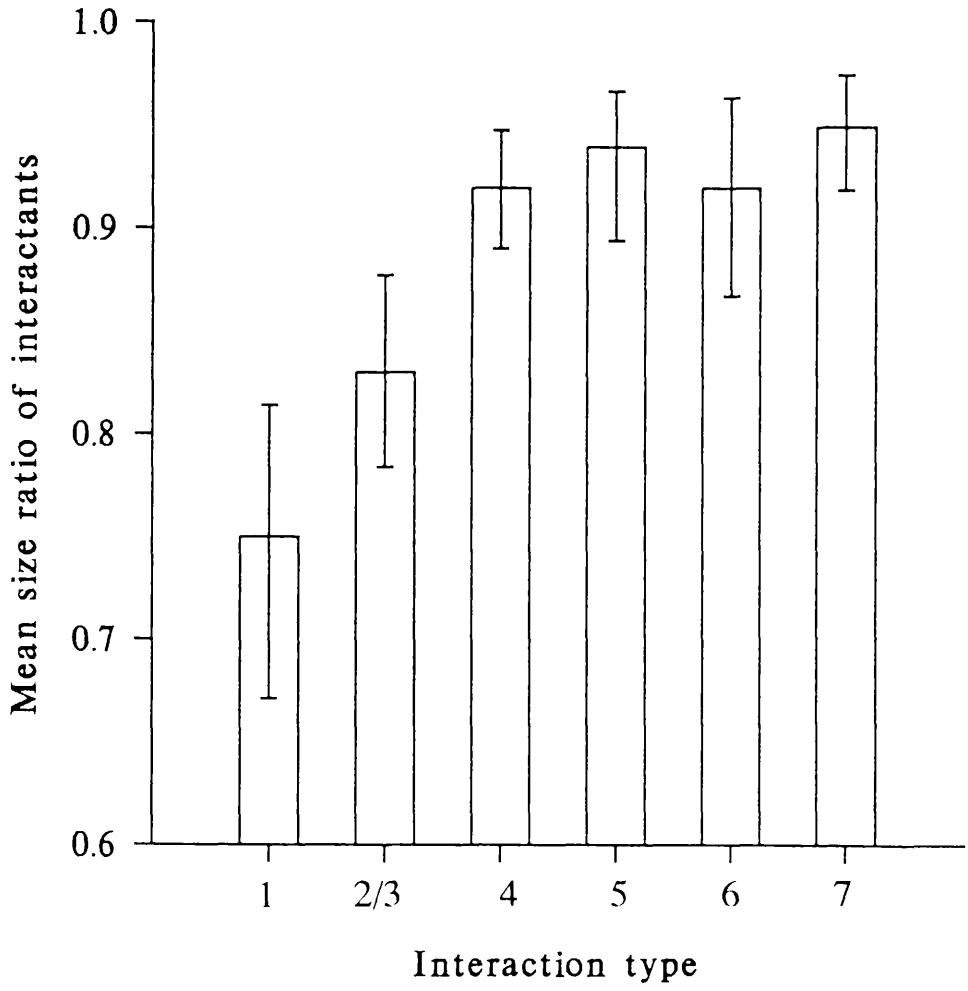


Table 2.2 Multiple comparisons of mean size ratios in different interaction types by Ramsey's revision of Ryan's Q test with Kramer's modification for unequal sample sizes. Size ratios were arcsine transformed before analysis.

No. of means	Comparison	b	$Q_{b(p,v)}$	SE_c	CV	Difference between means	P
6	7 - 1	0.05	4.110	0.0534	0.1552	0.3051	<0.05
5	5 - 1	0.05	3.930	0.0561	0.1559	0.2717	<0.05
5	7 - 2/3	0.05	3.930	0.0459	0.1276	0.1977	<0.05
4	7 - 4	0.034	3.899	0.0431	0.1188	0.0612	>0.05
4	5 - 2/3	0.034	3.899	0.0490	0.1351	0.1643	<0.05
4	6 - 1	0.034	3.899	0.0620	0.1709	0.2453	<0.05
3	6 - 2/3	0.025	3.726	0.0557	0.1468	0.1379	>0.05
3	4 - 1	0.025	3.726	0.0500	0.1317	0.2439	<0.05
2	2/3 - 1	0.017	3.417	0.0524	0.1266	0.1074	>0.05

1. The interaction types are defined in section 2.3.4. Data from type 3 interactions were pooled with those from type 2 due to infrequent occurrence of type 3.

2. The critical value of the difference between means,

$$CV = Q_{b(p,v)} . SE_c . 2^{-0.5}$$

Where Q is the studentized range statistic, b is the adjusted significance level for a test of the equality of p means, v is the number of degrees of freedom (v = 99) for the Residual Mean Square in the ANOVA (MS_d = 0.0210) and SE_c is the standard error of the comparison,

$$SE_c = \sqrt{[MS_d . (1/n_i + 1/n_j)]}$$

Where n_i and n_j are the sample sizes of the two samples to be compared (given in section 2.3.4).

$$b = a \text{ for } p = m,\ m - 1 \text{ and}$$

$$b = 1 - (1 - a)^{p/m} \text{ for } p < m - 1$$

Where a is the chosen experimentwise error rate (5%) and m is the number of means in the analysis of variance (6).

Figure 2.4 The mean durations of different types of interaction. See text for definitions of interaction types. Means and 95% confidence intervals were calculated from log-transformed data, but are presented in their original units (seconds).

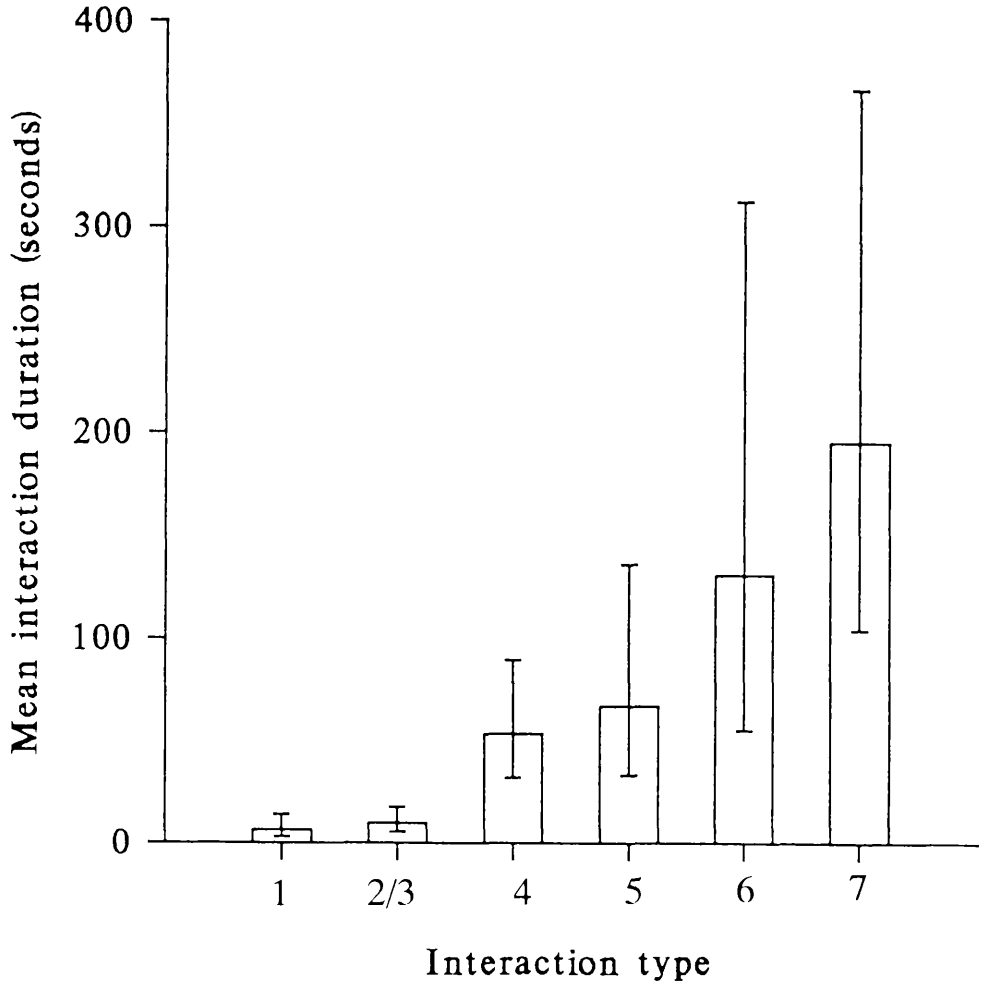


Table 2.3 Multiple comparisons of mean durations of different interaction types by Ramsey's revision of Ryan's Q test with Kramer's modification for unequal sample sizes. Durations were log transformed before analysis.

No. of means	Comparison	b	$Q_{b(p,v)}$	SE_c	CV	Difference between means	P
6	7 - 1	0.05	4.110	0.2222	0.6456	1.4914	<0.05
5	7 - 2/3	0.05	3.930	0.1908	0.5301	1.3079	<0.05
5	6 - 1	0.05	3.930	0.2580	0.7169	1.3180	<0.05
4	7 - 4	0.034	3.899	0.1791	0.4937	0.5656	<0.05
4	6 - 2/3	0.034	3.899	0.2315	0.6382	1.1345	<0.05
4	5 - 1	0.034	3.899	0.2333	0.6433	1.0259	<0.05
3	7 - 5	0.025	3.726	0.2081	0.5483	0.4655	>0.05
3	6 - 4	0.025	3.726	0.2220	0.5848	0.3922	>0.05
3	5 - 2/3	0.025	3.726	0.2037	0.5366	0.8424	<0.05
3	4 - 1	0.025	3.726	0.2079	0.5477	0.9258	<0.05
2	4 - 2/3	0.017	3.417	0.1739	0.4202	0.7423	<0.05
2	2/3 - 1	0.017	3.417	0.2180	0.5268	0.1835	>0.05

1. The interaction types are defined in section 2.3.4. Data from interaction type 3 were pooled with those from type 2 due to infrequent occurrence of the former.

2. The critical value of the difference between means,

$$CV = Q_{b(p,v)} . SE_c . 2^{-0.5}$$

Where Q is the studentized range statistic, b is the adjusted significance level for a test of the equality of p means, v is the number of degrees of freedom (v = 99) for the Residual Mean Square in the ANOVA (MS_d = 0.363) and SE_c is the standard error of the comparison,

$$SE_c = \sqrt{[MS_d . (1/n_i + 1/n_j)]}$$

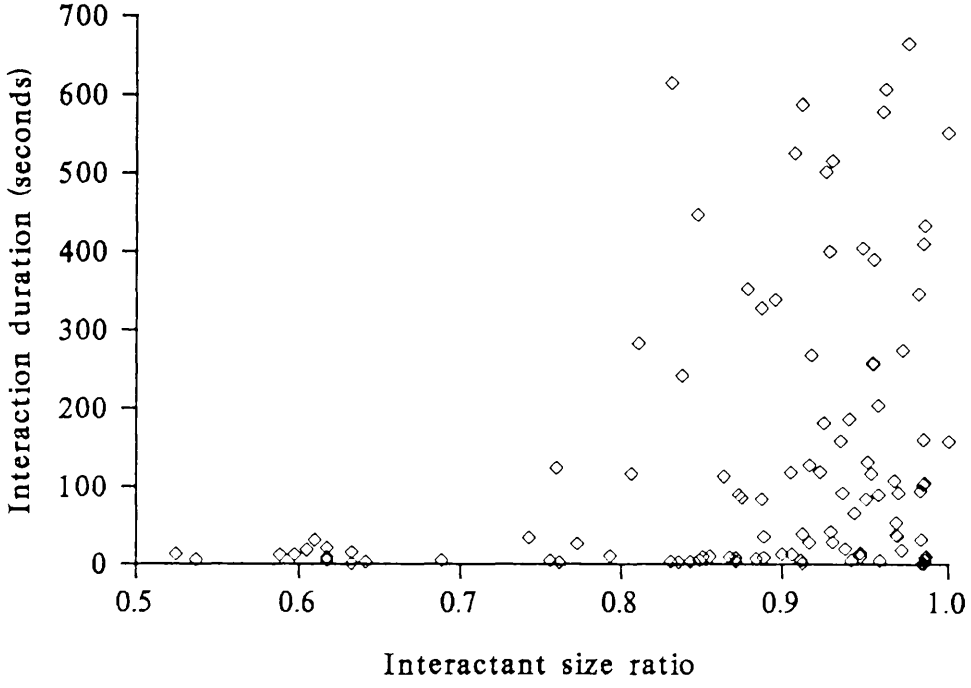
Where n_i and n_j are the sample sizes of the two samples to be compared (given in section 2.3.4).

$$b = a \text{ for } p = m,\ m - 1 \text{ and}$$

$$b = 1 - (1 - a)^{p/m} \text{ for } p < m - 1$$

Where a is the chosen experimentwise error rate (5%) and m is the number of means in the analysis of variance (6).

Figure 2.5 The relationship between interaction duration and the ratio of the carapace width of the smaller crab to that of the larger.



The data were insufficient to analyze the frequencies of initiation and success with respect to relative size for each interaction type separately, so the interactions have been grouped into those that involved strikes or grasps ("contact interactions") and those that did not ("non-contact interactions"). The occurrence of strikes or grasps during interactions was independent of the relative size and success of the initiator. 41.0% of interactions initiated by the larger crab involved strikes or grasps in comparison with 50.0% of interactions initiated by the smaller crab (G_{adj} = 0.83, df = 1, P>0.50). 40.3% of the interactions won by the initiator involved strikes or grasps compared with 52.6% of those lost by the initiator (G_{adj} = 1.47, df = 1, P>0.05).

Overall, 63.6% of the interactions won by the smaller crab were contact interactions, compared with 39.8% of the interactions won by the larger crab (G_{adj} = 3.91, df = 1, P<0.05). However, this result has been biased by the large proportion of non-contact interactions won by crabs much larger than their opponent. In the size ratio range where smaller crabs had some success (0.80-1.00), there was not a significant difference between the proportion of interactions won by the smaller that involved contact (63.6%) and the proportion won by the larger that involved contact (48.4%: G_{adj} = 1.50, df = 1, P>0.25).

2.3.5 The effects of the absolute size of participants on interaction content and duration

In order to separate the effects of size differential and absolute size, the content of interactions between size-matched opponents (size ratio 0.90-1.00) of various carapace widths has been analyzed. In this size ratio range, there was no correlation between the size ratio and the mean absolute size of participants (mean size = 0.5 • [sum of carapace widths of the two crabs]) (r = -0.120, df = 59, P>0.10).

In these encounters between more or less size-matched crabs, interaction duration was negatively correlated with interactant size (Figure 2.6, correlation between log transformed durations and mean carapace width of interactants, r = -0.418, df = 59, P<0.001). Large crabs resolved their encounters after shorter periods of time than small crabs, on average. However, the mean size of interactants involved in interactions of different intensity did not vary significantly (Figure 2.7, $F_{(4,56)}$ = 1.15, P>0.05, data from interaction types 1, 2 and 3 were pooled due to low incidence of each of these types in this size ratio range). These data suggest that although large

Figure 2.6 The relationship between the duration of interactions involving evenly size-matched crabs (size ratio = 0.90-1.00) and the mean carapace width of these crabs.

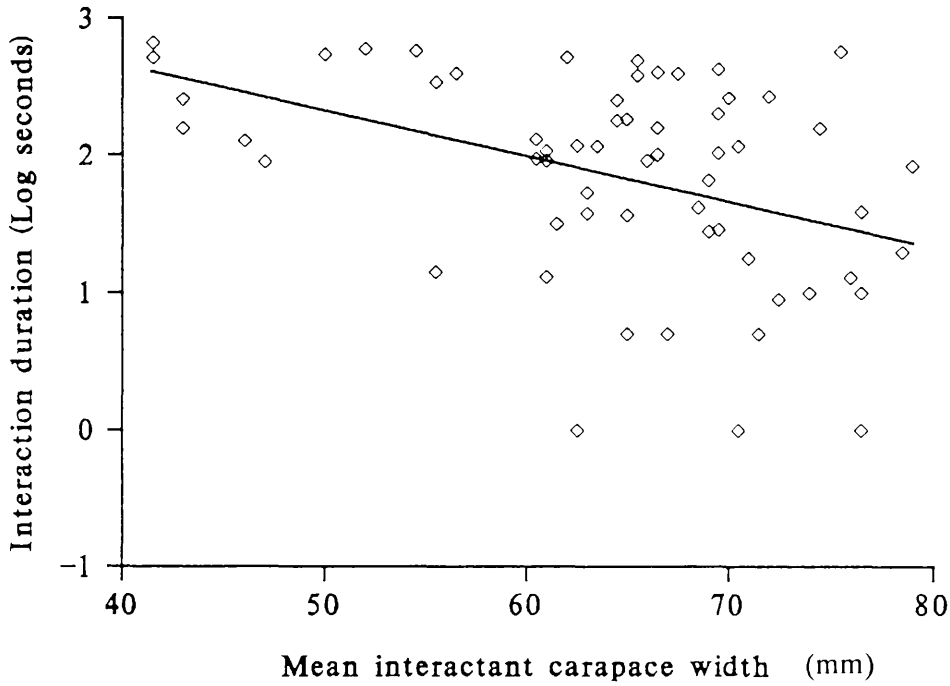
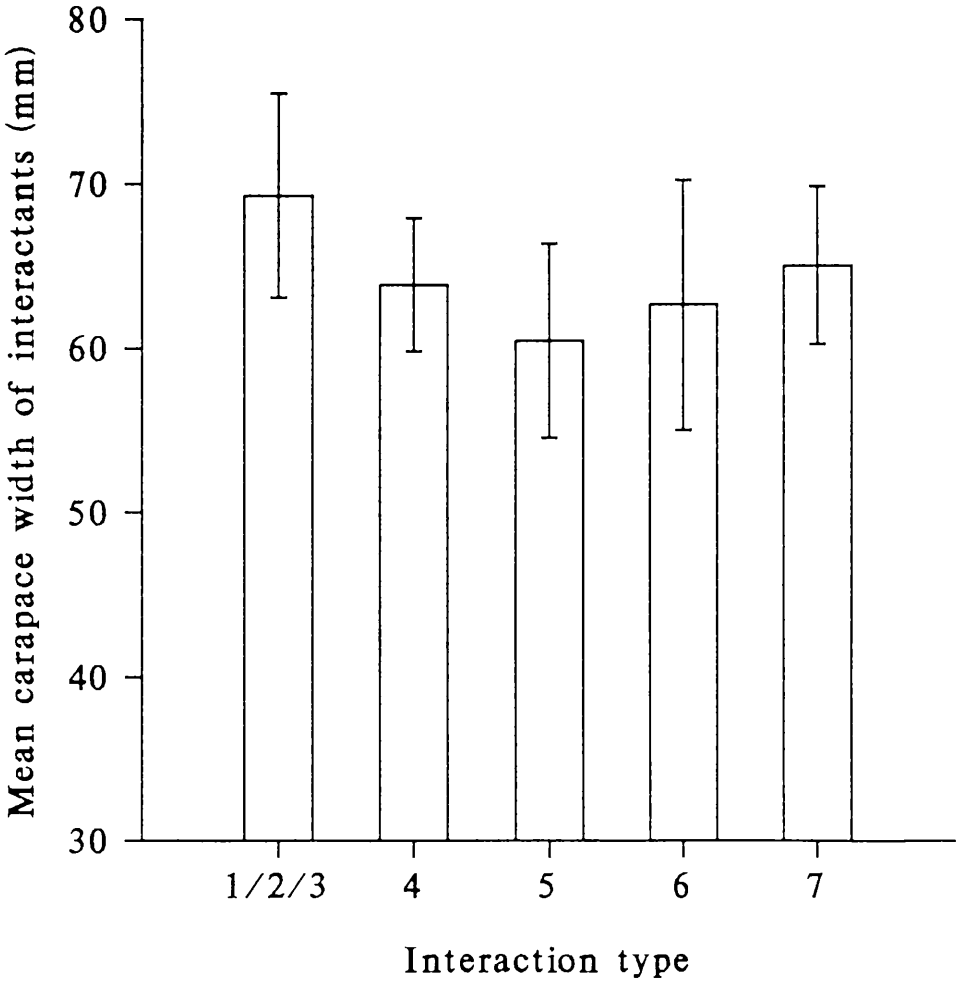


Figure 2.7 The mean carapace width of evenly size-matched crabs involved in different types of interaction. See text for definitions of interaction types. Error bars are 95% confidence intervals.



crabs engaged in shorter contests, the types of acts involved did not differ significantly from those in contests between small crabs.

2.3.6 Is cheliped size a better predictor of the outcome of contests than carapace width ?

In common with other crustaceans, there is usually slight asymmetry between the left and right chelipeds of individuals (heterochely). The length of the major cheliped was highly correlated with carapace width in the size range of crabs in this study ($r = 0.97$, $df=73$, $P<0.001$). Consequently, the proportion of interactions won by the crab with the greater carapace width (79.5%) was not significantly different from that won by the crab with the greater cheliped length (83.6%) (Normal approximation to binomial distribution, $d = 0.639$, $P>0.10$).

2.4 DISCUSSION

The intraspecific agonistic behaviour of *Liocarcinus puber* is similar to that of other portunids and nearly identical to that of *Liocarcinus depurator* (Glass and Huntingford, 1988). The extended cheliped display of *L. puber* may have several functions during an interaction. Raising the cephalothorax and extending the chelipeds probably gives a visual indication of the crab's size to an opponent. Crabs much smaller than their opponent usually withdrew immediately after display by the larger individual. This response may have been the result of a visual assessment which was only possible when the opponent displayed. When crabs of similar size extended their chelipeds in close proximity to each other, they may have been able to use tactile cues to assess their relative sizes. In this position, closely size-matched crabs often engaged in pushing bouts which may have been a form of trial of strength. In encounters involving strikes or grasps with the chelae, the extended cheliped display may have offensive and defensive uses. Offensively, this display is a suitable posture from which to deliver strikes with the chelipeds. Defensively, crabs displaying in close proximity often gripped each others chelae, which appeared to hinder the execution of strikes. In addition, some crabs "parried" strikes by their opponent by striking the opponent's chelipeds with their own during execution of the strike.

As found for many other crustaceans, larger individuals were more likely to defeat their opponents than *vice versa*. The success of smaller crabs only approached 50% when the interactants were nearly the same size. Relative size was therefore highly correlated with agonistic ability in this sample of crabs. When the carapace width of the smaller crab was less than 70% of that of the larger, all interactions were initiated and won by the larger crab. However, in interactions where the crabs were more evenly matched, the smaller crab was just as likely to initiate as the larger one. Why should crabs have initiated interactions in which they had little chance of success? Firstly, in most cases the initiator was defined as the first crab to adopt an extended cheliped display. This definition may not have always accurately reflected the relative aggressive motivation of the crabs, as extended cheliped displays could have been defensive as well as offensive. However, it seems likely that crabs cannot accurately assess the size of their opponent until it displays. Regardless of which crab initiated an interaction, in many cases the smaller continued offensively against an

opponent it apparently had little chance of defeating. Crabs as small as 84% of the size of their opponent engaged in interactions involving strikes or grasps by both crabs. It is impossible to know if the smaller crab had accurately assessed the size of its opponent. Although closely matched crabs may have been unable to assess their size differential without recourse to pushing bouts or strikes, it seems likely that the more unevenly matched crabs that engaged in escalated encounters could visually detect their size difference. If this is so, the decision about whether to continue or retreat was unaffected by the size of the opponent in some crabs. In this study, intermoult, undamaged males were selected. In natural populations, however, injury, disease, gender and recent ecdysis may introduce substantial variation into the relationship between size and agonistic ability. In their natural environment, therefore, crabs may have greater success against larger opponents.

Variation in the relationship between size and agonistic ability also allows the possibility of individuals signalling greater relative fighting ability than they actually possess, i.e. bluffing. Smaller stomatopods (*Gonodactylus viridis*) used a greater proportion of threat displays than larger animals (Caldwell and Dingle, 1979). These displays were sometimes exaggerated, suggesting that some smaller animals were attempting to bluff their opponents. However, Caldwell and Dingle (1979) could not test this suggestion, as they had no way of knowing if these smaller contestants had accurately assessed their relative fighting ability. Steger and Caldwell (1983) assumed that recently moulted *Gonodactylus bredini* accurately assessed their inferior fighting ability in relation to intermoult conspecifics. In defence of their cavities, newly moulted stomatopods initiated interactions against intermoult animals, but retreated if their opponent advanced. They were therefore presumed to be bluffing. Adams and Caldwell (1990) have examined this phenomenon further and report that bluffing inhibited escalation to physical aggression by intermoult animals and resulted in an increased probability of successful cavity defence. Bluffing was more successful against smaller opponents.

Recent game theory analyses have illustrated circumstances in which bluffing may be a viable competitive strategy (Bond, 1989; Gardner and Morris, 1989). The model developed by Gardner and Morris (1989) predicted that the behaviour of recently moulted *G. bredini* was viable when the cost of bluffing and that of losing a contest were both low. The costs of bluffing and of losing a contest probably vary between individuals so that bluffing may be disfavoured for some (Adams and

Caldwell, 1990). Bond (1989) suggested that bluffing could be detected by a comparison of logistic regressions of the probability of success against a "composite indicator of actual fighting ability" for escalated and display-only interactions respectively. Bluffing should result in a weaker relationship between actual fighting ability and probability of success for display-only interactions. In the present study there were too few escalated interactions in too limited a size ratio range for such an analysis to be feasible (19 interactions in the size ratio range 0.84-0.98). However, the fact that smaller crabs were more successful in escalated contests than in display-only interactions - even though the success of smaller crabs may have been coincidental with the higher intensity interactions of relatively size matched crabs - suggests that successful bluffing by *L. puber* was not frequent.

Interactions between closely matched *Liocarcinus puber* were of longer duration and involved more potentially injurious behaviour than those between disparate crabs. The probability of success for the smaller crab decreased with increasing size difference between the opponents. The duration of interactions between *L. depurator* and the probability of success for the smaller crab were also negatively related to the size differential, but no systematic variation in the behavioural content of interactions was detected (Glass and Huntingford, 1988). In these respects, the interactions of *L. puber* accord with the predictions of the "sequential assessment game" (Enquist and Leimar, 1983,1987), a game theoretic analysis in which contestants are assumed to assess their relative fighting ability by successively sampling correlates of fighting ability in their opponent. Detection of smaller differences in relative fighting ability is assumed to require a greater number of repetitions, or a greater duration of behaviour that facilitates assessment and the probability of success for the weaker individual is predicted to increase with decreasing size differential, due to random errors in this sampling process. The model is based on the assumption that contests are structured in phases, successive phases corresponding to more intense behaviours (performed at the same rate within phases), leading eventually to direct sampling of fighting ability in an escalated contest. As matched individuals require more or longer acts to resolve their contests, they progress through more phases, achieving greater intensity than disparate individuals. Although the behaviour of matched *L. puber* was more intense than that of disparate crabs, the interactions were not structured into a series of escalating phases. Intense acts could occur at any stage in a contest and could be followed by resumption of display-only tactics. The assumptions of the

sequential assessment game therefore do not hold for interactions between male *L. puber*. The same was true of interactions between male *L. depurator* (Glass and Huntingford, 1988).

Interactions between large *L. puber* were resolved quicker than those between small crabs, but there was no significant association between interactant size and the types of act that were executed. Time spent in long interactions is not available for fitness-promoting activities such as feeding and mate location. Size correlates with age in crustaceans (Hartnoll, 1982). It is possible that the behaviour of crabs develops as they age in a way that leads them to resolve interactions quicker. Another possibility is that there is differential survival of crabs with different behavioural phenotypes. One aspect of a successful phenotype might involve spending little time in competition for space. Alternatively, behaviour that is optimal for large or old crabs may not be so for small or young crabs. Since the behavioural content of interactions did not change appreciably with interactant size, the shorter interactions of large crabs involved less potentially injurious behaviour, on average, than those between small crabs. This adjustment of agonistic behaviour may be adaptive if large crabs have greater ability to inflict injury. Jacoby (1983) noted that large male *Cancer magister*, which could inflict serious injury on conspecifics, used a greater proportion of extended cheliped pushing tactics than strikes or grasps compared with juveniles or females, which were less able to inflict injury. The agonistic behavioural repertoire of juveniles, females and males contained the same acts, but the frequencies of individual acts varied between these groups (Jacoby, 1983). Glass and Huntingford (1988) found that the duration of agonistic interactions between male *Liocarcinus depurator* increased with the absolute size of the interactants. The addition of food extract to stimulate locomotor activity in their study may have resulted in crabs competing for food rather than space. Optimal behaviour may be different in competition for food and space.

The interactions in the present study occurred in the absence of any tangible resources. In other crustaceans, agonistic interactions occur in the context of competition for resources such as food or shelter, as well as resulting from chance encounters between individuals (Hazlett, 1968; Warner, 1970; Hazlett, 1974; Jachowski, 1974; Rubenstein and Hazlett, 1974; Abele *et al.*, 1986; Glass and Huntingford, 1988). In the observation tank, *L. puber* invariably interacted agonistically when they encountered each other and this is representative of the

situation in the field (chapter 6). There may be several reasons why it is disadvantageous for crabs to be close to conspecifics. Aggregations may attract predators or facilitate the spread of parasites or disease. Crustaceans are often cannibalistic, especially when the victim is much smaller or at a vulnerable stage in the moult cycle, so conspecifics may represent a constant threat. American lobsters, *Homarus americanus*, become more aggressive prior to moulting, which suggests that exclusion of conspecifics from the vicinity by agonistic behaviour is a means of reducing the threat of cannibalism (Tamm and Cobb, 1978). Lastly, an individual may have a greater probability of exclusive access to requisite resources if conspecifics are excluded from the immediate vicinity. Evans and Shehadi-Moacdieh (1988) postulated that the individual space defended by prawns, *Palaemon elegans*, functioned as a "food collector" in an environment where food items were small and randomly distributed in space and time.

The results of the present study have implications for the design of experiments to investigate other influences on agonistic behaviour in *L. puber*. Since both relative and absolute size affect agonistic interactions in this species, they must be accounted for in investigations of other influences on this behaviour. In addition, statements about the proportion of interactions initiated or won by the larger crab are only meaningful with a specification of the distribution of sizes observed.

3. THE EFFECTS OF HUNGER ON THE AGONISTIC BEHAVIOUR OF *LIOCARCINUS PUBER*

3.1 INTRODUCTION

3.1.1 Resource value and agonistic behaviour

An animal's chances of survival and reproduction depend on the availability and quality of resources such as food, shelter or mates. The value of these resources to an animal can be considered in terms of the change in the animal's fitness after acquiring them. The increase in fitness due to a resource may be offset by a reduction resulting from activity necessary to acquire the resource. This cost of resource acquisition may be manifested, for example, as time and energy expenditure, as risk of injury or death through physical combat, or in terms of increased exposure to predators. The net value of a resource can therefore be thought of as the difference between the gross value and the cost of resource acquisition. The gross value will vary with the quantity and quality of the resource, while the cost will depend on the activity required for resource acquisition.

Investigation of the influence of resource value on agonistic behaviour requires the investigator to have a prior estimate of the value of the resource to the contestants. Measurement of resource value in terms of fitness is not usually possible, since lifetime reproductive output and survival of offspring cannot be easily monitored or predicted. Even if they could, it would be difficult to isolate the influence on them of any one resource. However, assumptions can often be made about the relative value of particular resources to each of the contestants. The agonistic behaviour of a wide variety of animals is influenced by resource value (Enquist and Leimar, 1987). In these species, the individual's perception of the value of the contested resource is presumably important in determining its behaviour. An individual's estimate of resource value probably varies with attributes of the resource itself and with internal variables such as hunger, thirst or reproductive history. An individual's estimate of net value may change during competition as more information becomes available about the gross value of the resource and the costs of acquisition. Individuals competing for the same resource may have different estimates of its value. Differences between individuals in physiological variables may result in

different estimates of gross resource value. Asymmetry in resource value assessment may also arise because assessment involves error which depends on the information available about the resource (Leimar and Enquist, 1984). In interactions between the owner of a resource and a challenger, the owner may have more information and therefore a more accurate assessment of the resource value than its opponent, whose initial estimate may be based on the average value of such resources (Enquist and Leimar, 1987).

Several game theory models predict that an agonistic interaction is more likely to escalate from display to physical aggression when the value of the contested resource is high (Hammerstein and Parker, 1982; Maynard Smith, 1982; Enquist and Leimar, 1987). Additionally, models of a variety of competitive situations predict that an interaction between opponents of equal fighting ability will be won by the individual with the higher estimate of resource value (Maynard Smith and Parker, 1976; Bishop *et al.*, 1978; Leimar and Enquist, 1984; Enquist and Leimar, 1987). In a survey of empirical studies of the effects of resource value on agonistic behaviour in a variety of animals, Enquist and Leimar (1987) found qualitative agreement with these predictions.

3.1.2 Resource value and agonistic behaviour in crustaceans

Shelter is an important resource for many species of Crustacea and is one which can easily be manipulated experimentally. The rôle of agonistic behaviour in competition for shelter has therefore received considerable attention. In several species of Crustacea, agonistic behaviour is more intense when shelter is in limited supply, or if much time or energy is expended in acquiring shelter (Atema and Cobb, 1980; Dingle, 1983; Scully, 1983; Capelli and Hamilton, 1984; Shuster and Caldwell, 1989). Food is obviously a vital resource for crustaceans, but the importance of agonistic behaviour in competition for food has been studied in only a few species (Hazlett, 1966; Hazlett and Estabrook, 1974; Hazlett *et al.*, 1975; Capelli and Hamilton, 1984). Several of these studies involved pairing fed individuals with animals deprived of food for a fixed period of time (Hazlett, 1966; Hazlett and Estabrook, 1974; Hazlett *et al.*, 1975). This procedure was designed to investigate the probability of hungry individuals initiating or winning agonistic interactions. Hermit crabs, *Calcinus tibicen*, were more likely to initiate and win fights when starved (Hazlett, 1966); spider crabs, *Microphrys bicornutus*, were also more likely to win

(Hazlett and Estabrook, 1974) and crayfish, *Orconectes virilis*, initiated more fights and showed more offensive behaviour when deprived of food for seven days (Hazlett *et al.*, 1975). These findings agree with the game theory prediction that differing resource value assessments between contestants should result in the individual with the higher value assessment being more likely to initiate and win aggressive interactions. However, the design of these experiments is not appropriate for testing the prediction that the costs of agonistic encounters should be positively correlated with the value of the contested resource (Enquist and Leimar, 1987). This test requires analysis of interactions between individuals with similar resource value assessments. Hazlett *et al.* (1975) paired *Orconectes virilis* that had been treated identically. Those starved for seven days spent more time in a greater number of agonistic encounters than fed crayfish. However, the aggressive activity of crayfish declined after fourteen days of food deprivation, when their agonistic behaviour was similar to that of fed animals.

3.1.3 Food and agonistic behaviour in *Liocarcinus puber*

Liocarcinus puber feeds on mussels and other bivalves, gastropods, crustaceans and echinoderms (Kitching *et al.*, 1959; Ebling *et al.*, 1964; Muntz *et al.*, 1965; Romero *et al.*, 1982). Analyses of the foregut contents of *L. puber* from South Wales and the south of England revealed brown algae to be a major component of the diet (Choy, 1986, Norman and Jones, 1990). Mussels and crustaceans were of secondary importance, despite a preference for animal prey in the laboratory. It was not clear whether algae were ingested as food or as a consequence of feeding on attached organisms. The activity of the enzyme laminarase in *L. puber* indicated that this species has the ability to hydrolyse laminarin, a carbohydrate present in the type of algae found in the crabs' foreguts (Norman and Jones, 1990).

Direct observations of *L. puber* in Lough Hyne (=Ine), Northern Ireland indicated nocturnal, high tide feeding during summer, with diurnal, sub-tidal feeding to a lesser extent (Kitching *et al.*, 1959; Ebling *et al.*, 1964). Choy's (1986) analysis of foregut contents indicated peaks of feeding activity on nights when there was a high tide. I have observed nocturnal high tide feeding in the intertidal zone in the Firth of Clyde during summer and agonistic interactions occur at these times (chapter 6). Bait placed sub-tidally attracts crabs and agonistic interactions occur in this situation also (chapter 6). Agonistic behaviour therefore appears to play a rôle in intraspecific competition

for food by *L. puber*.

Choy (1986) estimated an exponential function describing foregut clearance rate in *L. puber* that indicated a clearance time of approximately 20 hours at 13 ± 1°C for the size range of crabs used in the present study. The length of periods of fasting undergone by *Liocarcinus puber* in natural conditions has not been quantified, but there is indirect evidence that starvation for several days is not uncommon. The incidence of *L. puber* with empty foreguts varies seasonally. Both González Gurriarán (1978) and Choy (1986) recorded a high incidence of crabs with empty foreguts during winter, suggesting that some crabs do not feed for several days. Fasting at that time of year may be related to reduced availability of prey organisms or to reduced metabolic rate at low temperature. Feeding also varies in relation to stage in the moult cycle. *L. puber* do not feed for up to 5 days after ecdysis (González Gurriarán, 1978).

In the present study, food was assumed to be a resource that becomes more valuable to *L. puber* the longer they are deprived of it. Agonistic interactions were staged in the laboratory between pairs of crabs which had been deprived of food for the same period of time to investigate the effects of variation in resource value on agonistic behaviour. The duration of interactions and the occurrence of potentially injurious behaviour have been used as indicators of the costs of this activity. Published studies of the relationship between food and agonistic behaviour in crustaceans have differed in whether or not food or a stimulus associated with it was present during interactions. Therefore, the effects of the presence of food odour on the behaviour of crabs deprived for various periods have also been investigated.

3.2 MATERIALS AND METHODS

3.2.1 Experimental animals

Male *Liocarcinus puber* were collected by divers from shallow, rocky, sublittoral sites in the Firth of Clyde and were maintained as described in section 2.2.1. Four sets of 20 crabs were collected: two sets in August and October 1987, the other two in November and December 1988 and January 1989. Crabs were allowed to settle in the aquarium for one week prior to observations and were used only if the exoskeleton was hard, with a full compliment of appendages and without excessive epifaunal growth. Due to uncontrollable fluctuations in the sea water system, crabs collected in August and October were maintained in seawater of temperature 13-14°C and salinity 30-32°/$_{oo}$; those collected in November to January were maintained at a temperature of 9-11°C and a salinity of 28-30°/$_{oo}$. During the settling period, they were fed whitebait every other day. Carapace widths (CW) were measured with vernier callipers. After completion of behavioural observations, crabs were held for a further two weeks to ensure that none was in proecdysis (Stevenson, 1985). None moulted in this period.

3.2.2 Experimental manipulation

The hunger of crabs was manipulated by depriving them of food for 1 day, 2, 3, 5 or 12 days before behavioural observations. At the last feed before observations, crabs were given excess food and that not eaten within 24 hours was removed. The period of deprivation was deemed to start after this 24 h period.

Limitations on the number of crabs available necessitated more than one observation of each crab. Each of the four sets of 20 crabs was divided into five groups of four crabs in such a way that all possible pairs within a group were relatively evenly size matched (ratio of smaller CW to larger CW = 0.91 ± 0.02), but there was no difference between groups in terms of the mean carapace width or mean size ratio. Each of the five groups in each set corresponded to one of the five deprivation periods. All crabs were paired with each of the other three in its group to give 6 pairings per group and 24 per deprivation period. Each crab in the study was therefore involved in no more than 3 agonistic interactions. Ideally, the interval between replicate observations should have been the same for each crab in the study.

This would dictate a minimum interval equivalent to the longest deprivation period, i.e. 12 days. Three replicate observations of each crab would therefore involve holding the crabs in the aquarium for at least 31 days (7 days settling period and two inter-observation periods of 12 days). The effect of captivity on the behaviour of *L. puber* is not known. To minimise potential changes in behaviour resulting from the artificial conditions of the aquarium, replicate observations of crabs in the 1, 2, 3 and 5 day groups were made at intervals of 6 days. Crabs in the 12 day groups were each observed once on three consecutive days, after 11, 12 and 13 days of food deprivation. The average deprivation period in this category was therefore 12 days.

3.2.3 Observations of agonistic behaviour

Crabs collected in November to January were allowed a 15 minute settling period after transfer from the holding tanks to the observation tank, while separated by an opaque partition. Sea water from the recirculating system was supplied to each half of the observation tank. The rates of flow through outlets at each end of the tank were approximately balanced. After the settling period, 5 ml of food extract (see below) was administered next to the water inlets to the tank from outside the screen with a 10 ml syringe and a 2.5 m length of polythene tubing (bore = 4 mm). A Y-connector was used to deliver the extract into each half of the tank. The tubing was then flushed with 40 ml of sea water. After addition of the food extract, the sea water supply to the observation tank was switched off so that the extract was not diluted further during observations. Five minutes after the addition of food extract the partition was raised and observations were made as described in section 2.2.2.

Food extract was prepared by homogenising 50 g of whitebait in 150 ml of sea water using a mortar and pestle. The resultant mixture was centrifuged at 245 ***g*** for 10 minutes. The residue was discarded and the supernatant was used as the food extract.

Crabs collected in August and October were observed as described in section 2.2.2 after the appropriate deprivation period. Food extract was not added. The sea water supply to the observation tank was switched off during observations.

Records of the interactions on video tape or from the event recorder were examined to determine the length of time between removal of the partition and initiation of agonistic interactions (the latency), the time between initiation and resolution of agonistic interactions (the duration), the initiator and winner of agonistic

interactions (as defined in section 2.3.2) and the behavioural content of interactions (in terms of the behaviour patterns described in section 2.3.1).

3.2.4 Statistical methods

The variances were correlated with the means for the latency and duration of interactions. They were therefore log transformed before 2 way analysis of variance with food deprivation period and presence/absence of food extract as factors (Sokal and Rohlf, 1981). The relationships between the food deprivation period and the proportion of interactions initiated by the larger crab, the proportion won by the larger crab and the proportion of interactions involving strikes or grasps ("contact interactions") were investigated by regression analysis. Since some of these proportions were greater than 70% or less than 30%, they were all arcsine transformed before analysis so that these data were more normally distributed (Sokal and Rohlf, 1981).

There was no interaction after 30 mins between two pairs in the 5 day group and between one pair in the 12 day group when no food extract was present. There were therefore totals of 10 and 11 interactions in these treatments respectively. There were 12 interactions in all other combinations of deprivation period and presence of food extract.

3.3 RESULTS

3.3.1 Latency of initiation of interactions

The time between removal of the partition separating the crabs and the initiation of an agonistic interaction did not differ significantly between food deprivation periods (Figure 3.1, 2 way ANOVA, $F_{(4,106)} = 0.121$, $P>0.05$). The mean latency of initiation of interactions when food extract was present in the water ± 95% confidence limits calculated from log transformed data (116 +39.9 -29.7 s) was significantly shorter than when extract was not present (311 +117.3 -85.2 s) ($F_{(1,106)} = 20.56$, $P<0.001$).

3.3.2 Initiation of interactions

The proportion of interactions initiated by the larger crab was positively related to the deprivation period when food extract was absent (regression of arcsine transformed proportions against deprivation period, $F_{(1,3)} = 12.52$, $P<0.05$) and negatively related to deprivation period when food extract was present ($F_{(1,3)} = 21.47$, $P<0.05$) (Figure 3.2).

3.3.3 Outcome of interactions

The proportion of interactions won by the larger crab was not related to food deprivation period whether food extract was present ($F_{(1,3)} = 0.08$, $P>0.50$) or absent ($F_{(1,3)} = 0.40$, $P>0.50$) (Figure 3.3).

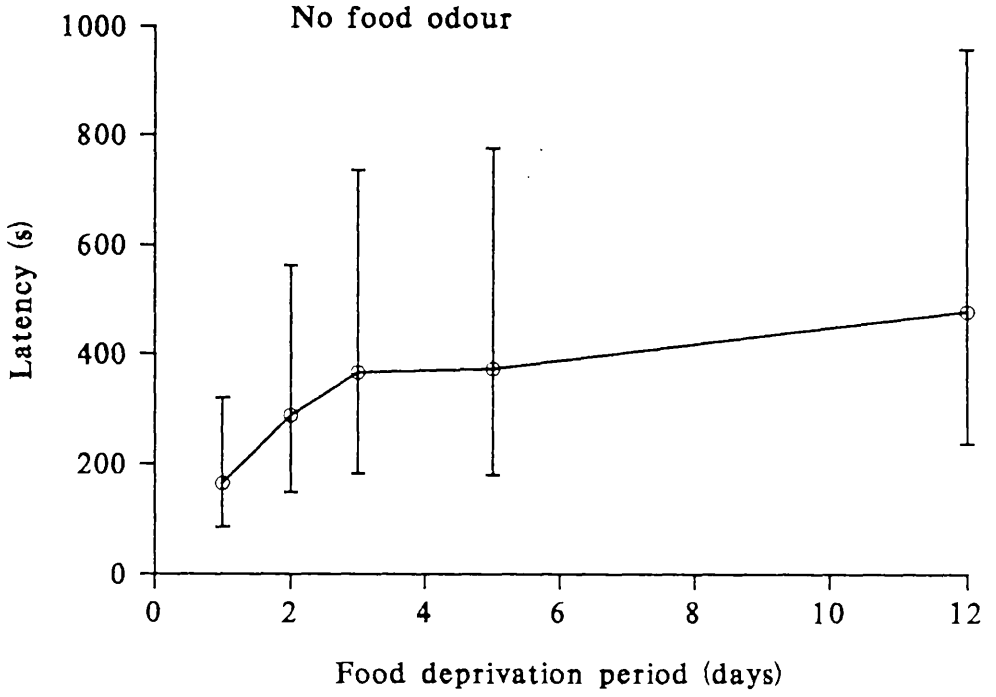
3.3.4 Duration of interactions

As with the latency, the duration of interactions did not vary significantly with deprivation period (Figure 3.4, $F_{(4,107)} = 1.43$, $P>0.05$). Interactions where food extract was present were shorter, on average, than those where it was absent (mean duration where extract was present ± 95% confidence limits calculated from log transformed data = 34.2 +23.8 -14.0 s, mean duration ± 95% confidence limits where extract was absent = 74.6 +34.7 -23.7 s, $F_{(1,107)} = 5.51$, $P<0.025$).

3.3.5 Content of agonistic interactions

The distribution of interaction types (as defined in section 2.3.4) with respect to

Figure 3.1 Mean latency of initiation of agonistic interactions between *L. puber* deprived of food for different periods. Means and 95% confidence intervals were calculated from log transformed data.



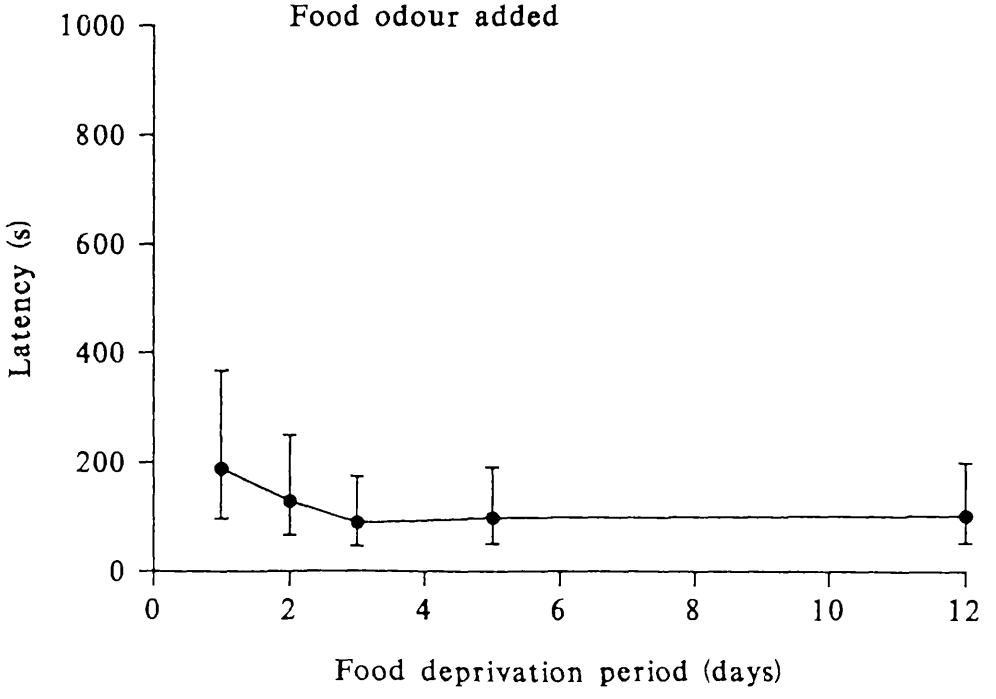


Figure 3.2 The proportion of interactions initiated by the larger crab in interactions between *L. puber* deprived of food for different periods, in the presence and absence of food odour.

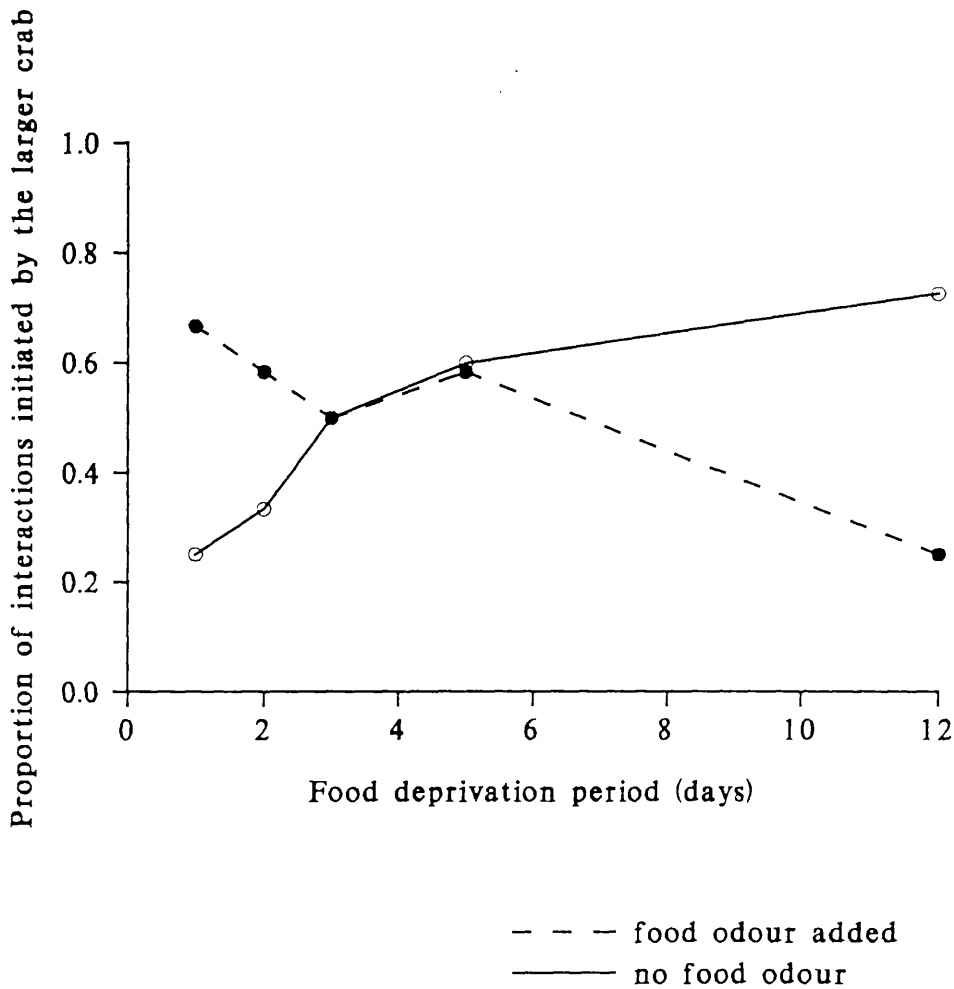


Figure 3.3 The proportion of interactions won by the larger crab in interactions between *L. puber* deprived of food for different periods, in the presence and absence of food odour.

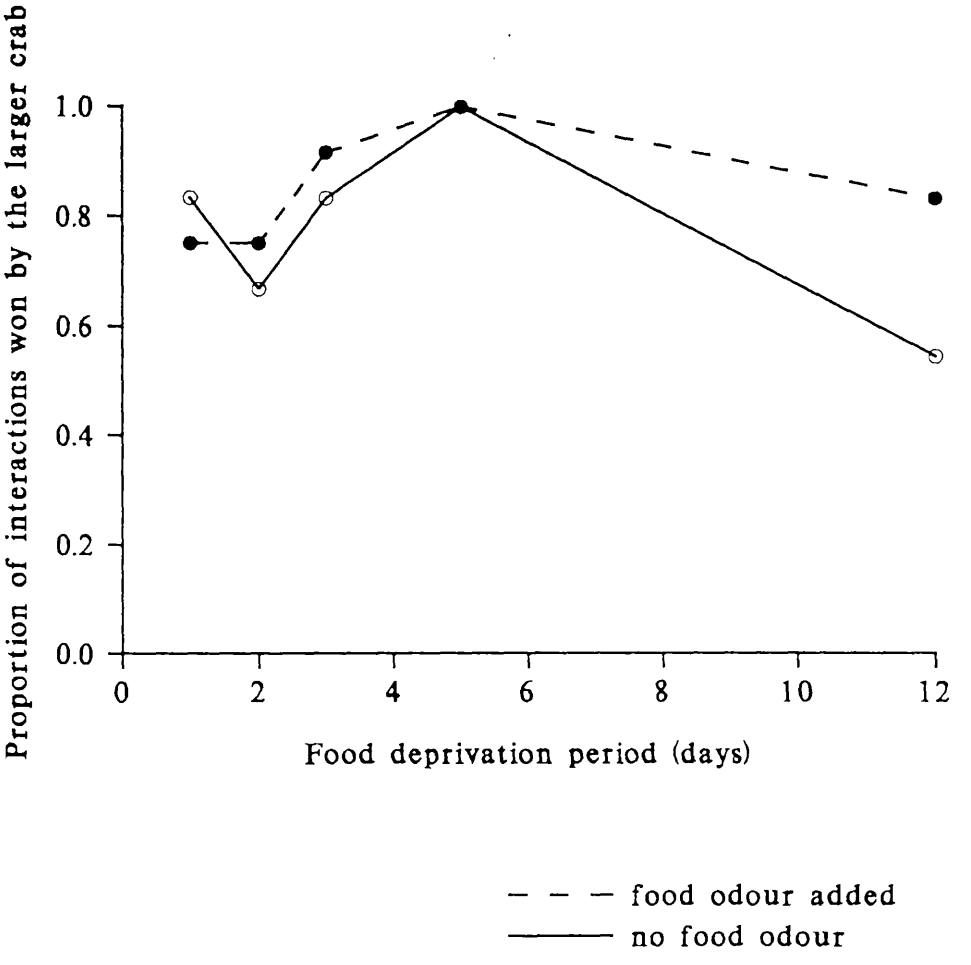
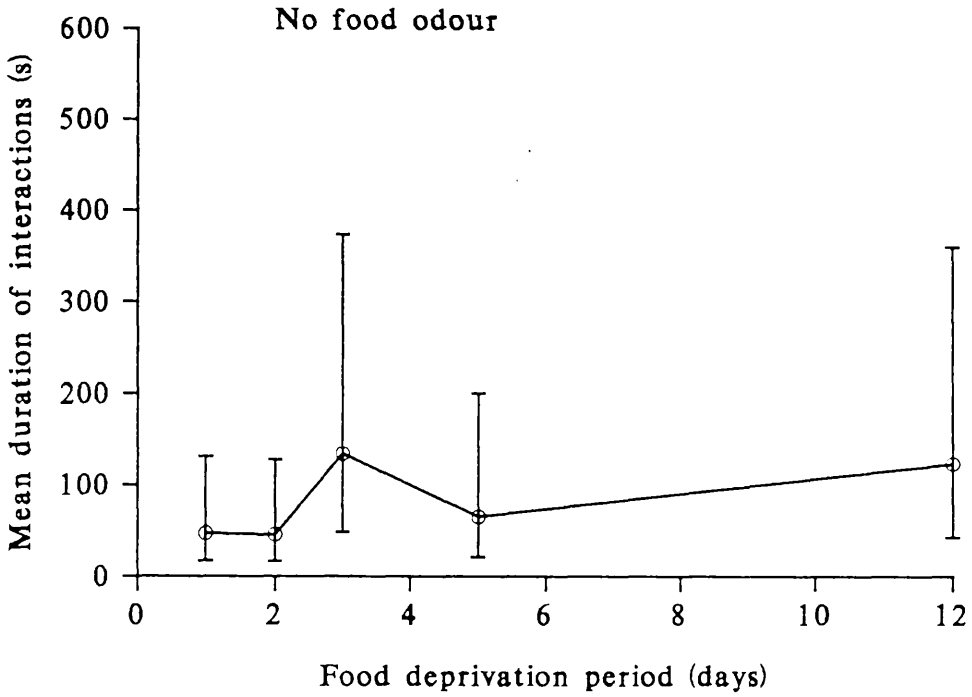
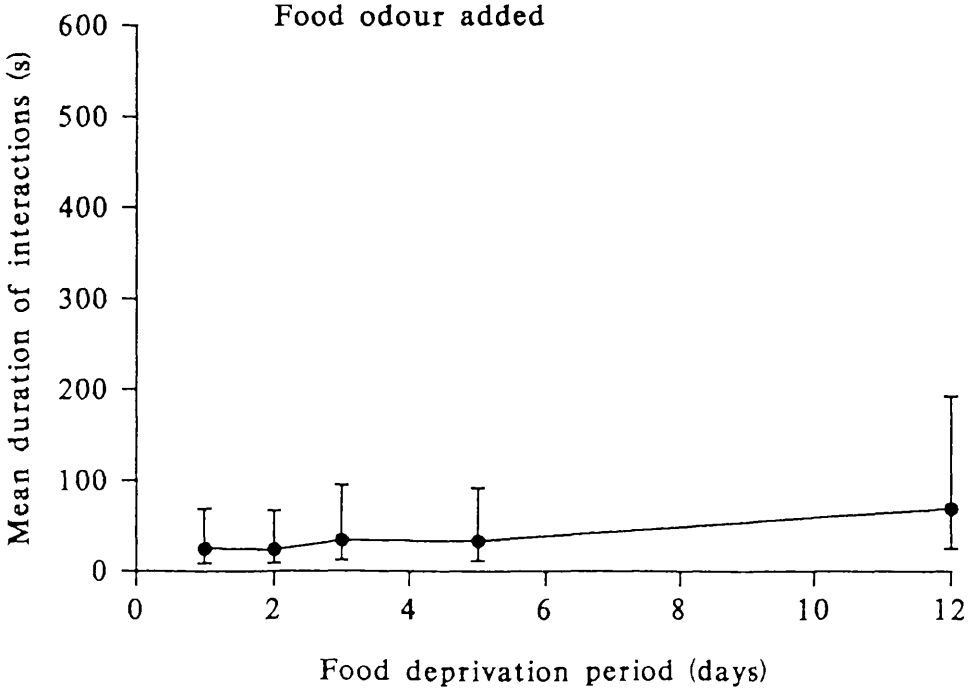


Figure 3.4 Mean durations of agonistic interactions between *L. puber* deprived of food for different periods. Means and 95% confidence intervals were calculated from log transformed data.

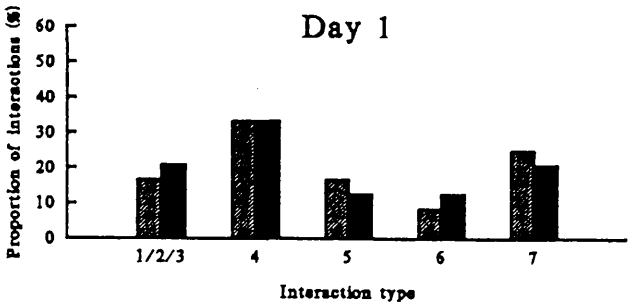


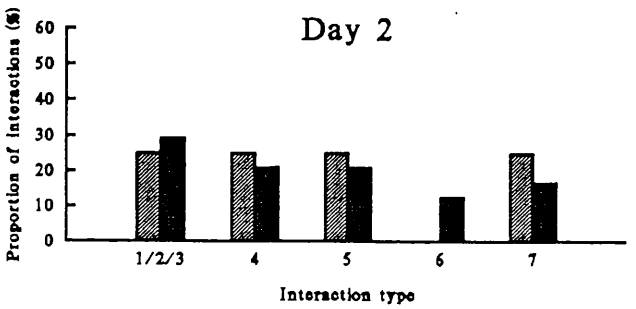


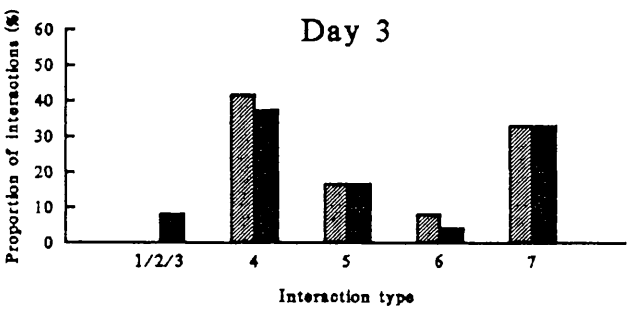
deprivation period and presence/absence of food extract is illustrated in Figure 3.5. There were too few data to analyze the effects of these two factors on the behavioural content of interactions on the basis of this classification. The interaction types have therefore been combined into those involving strikes or grasps ("contact" interactions, types 3, 5, 6 and 7) and those not involving such acts ("non-contact" interactions, types 1, 2 and 4).

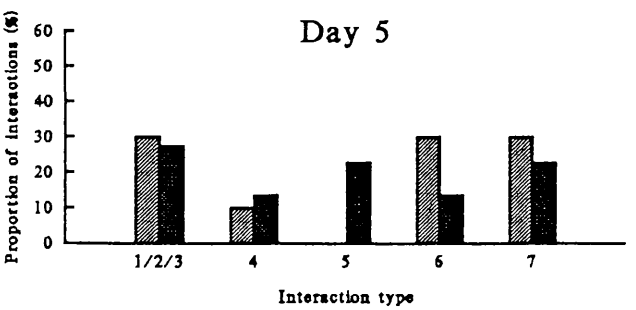
Regardless of the presence or absence of food extract in the observation tank, the proportion of contact interactions increased during the first 5 days of food deprivation (Figure 3.6). Where food extract was not added, there was a further slight increase in the proportion of contact interactions in the 12 day group. Where extract was added there was a reduction in this proportion in the 12 day group. An asymptotic relationship was suggested by a significant regression of arcsine transformed proportion of contact interactions against log transformed deprivation period ($F_{(1,8)} = 12.50$, $P<0.01$).

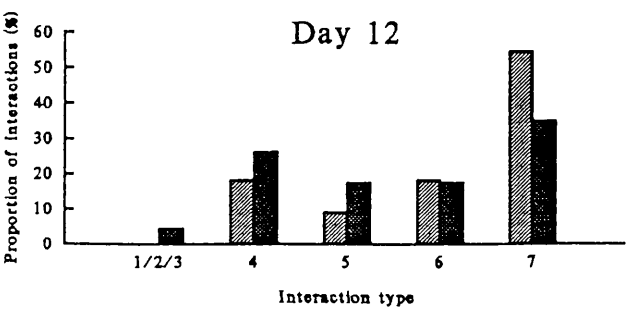
Figure 3.5 The distribution of interaction types with respect to food deprivation period and presence of food extract. See text for definitions of interaction types.


Day 1
Proportion of interactions (%)
60
50
40
30
20
10
0
1/2/3
4
5
6
7
Interaction type


Day 2
Proportion of interactions (%)
60
50
40
30
20
10
0
1/2/3
4
5
6
7
Interaction type


Day 3
Proportion of interactions (%)
60
50
40
30
20
10
0
1/2/3
4
5
6
7
Interaction type


Day 5
Proportion of interactions (%)
60
50
40
30
20
10
0
1/2/3
4
5
6
7
Interaction type


Day 12
Proportion of interactions (%)
60
50
40
30
20
10
0
1/2/3
4
5
6
7
Interaction type

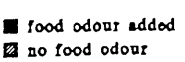
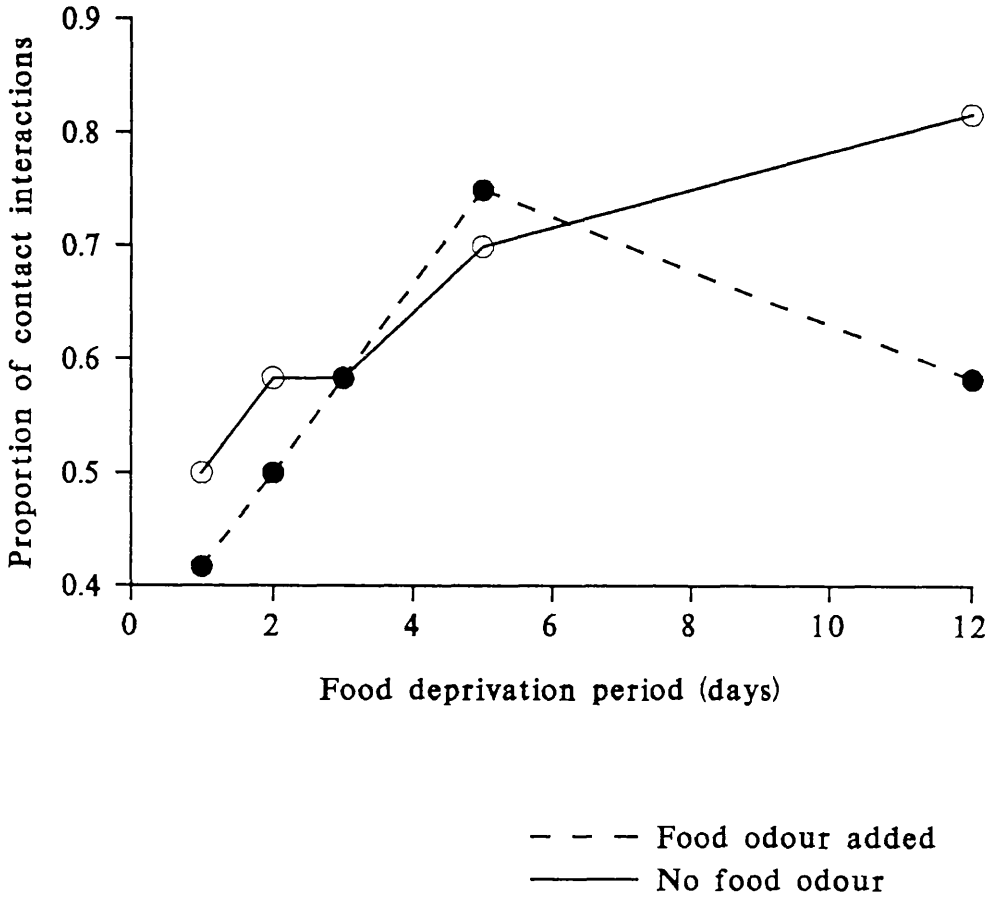

food odour added
no food odour

Figure 3.6 The proportion of "contact" interactions between *L. puber* deprived of food for different periods, in the presence and absence of food odour.



3.4 DISCUSSION

Crabs observed in the presence of food extract were collected in winter and were maintained in slightly colder, less saline water than those observed in the absence of food extract, which were collected in late summer and autumn. It is not known if there are seasonal variations in the occurrence and nature of agonistic behaviour in *Liocarcinus puber*, or in what way environmental conditions affect this behaviour. It is possible that some of the differences in agonistic interactions in these two groups were not solely due to the presence or absence of food odour. However, the rapid response of crabs to food extract indicated that it had a significant influence on their behaviour. At the end of the settling period in the observation tank, before addition of food extract, crabs were usually quiescent. Shortly after administering extract, most crabs increased the rate of antennular flicking and tended to start moving around the tank. This response is identical to that observed when food is placed in an aquarium with *L. puber*. Food capture usually follows contact of the pereiopods with the food item (personal observations). Treatment of the water in the observation tank with food extract was therefore probably the main reason for differences between these two groups.

The differences between interactions in relation to the presence or absence of food odour are consistent with an increased rate of activity when food odour is present. In most cases, agonistic interactions resulted when the movement of one or both crabs brought them in close proximity to each other. Since addition of food extract was followed by increased locomotor activity, the time between removal of the partition and the initiation of an agonistic interaction was shorter when extract was present. The faster resolution of interactions in the presence of food odour may also be attributable to this increased rate of activity.

The pairs of crabs in this study were size matched as far as possible, but in few cases were the carapace widths of paired crabs equal. This permitted the initiation and outcome of interactions to be analyzed in terms of the relative sizes of the interactants. As each crab in a pair had been subjected to the same treatment before behavioural observations, no relationship was expected between food deprivation period and either the relative size of the initiator or the winner. The conflicting trends in the relative size of the initiator with food deprivation period in the presence and

absence of food odour are therefore puzzling and no significance can be attached to them at this time. The period of food deprivation did not appear to affect the relative size of the winner, whether or not food extract was present.

The duration of interactions and the incidence of strikes are considered here to be correlates of the cost of this behaviour. *L. puber* are capable of damaging each other with strikes and grasps (see section 4.3.4.4). Interactions involving these acts therefore have a higher risk of injury than those involving exclusively non-contact display. The duration of interactions may represent several types of cost. Time spent in agonistic interactions cannot be spent in fitness promoting activities. Agonistic interactions are visually conspicuous and may therefore attract predators. If such a risk exists, it would be related to interaction duration. The duration of interactions may also be related to the energetic cost of this activity (chapter 5). The relative magnitude of the costs represented by interaction duration and incidence of strikes is unknown. The effects of hunger on the duration of interactions and the incidence of strikes have been interpreted on the basis of comparisons between experimental treatments and are not assumed to be comparable in absolute terms with naturally occurring interactions.

The increasing urgency for crabs to acquire food the longer they are deprived of it is assumed to result in an increase in their estimate of the value of this resource. In common with other crustaceans, *L. puber* appear to defend an individual space that excludes other crabs from resources within that space (chapter 2). This space may therefore also be a resource, the value of which varies with food deprivation period.

Contrary to the predictions of certain game theory models (Parker, 1974; Maynard Smith and Parker, 1976; Hammerstein and Parker, 1982; Enquist and Leimar, 1987), the durations of interactions were not significantly related to the length of the food deprivation period. In the presence of food extract there was an increase in mean duration with deprivation period, but this trend was insignificant compared with the residual variation in the data. However, the finding that the incidence of potentially injurious behaviour increased with food deprivation period was in accord with the predictions of game theory. Over the first five days of food deprivation, the increase in incidence of interactions involving strikes was remarkably similar when food odour was present and when it was absent. After this period, the incidence of contact interactions did not increase linearly (food odour absent), or it declined (food odour present). Hazlett *et al.* (1975) reported that aggressive activity

in the crayfish, *Orconectes virilis* increased after seven days of starvation, but after fourteen days there was a decline in the number of fights and the time spent fighting. There are several possible explanations for these results. Firstly, there is a methodological consideration to be made in interpreting the results of the present study. Each crab was tested three times. In the categories corresponding to one, two, three and five days of starvation there were six days between replicate observations of each crab. In the twelve day category, however, each crab was tested on three successive days, with twenty-four hours between replicate observations. The reduction in the proportion of interactions with strikes in this category could therefore have been due to the short period between observations of individual crabs.

Depletion of energy reserves may eventually limit an increase in agonistic intensity with hunger in crustaceans. Many crustaceans can survive weeks or months of fasting, but there is conflicting evidence about the nature of energy storage and utilisation (Dall, 1981; Dall and Moriarty, 1983; Barclay *et al.*, 1983; Whyte *et al.*, 1986). In most crustaceans in which this has been studied, proteins, lipids or both are the major reserves of energy used during starvation (Barclay *et al.*, 1983). In contrast, Cuzon *et al.* (1980) reported that utilisation of carbohydrate reserves was significant during the early stages of starvation in *Penaeus japonicus*. Respiratory adjustments which may affect activity also occur during starvation. A reduction in the resting rate of oxygen consumption was observed in *Carcinus maenas* (Marsden *et al.*, 1973; Wallace, 1973) and *Crangon crangon* (Regnault, 1981). Starvation of *Cancer pagurus* resulted in a decline in the resting rate of oxygen consumption which stabilised after the first week (Ansell, 1973). The maximum heart rate of *C. pagurus* recorded during successive 24 hour periods also fell and there was an increase in the prevalence of a heart beat pattern characteristic of quiescent crabs. Nocturnal activity diminished concurrently (Ansell, 1973). Similar results have been reported for *Carcinus maenas* (Depledge, 1985). This suppression of metabolic rate in times of food shortage may result from substrate limitation or may be an energy conservation strategy. A similar phenomenon in *L. puber* might prescribe a critical starvation period, beyond which the probability of energetic, escalated agonistic encounters diminishes rapidly. Measurement of the endurance of *L. puber* in other types of activity might indicate whether there is varying energetic constraint during twelve days of starvation.

The behaviour analyzed in the present study corresponds with that of crabs prior to food location. The subsequent response of crabs to conspecifics may depend on

the nature of the food item in addition to the time since they last fed. Observations in the aquarium and in the field show that the strategies used in competition for food by *L. puber* are influenced by the physical nature of the food items (personal observations; chapter 6). When food items are small and transportable, *L. puber* often respond to the approach of a conspecific by retreating with the food. When food items are immovable, they may be defended. An investigation by Capelli and Hamilton (1984) of the relationship between food availability and aggression in the crayfish, *Orconectes rusticus* was complicated by the animals' tendency to disintegrate discrete food items and redistribute the material over the observation area. When shelters were in limited supply and food items remained discrete, *O. rusticus* fought continually over food. The frequency of agonistic interactions declined when the food was dispersed.

4. THE RÔLE OF AGONISTIC BEHAVIOUR IN COMPETITION FOR MATES

4.1 INTRODUCTION

4.1.1 The rôle of agonistic behaviour in competition for mates

Intrasexual competition in the form of agonistic behaviour is known to be involved in the mating systems of many animals (Huntingford and Turner, 1987), including crustaceans (Dingle, 1983). In most crustaceans studied so far, this behaviour mediates male competition for mates or for the resources necessary for mating, such as shelter. Such behaviour is not confined to males, however. Montgomery and Caldwell (1984) described female aggression in relation to brood defence in the stomatopod *Gonodactylus bredini* and Atema (1986) suggested that the formation of dominance orders in female American lobsters, *Homarus americanus*, had implications for their reproductive success as they mated in order of dominance. Behaviour associated with reproduction may influence a species' ecology and evolution, yet the rôle of agonistic behaviour in the sexual activity of crustaceans has in most cases been inferred from indirect evidence. There are few direct observations of such behaviour and these are mainly from
laboratory or aquarium studies (e.g. Edwards, 1966; Jachowski, 1974; Berrill and Arsenault, 1982). Presumably the lack of field data on this important aspect of crustacean biology is due to their cryptic and often nocturnal activity patterns. Mating in many crustaceans occurs when the female is soft following ecdysis (Sastry, 1983). As this is a time when crustaceans are vulnerable - and therefore inconspicuous - observation of reproductive behaviour in the field is particularly difficult.

In those crabs in which mating takes place when the female is soft, copulation is often preceded by a period of "pre-copulatory attendance" where the male uses the ambulatory legs to hold the female, dorsal side uppermost, against his ventral side (Hartnoll, 1969). Copulation follows soon after the female has moulted and there is often a period of "post-copulatory attendance" (Hartnoll, 1969). Where these periods have been quantified, the pre-copulatory attendance is longer on average than the post-copulatory equivalent, which may be absent altogether (Edwards, 1966; Berrill and Arsenault, 1982). This pattern of mating is found in *Liocarcinus puber* (González

Gurriarán, 1985, Choy, 1988).

4.1.2 Indirect evidence for agonistic behaviour in crustacean reproduction

Field data on the abundance and size distribution of some species indicate that agonistic behaviour may influence which individuals successfully pair and mate. The sex ratios of some field populations of crabs are male biased (Wilber, 1986; Choy, 1988; Sekkelsten, 1988; Norman, 1989, chapter 6). Although this may be partly a result of under-sampling of females due to their lesser activity and cryptic habits, a paucity of females, combined with the short period of female sexual receptivity may result in an operational sex ratio which is extremely male-biased. In such populations there is presumably great potential for intense competition among males for mates.

In several crab species it has been noted that males paired with females in pre- or post-copulatory attendance or in actual copulation are larger on average than unpaired, adult males in the population eg. *Cancer pagurus* (Edwards, 1966); *Cataleptodius floridanus* (Hazlett *et al.*, 1977); *Panopeus herbstii* and *Mithrax sculptus* (Hazlett, 1979); *Menippe mercenaria* (Wilber, 1986) and *Carcinus maenas* (Sekkelsten, 1988). This was also found to be the case in a population of *Liocarcinus puber* in the south of England (Norman, 1989), but not in a population in the Firth of Clyde (chapter 6). Since larger individuals generally dominate smaller ones in agonistic contests (Hyatt, 1983), it may be that this distribution is brought about by direct male competition in the form of agonistic behaviour. However, present knowledge is insufficient to rule out other explanations such as female mate choice, or size-related male ability to subdue potential mates.

Differences between the sexes in the appendages used in agonistic display also suggest that such behaviour is related to sexual activity. It is common in crustaceans for males to have relatively larger chelipeds than females. Furthermore, in those sexually dimorphic species for which behavioural data are available, it transpires that only males fight, or that they fight more (Dingle, 1983).

4.1.3 Observations of male competition for mates in crustaceans

Direct observations of male competition for mates are available for only a few species of Crustacea. Agonistic behaviour of the caprellid *Caprella gorgonia* involves the use of a poison spine on the enlarged gnathopod (Lewbel, 1978). Intense competition for receptive females in that species results in high mortality of males

and consequently a female-biased sex ratio. The stomatopod *Gonodactylus bredini* relies on cavities in coral rubble for shelter in which to mate, these cavities being defended predominantly by the male when male and female are cohabiting (Shuster and Caldwell, 1989). Paired males show a greater tendency to strike intruders and are more successful in cavity defence than their unpaired counterparts. Intruders encountering paired males are more likely to be injured than when they encounter single males. Since agonistic success correlates with body size in gonodactylids (Caldwell and Dingle, 1979) this behaviour would lead to greater reproductive success for larger males.

Direct observations of male crabs competing for mates have been made for *Carcinus maenas* (Berrill and Arsenault, 1982), *Cancer pagurus* (Edwards, 1966) and *Callinectes sapidus* (Jachowski, 1974). This competition involves displacement of a male from pre- or post-copulatory attendance and takeover of the female by the dominant male.

4.1.4 Reproduction, resource value and agonistic behaviour

Behaviour associated with mating can have a direct influence on the probability of reproduction and therefore, if genetically determined, the genes responsible for behaviour which improves reproductive success have a high probability of being transmitted to the next generation. One of the major premises of cost-benefit analyses of animal behaviour such as evolutionary game theory (Maynard Smith, 1982) is that there is selection for behavioural phenotypes that maximise the lifetime reproductive output (the product of the rate of offspring production and longevity) of individuals. Natural selection results in organisms having a collection of traits that enhance lifetime reproductive output. Therefore, where one sex is limiting, natural selection will favour individuals with those characters that promote efficiency of locating and competing for mates.

The value of resources required for reproduction can be defined in terms of the increment to an individual's fitness that is gained by acquiring them. Game theory predicts that animals should modify their aggressive behaviour according to variations in resource holding power and resource value - in particular, they should fight more fiercely over valuable resources (Hammerstein and Parker, 1982; Enquist and Leimar, 1987). In sexually reproducing animals a mate is an essential requirement for reproduction and as such is a valuable resource. It is therefore possible for an animal

to incur considerable costs in acquiring a mate before the benefit from so doing (in terms of lifetime reproductive output) is outweighed. Aggressive behaviour used in competition for mates should therefore be more intense than that used in competition for resources having less influence on reproductive output.

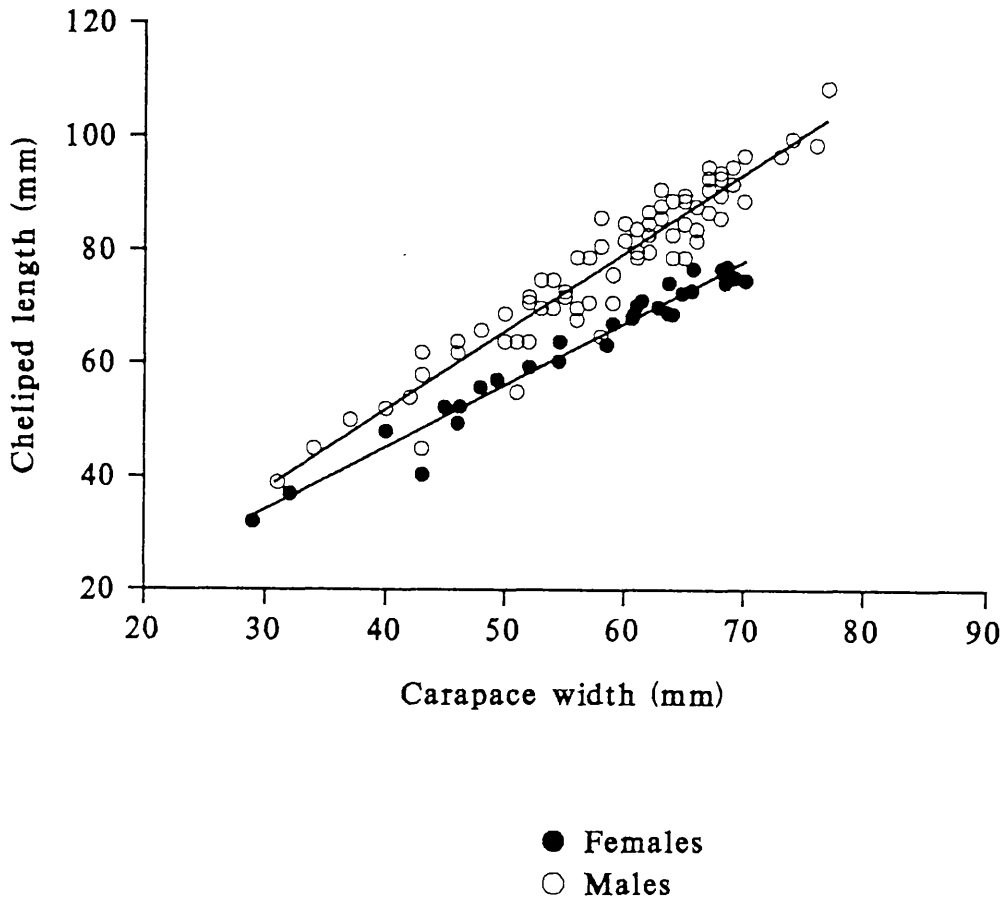
4.1.5 Sex pheromones in the Brachyura

Successful sexual reproduction requires that potential mates recognise each other not only as the same species, but also as being physiologically capable of reproduction. Crustaceans have been shown to use visual, acoustic and tactile cues for this purpose (Salmon and Hyatt, 1983). Additionally, in more than twenty species release of a sex pheromone by females has been demonstrated or is suspected (Bachau, 1986). Among the Portunidae, Ryan (1966) found that male *Portunus sanguinolentus* responded with searching behaviour and a characteristic courtship display to both pre-moult females and to water from tanks that had contained them. These males also attempted to seize and carry other crabs in the area, regardless of sex. The active substance was found to be associated with the females' urine and the response of male *P. sanguinolentus* to crab urine was sex and species specific. *Carcinus maenas* and *Liocarcinus holsatus* females also release a pheromone when in pre- and early post-moult, which elicits searching behaviour in conspecific males (Eales, 1974). As in *P. sanguinolentus*, the pheromone was shown to be associated with the female's urine in *C. maenas*. Sex pheromone release in female urine has also been demonstrated in *Callinectes sapidus* and ablation experiments indicated that males detect this substance with chemoreceptors on the outer flagellae of the antennules (Gleeson, 1980).

4.1.6 Agonistic behaviour and mating in *Liocarcinus puber*

Liocarcinus puber has sexually dimorphic chelae (Figure 4.1), there is often a male-biased operational sex ratio (Choy, 1988; Norman, 1989; chapter 6) and in one population at least, males successful in pairing with females were larger than average (Norman, 1989). These pieces of indirect evidence alone indicate that agonistic behaviour may be involved in competition for receptive females in *L. puber*. In addition, these phenomena are found in other species for which male competition for mates has been observed. The objects of this study were therefore to determine whether there is male competition for mates in the form of agonistic behaviour and

Figure 4.1 Cheliped length of male and female *L. puber* as a function of carapace width.



if so, to investigate how aggressive behaviour is modified by the presence of receptive females. Sex pheromone release by female *L. puber* has not been demonstrated previously, but seems likely since their reproductive behaviour is similar to other portunids in which it has. If females release a sex pheromone when receptive and males compete for mates, then game theory predicts that the aggressive behaviour of males should become more intense when exposed to such a stimulus. Dunham (1988) has suggested that one of the functions of a crustacean sex pheromone may be to reduce the aggressiveness of males, thereby reducing the chance of cannibalism when the female moults. An alternative hypothesis is therefore that a stimulus associated with a receptive female should diminish the intensity of agonistic behaviour between males.

In this chapter the results of an investigation of the effects of female odour on the agonistic behaviour of male *L. puber* are reported. The period of peak breeding activity of *L. puber* in the Firth of Clyde occurs between July and September (Allen, 1967), although mating does occur at other times of year (chapter 6). The effects of female odour on male agonistic behaviour were observed during this period in 1989 after preliminary control experiments were conducted outwith the main breeding period in October and November of 1988.

4.2 MATERIALS AND METHODS

4.2.1 Male competition for receptive females

In order to determine whether agonistic behaviour occurs between males when one is in the "pre-copulatory guarding position" (Hartnoll, 1969), interactions between paired and single males were observed. Pre-copulatory pairs collected by divers in September 1989 were allowed to settle in a 104 l glass observation tank, separated from a single male by a partition. The observation tank had an arena of 64 x 42 cm and a substratum of gravel approximately 2 cm deep.

The partition was raised and the crabs' behaviour was recorded with the remotely controlled video system described as System 2 in section 2.2.2. A time-date generator allowed time to be recorded on video tape simultaneously. Illumination of the observation tank was supplemented for the camera by two 40 W red lights. The partition was controlled remotely with the aid of an electric motor-driven winch (Como Drills, Deal, Kent).

Three replicates of this procedure were performed, the paired male being the smaller of the two males and the female being smaller than both males in each case.

4.2.2 Male agonistic behaviour outside the peak period of breeding activity.

Additional preliminary observations were made on male crabs collected by SCUBA divers from the Firth of Clyde in October andNovember1988. They were measured with vernier callipers and were placed in individual polypropylene tanks (30 x 16 x 20 cm) supplied separately with sea water from a recirculating system (10-12°C, $\approx 30^{o}/_{oo}$). They were allowed two weeks to settle before observations, during which time they were fed *ad libitum* with whitebait.

In addition to these crabs, 6 unpaired females and 6 males were collected. The sexes were separated into two tanks which were aerated but not supplied with running sea water. Water from these tanks was not allowed to enter the recirculating system. The crabs in these tanks were separated by perforated partitions to prevent them from injuring each other. Crabs used to condition water were not fed during the course of the experiment to avoid contamination of the water with food odour.

Observations of inter-male agonistic behaviour were made using the observation tank described above, screened from visual disturbance by plastic sheeting. The crabs were allowed a settling period of 15 minutes while separated by an opaque partition.

On commencement of the settling period one of the following was added to the tank:

1. Water from the tank containing females.
2. Water from the tank containing males.
3. Water from the recirculating system.
4. Nothing.

Test water was administered from a 4.5 l glass container, which was placed above the observation tank, via polythene tubing and a Y-connector which divided the water into each half of the tank. This apparatus delivered 4.4 l of water in about 5 minutes. After the 15 minute settling period, the partition was raised and subsequent behaviour of the crabs was recorded using a BBC-B microcomputer programmed as an event recorder or using the video system described as System 1 in section 2.2.2. After the interaction (or after 30 minutes if no interaction occurred in this time) the partition was lowered, the crabs were returned to their individual holding tanks and the observation tank was drained. The tank, glass container and polythene tubing were rinsed with sea water from the recirculating system.

Five male crabs were used in each of the four treatments. These crabs were observed in a round-robin design to give 10 pairings for each category. The crabs were allocated to categories in such a way that they were relatively evenly size matched and the mean carapace width of crabs and mean size ratio of pairs (carapace width of smaller crab divided by that of the larger) were not significantly different between categories. Each crab was observed 4 times with 4 different crabs, there being at least 2 days between replicate observations of any one crab. Crabs were fed 24 h before observations.

Several variables were determined from the records of agonistic interactions: the crab that first adopted a meral spread display ("the initiator"), the crab that elicited repeated retreats from the other ("the winner") and the occurrence of potentially injurious behaviour (strikes and grasps with the chelae). In addition, three measurements of time were made - the time between raising the partition and the initiation of an interaction (latency); the time between the first display and the first of repeated retreats (duration) and the time spent by each of the crabs in display postures (display time). These measurements were made with the elapsed time clock of the microcomputer.

4.2.3 Male agonistic behaviour during the period of peak breeding activity

Observations of inter-male agonistic behaviour during the period of peak breeding activity were made in July, August and September 1989. Crabs were collected by divers in July and August and were maintained in a "flow-through" sea water system (13-14°C, ≈ 32°/$_{oo}$). sea water supplied to the test males and to the male and female crabs used to condition the test water was allowed to drain to waste. Females which were paired with males in the "pre-copulatory guarding position" were assumed to be sexually receptive (Hartnoll, 1969): only these females were collected. When available in sufficient numbers, such females were held in a 150 l tank and were separated by partitions. If they moulted during the course of the experiment, they were used only until one day after their moult, since the period of sexual receptivity ends as the new exoskeleton hardens (González Gurriarán, 1985). Male-conditioned water was prepared by keeping males in a similar 150 l tank. If the number of receptive females available was considered too small to condition water in the 150 l tank, "female water" was prepared by placing a single receptive female in a 10 l tank with aeration but no water supply; the male-conditioned water for that observation session was prepared using a male in the same way.

Recordings were made as described in section 4.2.1. The crabs were allowed 1 hour to settle in the observation tank, with test water administered after 55 minutes, using the same water dispenser as before. The water dispenser was controlled remotely with the aid of a solenoid valve (RS 342-023) and the partition was actuated by the electric winch described above.

In this experiment one of three types of water were added:

1. female-conditioned water.
2. male-conditioned water.
3. unconditioned sea water.

The control of administering nothing was omitted from this experiment since a limited number of crabs was available and the results from the preliminary trials indicated that adding sea water and adding nothing were equivalent.

Each treatment was represented by four groups of four crabs. A round-robin design within each group gave 6 dyads per group and 24 per treatment. Each crab was therefore paired with three different opponents. The groups were arranged as before so that there were no significant differences in mean carapace widths of crabs or in mean size ratios of the pairs in different treatments. Observations were made

in sessions with one dyad from each treatment observed in a random order. Crabs were randomly assigned to each side of the observation tank. After each interaction (or 30 minutes if none occurred) the crabs were removed and the apparatus was drained and rinsed thoroughly with sea water.

The video tapes were used to derive the same variables as for the preliminary observations with the exception of display time. In one pair in each of the "female water" and sea water categories there was no agonistic interaction within 30 minutes of the partition being raised and in one interaction in the "male water" treatment the initiator could not be determined as both crabs displayed simultaneously.

4.2.4 Statistical methods

Analysis of frequencies was carried out using the Log-likelihood ratio test with William's correction (Sokal and Rohlf, 1981), unless the sample size was too small (more than 20% of the expected frequencies less than 5) in which case exact Binomial probabilities were computed. Time measurements were compared with Analysis of Variance (ANOVA) where possible. *A posteriori* comparisons were made with Ramsey's revision of Ryan's Q test, with Kramer's modification for unequal sample sizes (Day and Quinn, 1989). Where the assumptions of ANOVA did not hold a Kruskal-Wallis test was used.

4.3 RESULTS

4.3.1 Agonistic behaviour during "pre-copulatory guarding"

All three encounters of single males with pre-copulatory pairs resulted in long, vigorous agonistic interactions. Some characteristics of these interactions are shown in Table 4.1.

Interactions were initiated both by paired and single males. In one case the female was forcibly removed from her mate and taken over by the other crab. In the other two cases, the paired male successfully defended the female, despite being 85% and 95% of the size of the single crab, respectively.

All three interactions involved multiple, bilateral striking and two of them involved periods of grappling where the single male attempted to wrestle the female from the other male. One of these attempts was successful and the usurping male subsequently fended off the other male. The other grappling bout resulted in the propodus of one of the single male's chelae being cracked by a grasp by the paired male. These crabs later separated and when the paired male released the female, he made vigorous attempts to displace his opponent. During this behaviour, the female repositioned herself under the original mate, which gripped the female with its ambulatory legs in the pre-copulatory position and attempted to retreat from the other male by swimming with her.

At all times when the female was held by her initial mate, she was passive. Following the one successful takeover, the usurping male forced the female under him while she apparently attempted to escape.

4.3.2 Sex pheromone release by female *Liocarcinus puber*

The assumption was made in the design of this investigation that when sexually receptive, female *L. puber* produce a pheromone. Although not previously demonstrated for this species, existence of a sex pheromone seemed likely as the reproductive activity of *L. puber* is very similar to other crabs in which pheromone release by females is known (Bachau, 1986; González Gurriarán, 1985). Towards the end of the settling period, males were usually quiescent, but on addition of female-conditioned water they generally increased their rate of antennular flicking and began wiping their mouthparts and chelae with the palps of the third maxillipeds. There was a tendency for these males to begin moving around the observation tank, occasionally

Table 4.1 Attributes of interactions between single male Liocarcinus puber and males in pre-copulatory pairs.

Size Ratio[1]	Initiator[2]	Latency[3]	Winner	Duration	Grappling[4]
0.85	Single	72 s	Paired	1245 s	-
0.86	Paired	708 s	Single	1192 s	464 s
0.95	Single	210 s	Paired	930 s	228 s

1. Size ratio = carapace width of smaller crab divided by that of the larger.

2. The paired male was smaller than the single male in each case.

3. Latency is the time between removal of the partition and the initiation of an agonistic interaction.

4. See text for a description of grappling bouts.

orienting towards the test water inflow. In several cases in the female-water category agonistic behaviour between males was the result of one crab grappling with the other and attempting to force it under its body into a "pre-copulatory" position. In one case the subordinate male was relatively passive and the other managed to place it in this position. This last activity was never observed in the "male water" or sea water categories, nor has it been seen under any other experimental conditions (personal observations). This behaviour has only been described in response to female pheromone in other portunids (Eales, 1974; Gleeson, 1980; Jachowski, 1974; Ryan, 1966). There is therefore some evidence that female *L. puber* which had been paired with males in the field produced a pheromone which was detected by at least some males. However, since females may release pheromone intermittently (Eales, 1974) and males may not always respond visibly to pheromone, the proportion of tests where female pheromone was present and was detected by one or both males cannot be determined.

4.3.3 Agonistic behaviour outside the breeding season

Although the crabs were size matched as far as possible while not allowing absolute size to vary significantly between treatment groups, in only one pair were the carapace widths the same. The smaller crab's carapace width was on average 92% of the larger's and in the most disparate pair was 81% of the larger's. This allowed the interactions to be analyzed in terms of the relative sizes of the crabs. The frequencies of initiating and winning with respect to relative size in agonistic interactions observed outside the period of peak breeding activity are presented in Tables 4.2 a-d. The content of these interactions in terms of the occurrence of strikes and grasps is also given. There were no significant differences in the proportion of interactions initiated by the larger crab between the four treatment categories (G_{adj} = 2.541, P>0.10, df = 3) with 52.6% of the interactions overall being initiated by the larger crab. This proportion is not significantly different from 50% (G_{adj} = 0.051, P>0.10). There were also no significant differences in the outcome of interactions (G_{adj} = 3.626, P>0.10, df = 3), 71.1% overall being won by the larger (significantly greater than 50%, P = 0.007). The interactions in the four treatment categories were also comparable with regard to the incidence of potentially injurious behaviour (G_{adj} = 1.027, P>0.10, df = 3), with 60.5% of all interactions involving strikes or grasps.

Table 4.2. Initiation, outcome and content of agonistic interactions between male Liocarcinus puber outside the peak period of breeding activity. Contact interactions are those involving strikes or grasps.

(a) Crabs exposed to female-conditioned water

Initiating crab	Winning crab				Totals
	Non-contact		Contact		
	Larger	Smaller	Larger	Smaller	
Larger	1	1	2	1	5
Smaller	0	2	1	1	4
Totals	1	3	3	2	9

(b) Crabs exposed to male-conditioned water

Initiating crab	Winning crab				Totals
	Non-contact		Contact		
	Larger	Smaller	Larger	Smaller	
Larger	1	0	1	1	3
Smaller	2	0	3	1	6
Totals	3	0	4	2	9

Table 4.2 Continued

(c) Sea water added to observation tank

Initiating crab	Winning crab				Totals
	Non-contact		Contact		
	Larger	Smaller	Larger	Smaller	
Larger	4	0	2	1	7
Smaller	0	1	2	0	3
Totals	4	1	4	1	10

(d) Nothing added to the observation tank

Initiating crab	Winning crab				Totals
	Non-contact		Contact		
	Larger	Smaller	Larger	Smaller	
Larger	1	0	3	1	5
Smaller	2	0	2	1	5
Totals	3	0	5	2	10

None of the time measurements varied significantly between treatments - Latency, H_{adj} = 3.579; Duration, H_{adj} = 3.712; Display time, H_{adj} = 3.324. P>0.10, df = 3 for each. The display time was highly correlated with the interaction duration (Figure 4.2; regression of log-display-time on log-duration - $F_{(1,36)}$ = 769.18, P<0.001) and therefore provided little additional information.

4.3.4 Agonistic behaviour during the breeding season

4.3.4.1 Initiation, outcome and content

Categorization of the agonistic interactions observed during the breeding period according to the initiator, winner and occurrence of strikes and grasps is presented in Tables 4.3 a-c.

The initiating crab was larger in 13 out of 22 interactions when female-conditioned water was added and 12 out of 23 interactions in both categories where male-conditioned water and sea water were added. These proportions are not significantly different from each other (G_{adj} = 0.280, P>0.10, df = 2).

The larger crab won the interaction in 11 out of 22 cases in the "female water" category, 20 out of 23 cases in the "male water" category and 16 out of 23 cases in the sea water category (Figure 4.3). Pairwise comparisons of these proportions indicated that the success rate of the larger crab in both the "female water" and "male water" category was not significantly different from that in the control group (sea water added), (G_{adj} = 1.710 and G_{adj} = 1.983 respectively, P>0.10, df = 2). However the proportion of fights won by the larger crab was significantly greater in the "male water" category than in the "female water" category (G_{adj} = 7.094, P<0.05, df = 2). The equivalence of success rate of larger crabs in these two groups with the control group makes it difficult to determine whether the difference between the "female water" and "male water" categories is due to increased success of larger crabs in the "male water" category, increased success of smaller crabs in the "female water" category, or both. However, in the "male water" and sea water categories the success rate of larger crabs was significantly greater than 50%, as expected from previous studies (one tailed exact binomial probability - "male water" P<0.001, sea water, P<0.05), whereas in the "female water" category the success rate of larger crabs was 50%, suggesting that the result was due to increased success of smaller crabs in the "female water" category.

Agonistic interactions between male crabs exposed to water conditioned by

Figure 4.2 The relationship between the time spent in display by both crabs and interaction duration.

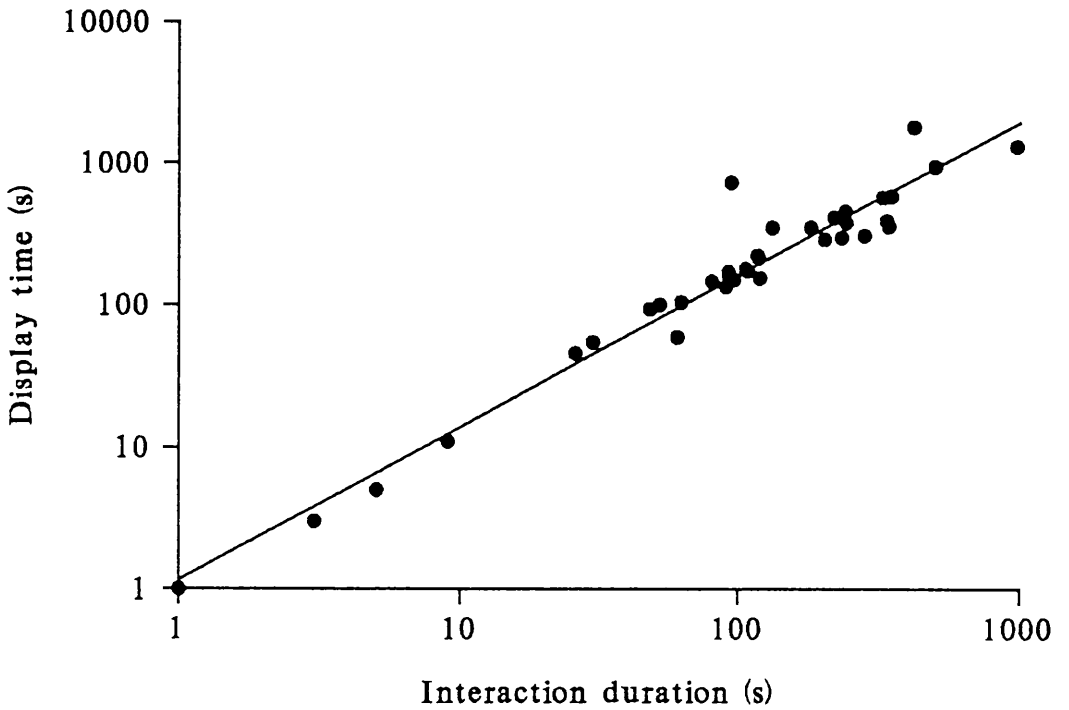


Table 4.3 Initiation, outcome and content of agonistic interactions between male Liocarcinus puber during the peak period of breeding activity. Contact interactions are those involving strikes or grasps.

(a) Crabs exposed to female-conditioned water

Initiating crab	Winning crab				Totals
	Non-contact		Contact		
	Larger	Smaller	Larger	Smaller	
Larger	1	3	3	6	13
Smaller	2	1	5	1	9
Totals	3	4	8	7	22

(b) Crabs exposed to male-conditioned water

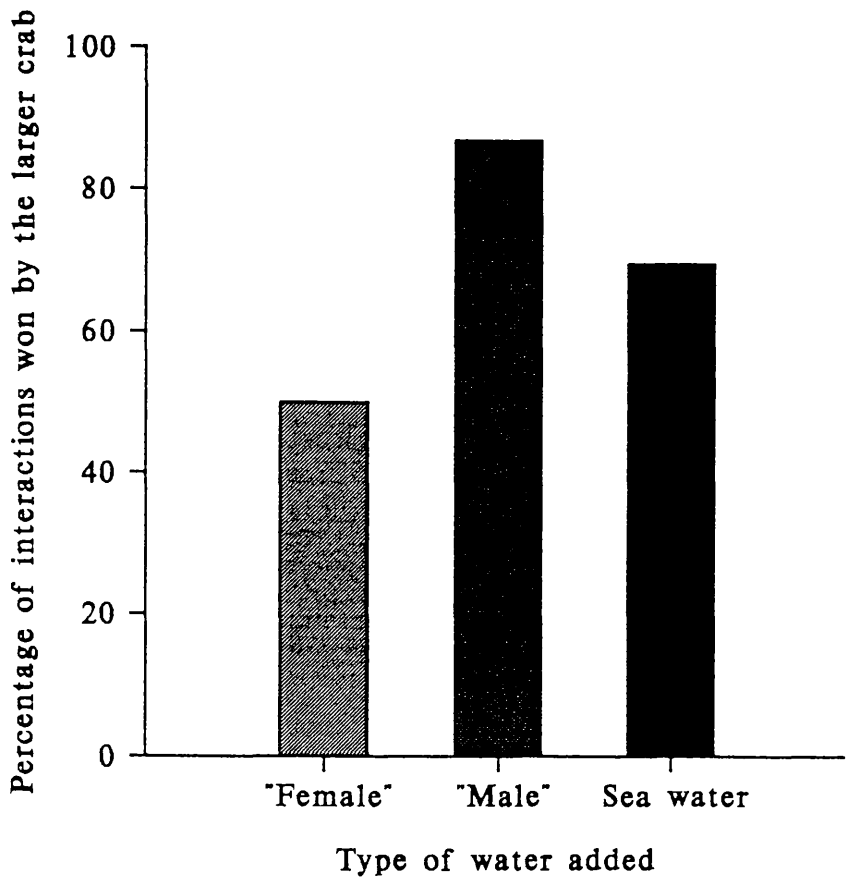
Initiating crab	Winning crab				Totals
	Non-contact		Contact		
	Larger	Smaller	Larger	Smaller	
Larger	5	1	6	0	12
Smaller	2	0	7	2	11
Totals	7	1	13	2	23

Table 4.3 Continued

(c) Sea water added to the observation tank

Initiating crab	Winning crab				Totals
	Non-contact		Contact		
	Larger	Smaller	Larger	Smaller	
Larger	6	1	4	1	12
Smaller	3	4	3	1	11
Totals	9	5	7	2	23

Figure 4.3 The proportion of interactions won by the larger crab in interactions between *L. puber* exposed to sea water (control) or water conditioned by females or males.



sexually receptive females exhibited a significant association between initiation and resolution (G_{adj} = 4.414, P<0.05, df = 1), where the proportion of fights won by responders (72.7%) was greater than that won by initiators (27.3%). This association was not found in the "male water" category (G_{adj} = 0.488, P>0.10, df = 1) nor in the sea water category (G_{adj} = 2.070, P>0.10, df = 1). In these treatment groups initiators were as likely to be successful as responders (Responder success - "male water" category = 43.5%, sea water category = 34.8%).

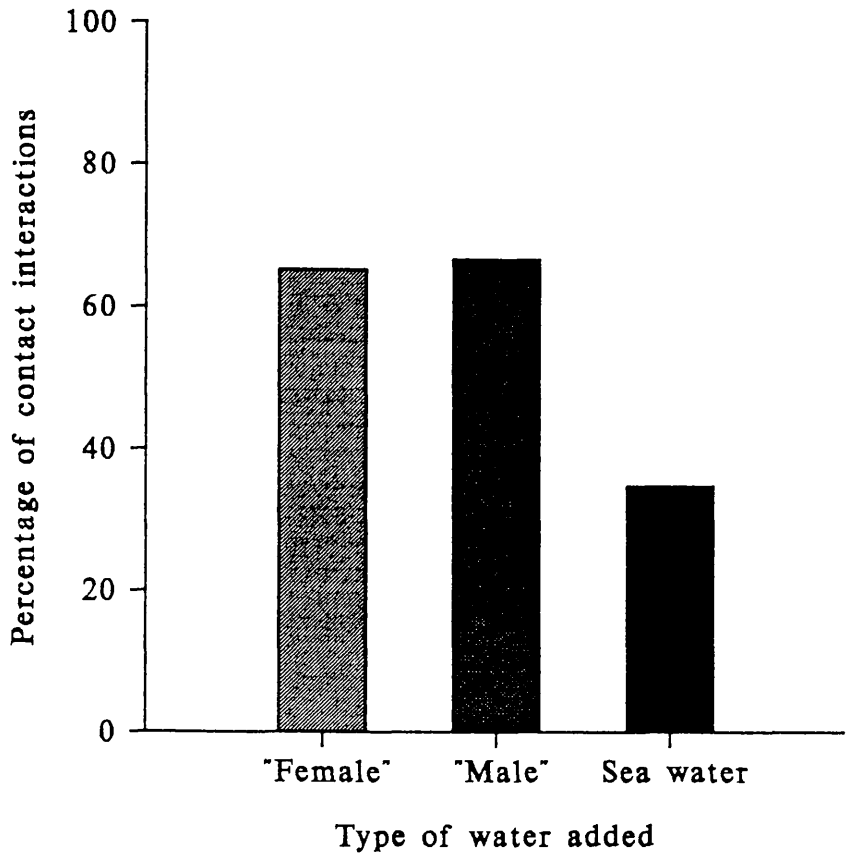
In order to determine whether the association between responding and winning in the "female water" category was related to the type of initiation, the proportion of fights won by crabs initiating by approach in display was compared with the proportion of fights won by crabs displaying in response to the non-display approach of another. (There were no significant differences in the frequencies of these initiation types between the three categories; G_{adj} = 4.381, P>0.10, df = 2). Of 12 "approach" initiations, 41.7% were won by the initiator, whereas 10.0% of the 10 "static display" initiations were won by the initiator. This difference is not significant (G_{adj} = 2.676, P>0.10, df = 1).

Interactions won by the responder in the "female water" category were not more likely to involve strikes or grasps than those won by the initiator (G_{adj} = 0.008, P>0.50, df = 1) and the probability of these acts occurring did not depend on which crab initiated (G_{adj} = 0.014, P>0.50, df = 1). Similarly, the incidence of unilateral as opposed to bilateral striking was unrelated to the success of the responder (G_{adj} = 0.457, P>0.50, df = 1).

The content of interactions in this category therefore appears unrelated to the relative size of and success of the initiator. These data therefore give no indication why responders are more successful when exposed to the odour of a sexually receptive female, although more data may show that static initiators are at a disadvantage.

65.2% of 23 interactions in the "female water" category involved strikes or grasps compared with 66.7% (n = 24) in the "male water" category and 34.8% (n = 23) in the sea water category (Figure 4.4). Comparison of these proportions indicates that the probability of strikes or grasps occurring when males are exposed to female-conditioned water was not significantly different from that when they are exposed to male-conditioned water (G_{adj} = 0.010, P>0.50, df = 2). The mean number of strikes/grasps per interaction in the "female water" ($\bar{x}$ = 2.0) and "male water"

Figure 4.4 The proportion of interactions between *L. puber* involving strikes or grasps (contact interactions) when exposed to sea water (control) or water conditioned by females or males.



($\overline{x}$ = 2.2) categories were also not significantly different (Poisson approximation to normal distribution, d = 0.496, P>0.10). However, interactions in both of these categories were more likely to result in strikes or grasps than those in the sea water category (G_{adj} = 4.106 and G_{adj} = 4.616 for "female water" and "male water" categories respectively. P<0.05, df = 2 for both comparisons.)

4.3.4.2 Latency

The time between raising the partition and the initiation of an agonistic interaction was extremely variable (Table 4.4) and the distribution of the data did not permit Analysis of Variance. A Kruskal-Wallis test indicated that the median latencies of interactions in the three treatment categories were not significantly different (H_{adj} = 3.832, P>0.10, df = 2).

4.3.4.3 Duration

The lengths of interactions were also extremely variable, ranging from 1 s (sea water category) to 922 s ("female water" category) (Figure 4.5). A Log-transformation resulted in the data becoming approximately normally distributed and Analysis of Variance of these transformed data indicated significant differences among the means ($F_{(2,67)}$ = 5.56, P<0.01). Comparisons of the means (Table 4.5) indicated no significant difference between the "male water" and sea water categories, but interactions between crabs exposed to water conditioned by sexually receptive females were significantly longer than those between crabs exposed to male-conditioned water or sea water.

Durations of different classes of interaction are given in Table 4.6. The length of interaction was unrelated to the relative size of the eventual winner in any of the categories ("female water" $F_{(1,20)}$ = 1.51; "male water" $F_{(1,22)}$ = 0.95; sea water $F_{(1,21)}$ = 0.19, P>0.10 for each). However, in the "female" and "male water" categories, fights involving strikes or grasps were longer on average than less intense types of interaction ($F_{(1,21)}$ = 4.65 and $F_{(1,22)}$ = 5.87 for "female" and "male water" categories respectively, P<0.05 for both). This was not true of interactions in the sea water category ($F_{(1,21)}$ = 3.68, P>0.05). In some interactions strikes or grasps occurred after a period of display, the interaction being resolved soon after. In others however, strikes occurred long before the end of the fight and no clear escalation was evident.

Interactions won by the smaller crab in the "female water" category were

Table 4.4 Latency of initiation of agonistic interactions between male L. puber during the breeding season in the presence of female conditioned water, male conditioned water or unconditioned sea water.

	Category		
	"Female water"	"Male water"	Sea water
Median (s)	313	410	281
Range	111 - 1211	7 - 922	6 - 668

Table 4.5 Multiple comparisons of mean durations of interactions during the breeding season in the presence of female conditioned water, male conditioned water or sea water. Comparisons have been made with Ramsey's revision of Ryan's Q test with Kramer's modification for unequal sample sizes. Durations were log transformed before analysis.

No. means	Comparison	b	$Q_{b(p,v)}$	SE_C	CV	$\bar{x}_1 - \bar{x}_2$	P
3	A - C	0.05	3.390	0.192	0.461	0.636	<0.05
2	A - B	0.05	2.822	0.190	0.380	0.389	<0.05
2	B - C	0.05	2.822	0.190	0.380	0.247	>0.05

Residual Mean Square in the ANOVA = 0.425, df = 67.

See Table 2.2 for an explanation of the method of comparison.

Figure 4.5 The mean durations of interactions between *L. puber* exposed to sea water (control) or to water conditioned by females or males. Means and 95% confidence intervals were calculated from log transformed data.

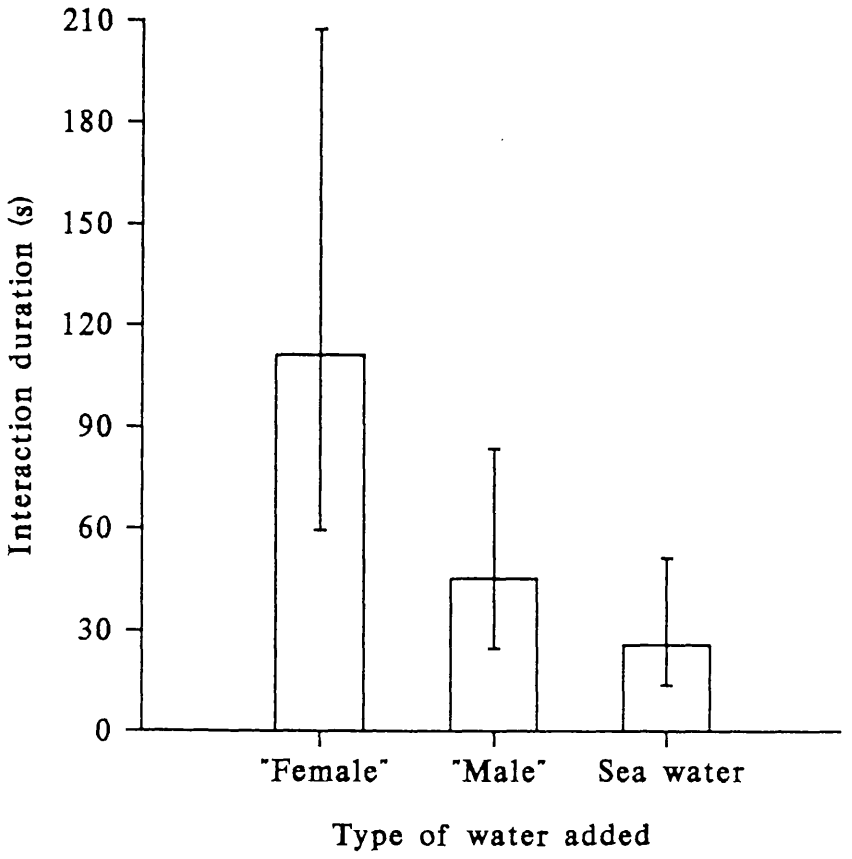


Table 4.6 Durations of agonistic interactions between male *Liocarcinus puber* - classified by resolution and content - in the three treatment categories during the breeding season.

Interaction type	Type of water added to observation tank[1] "female water"	"male Water"	sea water
Winner larger	**76.4** (25.04 - 233.23) n = 11	**40.8** (22.43 - 74.25) n = 21	**28.4** (11.42 - 70.65) n = 16
Winner smaller	**164.3** (73.98 - 356.02) n = 11	**95.3** (1.94 - 4669.19) n = 3	**20.5** (5.09 - 82.49) n = 7
Contact interactions[3]	**172.6** (89.53 - 332.67) n = 15	**71.0** (40.25 - 125.08) n = 16	**60.2** (12.01 - 301.47) n = 8
Non-contact interactions	**48.8** (13.30 - 178.72) n = 8	**18.5** (4.86 - 70.68) n = 8	**16.3** (8.05 - 33.19) n = 15
Initiator winner	**121.2** (16.60 - 884.75) n = 6	**37.0** (13.69 - 100.20) n = 12	**18.3** (8.11 - 41.31) n = 15
Responder winner	**108.8** (54.08 - 218.97) n = 16	**58.4** (24.74 - 138.01) n = 11	**48.6** (10.81 - 218.84) n = 8

1. In the "female" and "male water" treatment categories, test males were exposed to water conditioned by sexually receptive females and males respectively. In the sea water control, untreated seawater was added to the observation tank.

2. Figures are mean durations with 95% confidence intervals in parentheses. These values were calculated from log-transformed data and are presented in their original units of measurement (seconds).

3. Contact interactions are those involving strikes or grasps.

significantly longer than equivalent interactions in the "male water" and sea water categories (data pooled due to the low number of interactions won by the smaller crab in the "male water" category; $F_{(1,19)} = 6.09$, $P<0.05$). Those won by the larger crab in the "female water" category were not significantly longer than such interactions in the "male water" ($F_{(1,30)} = 1.35$, $P>0.10$) or the sea water category ($F_{(1,25)} = 2.20$, $P>0.10$). This suggests that the larger crab was less inclined to retreat from a smaller opponent when exposed to receptive female odour.

In none of the categories was there a relationship between the success of the initiator and the interaction duration ($F_{(1,20)} = 0.02$, $P>0.50$; $F_{(1,21)} = 0.57$, $P>0.45$; $F_{(1,21)} = 1.92$, $P>0.10$ for "female", "male" and sea water categories respectively).

4.3.4.4 Injuries

Five injuries were observed during this study, all of which occurred during the breeding season (Table 4.7, Figure 4.6). Grasps caused damage to chelae in two cases and to a second pereiopod in one case. Two of these injuries (to a chela and to an ambulatory leg) occurred in one interaction to the same crab. One strike caused damage to the abdomen and paralysis of the fifth pereiopod (the swimming leg) of a retreating crab. Another strike damaged a chela. Both injurious strikes occurred in the "male water" category, two of the above grasps occurred in the "female water" category and one occurred in an interaction between a paired and a single crab.

Table 4.7 Injuries resulting from agonistic behaviour in male *Liocarcinus puber*.

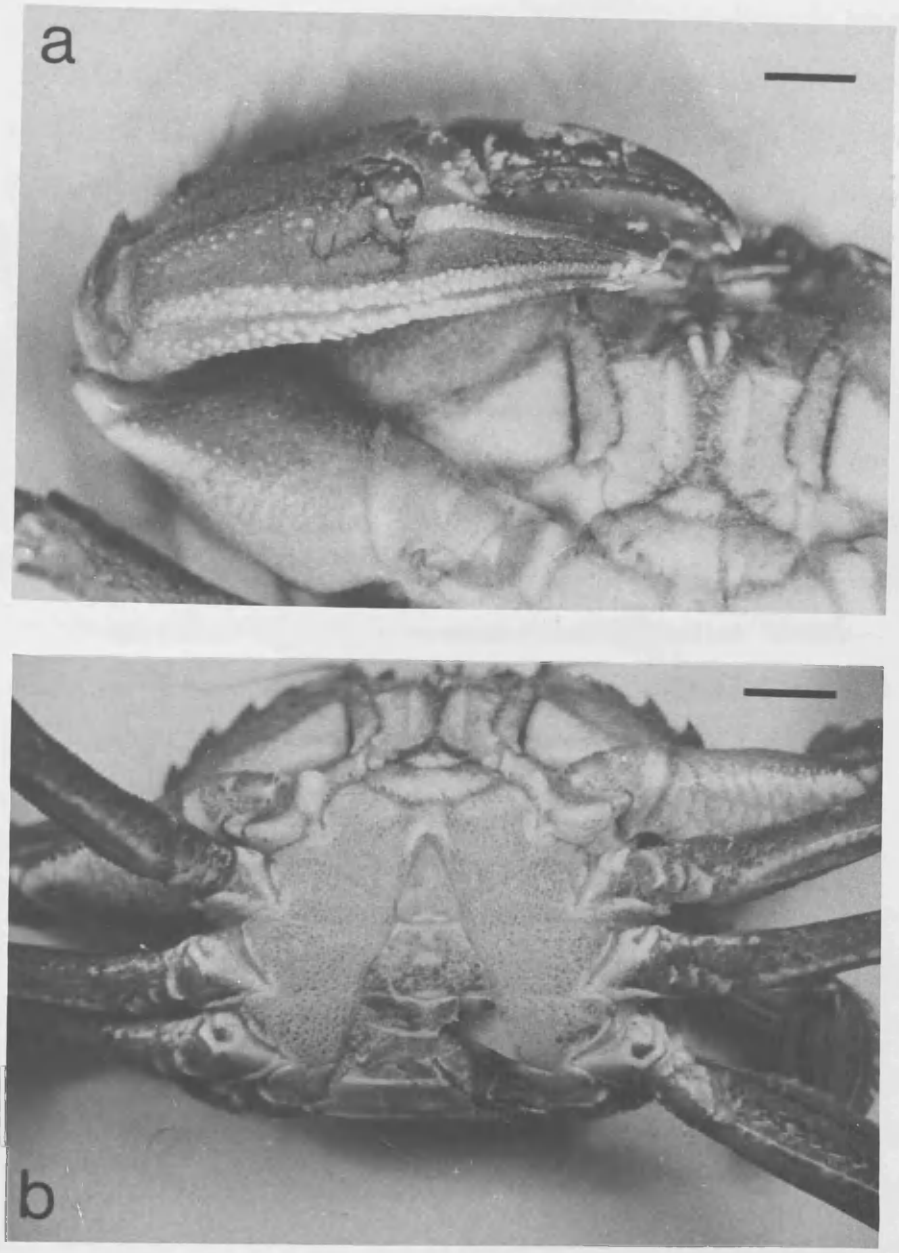
Type of injury	Cause	Size ratio	Injured crab	Treatment category
Damaged chela	Grasp	0.95	Single/Larger Loser	Single v. Paired male
Damaged chela	Grasp	0.96	Smaller/Loser	"female water"
Damaged second pereiopod	Grasp	0.96	Smaller/Loser	"female water"
Damaged chela	Strike	0.97	Smaller/Loser	"male water"
Damaged abdomen, paralysis of P5*	Strike	0.89	Smaller/Loser	"male water"

* P5: One of the fifth pereiopods (swimming legs).

Figure 4.6 Injuries sustained during agonistic interactions.

(a) Damage to propodus of cheliped caused by a strike. Scale bar ≡ 0.75 cm.

(b) Damage to the abdomen and cephalothorax caused by a strike. The left fifth pereiopod of this crab was paralysed as a result. Scale bar ≡ 1.00 cm.


a
b

4.4 DISCUSSION

4.4.1 Male competition for mates

Placing a male with a pre-copulatory pair indicated that, in the laboratory at least, male *Liocarcinus puber* compete for receptive females with aggressive behaviour. Such observations have been made for *Carcinus maenas* (Berrill and Arsenault, 1982), *Cancer pagurus* (Edwards, 1966) and *Callinectes sapidus* (Jachowski, 1974). The behaviour of *L. puber* in this situation is similar to that described for the portunids *C. maenas* and *C. sapidus*. These observations indicated that a male can successfully defend a female against a larger male. More observations are required to determine the relative success rates of single and paired males in agonistic interactions.

4.4.2 The effects of female odour on male aggressive behaviour

In several crab species (Bachau, 1986), female pheromone increases the locomotor activity of males, this response often being referred to as "searching behaviour" (Eales, 1974; Gleeson, 1980; Ryan, 1966). The behaviour of *L. puber* in the present study was consistent with these observations. Since agonistic behaviour virtually always occurs when males encounter each other in the laboratory, it seemed likely that the time between removing the partition and the start of agonistic behaviour would be shorter in the "female water" category. However there was found to be no relation between the type of water administered to the observation tank and the latency. The most probable explanation for this is that the removal of the partition caused a certain amount of disturbance to the crabs which caused locomotor activity to cease for a variable length of time. The response of crabs to the partition was probably related to their orientation and proximity to it.

The presence of female odour apparently had no effect on the pattern of initiation of agonistic interactions. As has been found for this species when closely size matched (chapter 2) and for the congener *L. depurator* (Glass and Huntingford, 1988), the smaller crab of a pair was as likely to initiate an interaction as the larger. However, the outcome of agonistic interactions was affected by the type of water administered to the observation tank. The reason for the increased success rate of smaller crabs when exposed to female-conditioned water is not known. The estimated probability of winning in this category, was 50% for either the larger or smaller crab

compared with the advantage that larger crabs usually have. Comparisons within categories indicated that interactions won by the smaller crab were not longer or more likely to involve injurious behaviour than those won by the larger. However, interactions between crabs exposed to female-conditioned water in which the smaller crab was dominant, were longer than equivalent interactions in the control categories; the same was not true for interactions won by the larger. It appears that the greater duration of interactions in the "female water" category was largely attributable to interactions which were won by the smaller crab. The duration of an interaction is presumably determined by the losing crab, which at some point "decides" to give up and retreat from its opponent. In this study larger losers did not persist longer on average than smaller losers. However, when exposed to female-conditioned water larger crabs were slower to submit to smaller opponents than when exposed to male-conditioned water or sea water. This is as predicted by game theory in view of the resource value of a receptive female. Conversely, despite a trend in the same direction, smaller crabs did not persist significantly longer before retreating when exposed to female-conditioned water. Few published data are available on contest durations in Crustacea, but Shuster and Caldwell (1989) found that in cavity defence by the stomatopod, *Gonodactylus bredini*, males paired with females did not fight longer than single males. However, paired males rarely lost interactions and it was not certain whether intruding (and therefore usually losing) males could detect the receptive female within.

Male-conditioned water was used in the design of this experiment to check whether responses to female-conditioned water were simply responses to the presence of a conspecific. The differences which were found between treatment categories were in the outcome of contests, in the relationship between initiation and outcome and in the duration and intensity of interactions. In all but the last-named, the "male water" category was not significantly different from the sea water control group but was different from the "female water" group. However, the incidence of potentially injurious behaviour was greater in the "male water" category than in the control group, but not significantly different from the "female water" category. It seems that the presence of a conspecific of either sex increased the likelihood of intense actions between males. This result does not support the suggestion of Dunham (1988) that crustacean sex pheromone serves to reduce male aggression. It is possible that *L. puber* are capable of chemosensory sex discrimination as distinct from simply being

able to detect receptive females. Such discrimination has been found in *Procambarus clarkii* (Ameyaw-Akumfi and Hazlett, 1975) and *Homarus americanus* (Atema and Engstrom, 1971; Atema and Cowan, 1986). Water conditioned by inter-moult conspecific males elicited agonistic behaviour in male *P. clarkii* (Ameyaw-Akumfi and Hazlett, 1975), but produced no detectable response in male *H. americanus* (Atema and Engstrom, 1971). Male *H. americanus*, however, did respond to water conditioned by recently moulted males with aggression and feeding behaviour (Atema and Cowan, 1986). In both these species, the responses to male odour were distinct from those to female odour. Consequently, it is not known whether the increase in agonistic intensity in response to male and female odour in this study is simply a response to conspecifics in general or whether there are different reasons for increased aggression in each case. Limitations on the number of crabs available in this study precluded more extensive controls such as addition of water conditioned by inter-moult females, pre-moult males and other species of crab. Further experimentation with such controls would clarify the possible existence of differential responses of males to conspecifics.

4.4.3 Costs of aggressive competition for females

The present data indicate that the costs incurred by *Liocarcinus puber* during agonistic interactions vary as a result of the crabs' perception of the contested resource. One of the most direct costs of agonistic behaviour is injury. Grasps and strikes with the chelae are potentially injurious as evinced by the five occurrences of injury observed during this study. Such injuries have obvious implications for future agonistic, feeding and predator avoidance capability. In addition, the growth rate of *L. puber* is reduced when regenerating limbs (Norman and Jones, in press). On this basis, contests in the presence of the odour of a receptive female were potentially more costly than those exposed to only sea water, but not different from those in the presence of male odour (assuming that strikes and grasps were delivered with the same force, on average, in each category).

The decrement to individual fitness represented by the interaction duration will be comprised of an energetic cost, a cost in terms of time spent away from fitness-promoting activities and possibly an increased predation risk, as agonistic displays are visually conspicuous. *L. puber* incur these costs to a greater degree in the presence of a stimulus associated with a receptive female than when such a stimulus

is not present.

4.4.4 Agonistic behaviour in natural populations

Field observations of competition for mates through agonistic behaviour are lacking for brachyurans and are required to determine the relevance of these laboratory observations to the natural habits of crabs. In a field study, Sekkelsten (1988) found that the reproductive success of male *Carcinus maenas* which were missing chelae was significantly lower than that of uninjured males. This was interpreted as being a consequence of reduced competitive ability through loss of appendages crucial to agonistic behaviour. A laboratory study of the stomatopod *Gonodactylus bredini* has shown that loss of appendages used in agonistic behaviour indeed results in competitive inferiority (Berzins and Caldwell, 1983).

There is evidence that agonistic behaviour is involved in competition for mates in at least some crustaceans and that there is a relationship between agonistic ability and reproductive success. The results of the present study indicate that the stimulus of a receptive female modifies the agonistic behaviour of male *L. puber*, suggesting a rôle for this behaviour in competition for mates. Preliminary laboratory observations have shown that males do compete for mates with agonistic behaviour. Quantification of the incidence of such competitive interactions in the field is required to elucidate the influence of agonistic ability on reproductive success and consequently the importance of such behaviour to population dynamics.

5. THE ENERGETIC COST OF AGONISTIC BEHAVIOUR IN *LIOCARCINUS PUBER*

5.1 INTRODUCTION

5.1.1 The costs of agonistic behaviour

The predictions of game theory models rest on the assumptions that the behaviour of an animal has detrimental and beneficial effects on its fitness and that behavioural phenotypes evolve through selection for those in which the net effect of these costs and benefits maximises the fitness of the animal (Maynard Smith, 1982). Interpretation of agonistic behaviour on this basis therefore requires an understanding of the nature of the costs and benefits incurred by competitors. It is often not possible to measure directly the changes in lifetime reproductive output due to particular behaviours, but the short term consequences of behaviour can be recorded and their probable effects on fitness estimated. For example, the risk of injury and exposure to predators are quantifiable consequences of behaviour and presumably have a directly detrimental influence on the reproductive output of an animal. Time spent engaged in various activities is also easily measured and may be related to fitness, particularly where the activity is mutually exclusive with feeding or mating. The energetic cost of behaviour may also have consequences for the fitness of the individual.

The energy expended on agonistic behaviour is not available for feeding or reproduction and therefore represents a decrement to fitness. In addition, depletion of energy reserves and accumulation of certain metabolites may limit the animal's subsequent activity. The duration and effectiveness of recovery is of vital consequence to the future performance of an animal. Incomplete recovery from anaerobic metabolism in crustaceans results in a reduced ability to engage in routine activities and in quicker onset of fatigue if "burst activity" such as escaping from a predator is necessary (Ellington, 1983).

The costs of agonistic behaviour in crustaceans have been analyzed in terms of the duration of contests and probability of injury (Dingle, 1983), but there is no information on the energetic cost of this activity. In this chapter, the energetic cost of the agonistic behaviour of *Liocarcinus puber* is investigated. There is a growing

body of data on the cost of locomotion in crustaceans which provides a useful reference for the study of the energetic cost of agonistic behaviour.

5.1.2 The energetic cost of exercise

Animals store energy in organic compounds. The energetic cost of an activity can therefore be considered as the resulting net reduction in these stores. Since aerobic animals normally derive energy by oxidation of these compounds, an indirect measure of energy utilisation which is frequently used is the excess oxygen consumption which is attributable to activity (Eckert *et al.*, 1988). The relationship between depletion of organic energy storage compounds and oxygen uptake depends on the substrate being catabolized and on the biochemical pathway by which it is converted into energy. For instance, the complete oxidation of 1 mole of glucose requires 6.0 moles of oxygen, but to derive the same energy from the oxidation of the fatty acid palmitate, approximately 6.3 moles of oxygen are required (McGilvery and Goldstein, 1983). Greater discrepancies may arise when the substrate is catabolized by different biochemical routes. In mammals, if glucose is catabolized anaerobically to lactate and this is subsequently regenerated *via* gluconeogenesis, 14.2 moles of oxygen must be consumed following the production of the same amount of energy as the complete oxidation of 1 mole of glucose, assuming that the ATP (adenosine triphosphate) required for gluconeogenesis is derived from the oxidation of a proportion of the lactate (McGilvery and Goldstein, 1983).

Estimation of the energy requirement of activity from oxygen consumption therefore requires knowledge (or assumptions) about the relative contributions of aerobic and anaerobic metabolism and their relative efficiencies of energy production. Difficulties in accounting for the relative energetic contribution of anaerobic metabolism led Crisp (1984) to advocate direct calorimetry for estimation of energy losses through respiration in the benthos. However, the use of calorimetry in the study of the energetics of activity requires an estimate of the thermodynamic efficiency of the energy metabolism involved (Gnaiger, 1983), or an independent estimate of the work done during the activity. The uncertainties involved in these estimates and the problems of rigorously controlling the activity of an animal inside a calorimeter seriously diminish the utility of the technique in this field.

Measurements of oxygen consumption are therefore still the most practical means of estimating energy expenditure during exercise (Schmidt-Nielsen, 1984).

Assessment of the contribution of anaerobic metabolism is necessary, however, and this requires knowledge about the capabilities of the system supplying oxygen to the respiring tissues and about the nature of the biochemical pathways involved in energy metabolism.

5.1.3 Respiratory and metabolic responses of crustaceans to exercise

The respiratory system of aquatic crustaceans is potentially limited in its ability to supply respiring tissues with oxygen due to the relative impermeability to gas exchange of the chitinous exoskeleton and the low oxygen capacity of the circulatory system (Taylor, 1982). The biochemical routes by which crustaceans derive cellular ATP appear similar to vertebrates in which these phenomena have been more extensively studied (Chang and O'Connor, 1983). In the last 10 - 15 years, stimulated by work on the exercise physiology of fish (reviewed by Beamish (1978)), there have been several studies of the responses to exercise of aquatic decapods (Phillips *et al.*, 1977; Burke, 1979; McDonald *et al.*, 1979; McMahon *et al.*, 1979; Booth *et al.*, 1982; England and Baldwin, 1983; Onnen and Zebe, 1983; Gäde, 1984; Houlihan *et al.*, 1984; Houlihan *et al.*, 1985) and their terrestrial or semi-terrestrial counterparts (Herreid *et al.*, 1979; Wood and Randall, 1981; Herreid *et al.*, 1983; Full and Herreid, 1983,1984; Herreid and Full, 1986; Greenaway *et al.*, 1988; Morris and Greenaway, 1989). The exercise regimes in these studies have differed widely. In most studies of aquatic species, locomotion has been induced by prodding the animals, either for a specified period of time or until exhaustion, which is usually defined as a state of unresponsiveness to tactile stimuli or loss of a righting response. *Callinectes sapidus* were induced to swim for up to an hour by suspending them above the substratum (Booth *et al.*, 1982). In studies of terrestrial and semi-terrestrial species it has been possible to control the intensity of exercise more rigorously by training the animals to walk on a treadmill (Herreid and Full, 1988).

Not surprisingly, the different species, experimental conditions and exercise regimes employed in these studies have produced a diversity of respiratory responses. These range from a predominantly aerobic response to sustained exercise (*Ocypode gaudichaudii*, Full and Herreid, 1983; *Coenobita compressus*, Herreid and Full, 1986) to the primarily anaerobic response to escape behaviour in macrurous decapods (*Cherax destructor*, Phillips *et al.*, 1977; England and Baldwin, 1983; *Crangon*,

Onnen and Zebe, 1983; *Homarus gammarus*, Phillips *et al.*, 1977; *Orconectes limosus*, Gäde, 1984). The aerobic response is characterized by a rapid rise in the rate of oxygen consumption at the onset of exercise to a steady state (short $t_{1/2\ on\text{-}response}$ - the time taken for the respiratory rate to increase to half of the steady state value - small oxygen deficit) which is maintained throughout the exercise bout and which may be several times the resting rate. On cessation of exercise there is a rapid return of the rate of oxygen consumption to resting values (short $t_{1/2\ off\text{-}response}$ - the time taken for the respiratory rate to decline to half of the steady state value - small oxygen debt) and presumably little lactate accumulation (lactate concentration was not measured in the studies of the two species exhibiting this response).

The prolonged recovery period in most crustaceans involves recharging of the oxygen, ATP and phosphagen (phosphorylated precursors of ATP) stores - which is a relatively rapid process - followed by slow removal of lactate (Ellington, 1983). The fate of lactate is not known, although gluconeogenesis has been demonstrated in some species (Phillips *et al.*, 1977; Gäde *et al.*, 1986; van Aardt, 1988; Hill, 1989). Bridges and Brand (1980) found no evidence of lactate excretion in 6 species of decapod and no excretion was detected from the xiphosuran, *Limulus polyphemus*, the brachyuran, *Menippe mercenaria* (Gäde *et al.*, 1986) nor from the River Crab, *Potamonautes warreni* (van Aardt, 1988). In contrast, de Zwann and Skjoldl (1979) reported that the isopod *Cirolana borealis* excreted 27 - 52% of the lactate produced during environmental anoxia. Comparison of the time courses of lactate removal and oxygen consumption recovery in the brachyuran, *Uca pugilator,* led Full and Herreid (1984) to conclude that gluconeogenesis was probably the major metabolic route for removal of lactate after exercise in this species. The fate of lactate may vary according to the physiological condition of the animal, as Gäde *et al.* (1986) found that the proportion of radio-labelled D-lactate oxidised by *Limulus polyphemus* was highly dependent on the activity of the animal.

The migratory portunid, *Callinectes sapidus*, is the only aquatic decapod studied so far which has been capable of sustained exercise in the laboratory (Booth *et al.*, 1982; Booth *et al.*, 1984; Houlihan *et al.*, 1985). This species also attained a stable rate of oxygen consumption with a relatively short $t_{1/2\ on\text{-}response}$ ($\approx$ 30 s). The factorial aerobic scope for activity (maximum oxygen consumption/resting oxygen consumption) was estimated by Booth *et al.* (1982) as 2.6 in animals of 90 - 190 g. Although the animals in this study were not swimming at their maximum speed, they

were perhaps near their maximum sustainable performance - "occasional tactile stimulation was usually necessary to maintain a full hour of swimming activity" (Booth *et al.*, 1982). Houlihan *et al.* (1985) found that factorial aerobic scope for activity was negatively related to crab size and declined from 6.3 - 3.6 in animals of 10 - 70 g. Extrapolation of their regressions to a crab with a mass of 140 g gives an estimated factorial aerobic scope of 2.7, agreeing closely with the data of Booth *et al.* (1982). Despite these aerobic characteristics, anaerobic metabolism played a significant rôle in energy production during exercise, as there was a 14 fold increase in haemolymph lactate concentration (Booth *et al*, 1982). Booth *et al.* (1982) reported that the rate of oxygen consumption was still elevated 30 minutes after exercise and that return to a quiescent state took several hours. Subsequent analysis of the recovery period indicated that lactate levels returned to pre-exercise levels after about 9 - 10 hours (Booth *et al.*, 1984).

Carcinus maenas did not reach a steady state of oxygen consumption before fatiguing, but did show a relatively quick recovery from exercise (8 - 25 minutes) (Houlihan *et al.*, 1984). The factorial aerobic scope for activity for this species (8 - 21 for 16 - 102 g animals) was also negatively related to crab size and anaerobic metabolism made a greater contribution to the energy produced during exercise in larger animals. Lactate returned to resting levels within 5 - 10 minutes.

In contrast, most other decapods studied so far have a limited aerobic capacity and are only able to raise their rate of oxygen consumption to 3 - 5 times the resting rate (McMahon, 1981). A steady state of oxygen consumption is never reached even during mild exercise and fatigue times are short. These species rely on stored oxygen and phosphagens and on anaerobic metabolism, accumulating large quantities of lactate during short periods of activity. Recovery from exercise in these species is characterized by a period of elevated oxygen consumption which is long in comparison with the exercise bout. Lactate concentrations may also take many hours to decline. This response to exercise has been recorded from *Cancer magister*, (McDonald *et al.*, 1979; McMahon *et al.*, 1979); *Cardisoma carnifex*, (Wood and Randall, 1981); *Cardisoma guanhumi*, (Herreid *et al.*, 1979); *Gecarcinus lateralis*, (Herreid *et al.*, 1983); and *Uca pugilator*, (Full and Herreid, 1984).

The figures for aerobic scope for activity must be interpreted with caution as the "resting" or "routine" rate used as the divisor in the calculation of this index is sensitive to the experimental procedures involved. For instance, Booth *et al.* (1982)

noted that after 2 - 3 days acclimation to the experimental situation, *Callinectes sapidus* still exhibited a ventilatory pattern characteristic of disturbed animals (bilateral scaphognathite beating). This disturbance was attributed to restraint of the animal, manipulations during measurements and to the mask used to separate inhalant and exhalant water currents. Houlihan *et al.* (1984) reported significantly lower "resting" rates for *C. maenas* which had been undisturbed for 12 h compared with those which had been handled 1 h previously. The factorial aerobic scopes for the two groups were 8 - 21 and 4 - 7 respectively. Houlihan *et al.* (1985) reported similar findings for *C. sapidus*. Increased respiratory rates in "resting" animals due to experimental disturbance result in lower estimates of the aerobic scope for activity.

The physiological mechanisms limiting exercise performance in crustaceans are not known (Full and Herreid, 1984), but in their study of the tail-flipping escape response of the shrimp *Crangon*, Onnen and Zebe (1983) found that fatigue coincided with depletion of phospho-arginine (an energy storage compound) in the tail muscle. In a similar study of the Australian Yabby, *Cherax destructor*, England and Baldwin (1983) reported that after an initial bout of rapid tail flipping which significantly reduced the level of phospho-arginine, there was a series of slower, less powerful flips that were apparently fueled by anaerobic glycolysis. Fatigue set in after failure to buffer pH changes in the muscle due to lactic acid production.

5.1.4 The energetic cost of activity in crustaceans

The energetic cost of activity has been evaluated in only a few species of decapods (Herreid and Full, 1988). Most data have been obtained from locomotion of terrestrial crabs. Due to the difficulty of rigorously controlling the exercise regime of aquatic species, the energetics of locomotion has been studied in only a few species of marine crab (Houlihan *et al.*, 1984; Houlihan *et al.*, 1985). Studies on the cost of locomotion began with mammals, which quickly attain a steady state of oxygen consumption during sustained exercise (Eckert *et al.*, 1988). For comparative purposes the cost of locomotion has been defined as the quantity of oxygen consumed in transporting a unit mass of animal over a unit distance. This is determined from the slope of a regression of steady-state mass-specific oxygen consumption against velocity of locomotion. In cases where this function is not linear, the minimum cost of transport is estimated by the slope of a tangent to the function that intersects the origin (Schmidt-Nielsen, 1984).

In only three of the crab species whose energetics have been studied was a steady state of oxygen consumption attained (*Ocypode gaudichaudii*, Full and Herreid, 1983; *Callinectes sapidus*, Houlihan *et al.*, 1985 and *Coenobita compressus*, Herreid and Full, 1986). In those in which sustained activity and steady state oxygen consumption was not achieved, the energy requirement of locomotion would be underestimated by the oxygen consumption due to significant contributions from anaerobic metabolism and from stored oxygen and phosphagens. As discussed earlier, attainment of a steady state of oxygen consumption over 1 hour in *C. sapidus* did not rule out significant anaerobic energy production. These contributions must be accounted for in assessments of energetic expenditure. The first attempt to estimate the energetic cost of locomotion in a crustacean that did not attain a steady state of oxygen consumption was based on the assumption that the excess post-exercise oxygen consumption was due to replenishment of oxygen and phosphagen stores and regeneration of lactate. Herreid *et al.* (1979) integrated the oxygen consumption curve of *Cardisoma guanhumi* during exercise and recovery to give the total quantity of oxygen consumed during this period and subtracted the resting oxygen consumption to give that quantity attributable to the exercise bout. Herreid *et al.* (1983) termed this estimate the "cumulative net oxygen consumption" and found that it increased linearly with velocity in *Gecarcinus lateralis*. Theoretical justification of this approach requires knowledge about the causes of excess post-exercise oxygen consumption. Although this knowledge is lacking, there is empirical support for this approach from data on recovery from exercise in *Uca pugilator* (Full and Herreid, 1984). In that study, estimates of the energetic contributions from aerobic and anaerobic metabolism were made from stoichiometric relationships between ATP production and oxygen consumption and whole body lactate production respectively. The rate of energy production increased throughout the exercise period. Since there was no reason to suspect an increasing work rate during exercise, it was concluded that oxygen and/or phosphagen stores made a significant contribution early in the exercise period. The final rate of ATP production was taken as the "best estimate of the energy demand of the exercise". The energetic requirement for exercise was estimated in three ways: the best estimate of the energy demand as described above; the estimate of the total ATP produced during exercise and the cumulative net oxygen consumption. These three estimates were in close agreement. A similar approach was adopted by Houlihan *et al.* (1984) with *Carcinus maenas*, but their data did not

permit detailed interpretation of the recovery period.

5.1.5 The energetics of agonistic behaviour in *Liocarcinus puber*

Measurements of oxygen uptake by aquatic crustaceans have previously been made by placing them in respirometers of open, closed or intermittently closed design (McMahon and Wilkens, 1983). Another method involves fitting a mask over the exhalant apertures to allow estimation of the ventilatory flow rate while the oxygen tension of inspired and expired water is monitored (McMahon *et al.*, 1974; Taylor, 1976; Butler *et al.*, 1978; McMahon *et al.*, 1979; Booth *et al.*, 1982; Wilkens *et al.*, 1984). None of these methods would allow the oxygen uptake of two crabs to be measured simultaneously and separately while engaged in agonistic behaviour without severely restricting their movements or impairing their senses.

The heart and scaphognathite beat rates are relatively easily measured in unrestrained crabs (Depledge, 1978). The scaphognathites are flattened exopodites of the second maxillae which generate a ventilatory current by a complex dorso-ventral undulation (Young, 1975). In several species a linear relationship has been demonstrated between the average scaphognathite rate (above a certain critical beat frequency) and the ventilatory flow rate (*Callinectes sapidus*, Booth *et al.*, 1982; *Cancer magister*, McMahon *et al.*, 1979; *Carcinus maenas*, Cumberlidge and Uglow, 1977; Wilkens *et al.*, 1984; *Orconectes virilis*, McMahon and Wilkens, 1983). These relationships indicate that the scaphognathites act as fixed stroke volume pumps in some species (Cumberlidge and Uglow, 1977; McMahon *et al.*, 1979; Mercier and Wilkens, 1984), but in others the stroke volume decreases with scaphognathite rate (Booth *et al.*, 1982) or varies from beat to beat (Wilkens, 1981; Wilkens *et al.*, 1984). Some of the differences between these studies may be due to the temporal resolution of the method of estimating ventilatory flow rate. Mercier and Wilkens (1984) collected measured volumes of expired water from *C. maenas* over 5 - 20 seconds and deduced that the stroke volume did not change significantly over a wide range of scaphognathite beat frequencies. In another of the same series of papers, Wilkens *et al.* (1984) presented data obtained with an electromagnetic flow probe which indicated a linear relationship between ventilatory flow rate and scaphognathite rate; however there was much scatter around the regression line which they interpreted as variation in stroke volume. The method used by Mercier and Wilkens may have averaged out such variation. Variations over a small time scale were also

demonstrated by instantaneous measurements of stroke volume in *Procambarus clarkii* (Wilkens, 1981).

Variation in stroke volume at low beat frequencies may be due to reflux of water past the scaphognathite and at higher frequencies to movements of appendages which alter the resistance to flow into and out of the branchial chambers - such as the epipodite of the first maxilla, which form the floor of the exhalant canal and the third maxilla, which varies the size of the inhalant openings (Wilkens, 1981). When average values are considered, however, it seems that the ventilatory flow rate may be predicted from the scaphognathite rate (Cumberlidge and Uglow, 1977; Booth *et al.*, 1982).

The relationship between ventilatory flow rate and oxygen consumption is determined by the efficiency of extraction of oxygen from the water (= percentage utilisation). Although the extraction efficiency is negatively correlated with the ventilatory flow rate in response to environmental hypoxia in some species (McMahon *et al.*, 1974; Batterton and Cameron, 1978; Butler *et al.*, 1978), changes in extraction efficiency during exercise in aquatic crabs are usually slight (McMahon, 1981). In the studies of aquatic crabs where ventilatory flow rate and oxygen consumption have been monitored during exercise and subsequent recovery, extraction efficiency has been shown not to change significantly with ventilatory flow rate (*Callinectes sapidus*, Booth *et al.*, 1982; *Cancer magister*, McMahon *et al.*, 1979). The oxygen uptake by these animals was therefore directly related to the ventilation volume and the scaphognathite rate.

Variation in cardiac output in crustaceans is mainly achieved by variation in stroke volume of the heart, heart rate alone being a less reliable predictor of cardiac output (McMahon and Wilkens, 1983). Therefore, although cardiac output increases with the rate of oxygen consumption, there may not be a linear relationship between heart rate and oxygen consumption.

In this chapter, the relationships between oxygen uptake and heart and scaphognathite rates were investigated during recovery from exhaustive exercise in *Liocarcinus puber*. A linear relationship was found between the scaphognathite rate and oxygen uptake. The respiratory behaviour of *L. puber* was then studied during agonistic interactions and subsequent recovery to estimate the relative energetic costs of winners and losers and of crabs engaged in interactions of differing intensity and duration. The response to exhaustive swimming activity also provides a reference for

the respiratory demand of agonistic behaviour.

5.2 MATERIALS AND METHODS

5.2.1 Experimental animals

Crabs were collected by SCUBA divers throughout the year from shallow, rocky, sublittoral areas in the Firth of Clyde. All crabs were maintained in a recirculating seawater aquarium (10-12°C, 30-32°/$_{oo}$) and were fed two or three times per week on whitebait, but were deprived of food for 24 h before respiratory measurements were made.

5.2.2 Measurement of oxygen consumption

The oxygen consumption of crabs at rest and during recovery from exhaustive exercise was estimated using a respirometer of intermittently-closed design. The respirometer was constructed from 6 mm thick acrylic and was cylindrical with a flat base and lid. The capacity of the respirometer was 1600 ml. The lid was held in place by four stainless steel wing nuts and sealed with a nitrile rubber O-ring. A 20 watt electric pump (1018, Gunther Eheim, Deizisau, West Germany) was used to circulate water through the respirometer from a reservoir of aerated seawater. The total volume of water in the system was approximately 10 l. The inlet and outlet pipes of the respirometer were made of acrylic tube (bore = 5 mm) and were sealed into the lid. The inlet pipe extended to within a few millimetres of the floor of the chamber to ensure efficient mixing. Water was conducted between the reservoir, pump and respirometer by polythene tubing (bore = 9.5 mm). Non-return valves (235/0355/00, BDH Ltd, Dagenham, Essex) were arranged at the inlet and outlet pipes so that when circulation ceased, they would be closed by water attempting to siphon back through the system, thereby sealing the enclosed volume of water in the respirometer. The valves also prevented water draining from the tubing, thus maintaining the prime of the pump.

Water from the reservoir was circulated through the chamber at regular intervals. The pump was operated by a time-switch (Sangamo Controls, Port Glasgow) usually programmed to switch the pump off for 15 or 30 minutes, followed by 15 minutes of circulation. These time intervals were chosen to ensure that the oxygen tension in the chamber did not fall below 120 Torr during closed periods. The 15 minute flushing period was sufficient to return the oxygen tension of water in the chamber

to initial levels.

The respirometer and the reservoir were placed in a water bath which maintained them at a temperature of 10.0 ± 0.1°C. The experimental medium was made to a salinity of 32°/$_{oo}$ with artificial sea salts (Tropic Marin, Tropical Marine Centre, Borehamwood, Herts.) and deionised water.

During closed periods, the fall in oxygen tension in the chamber was used to calculate the oxygen consumption of the animal. The oxygen tension was measured with an oxygen electrode (E5046, Radiometer, Copenhagen) connected to an oxygen meter (Model 781, Strathkelvin Instruments, Glasgow). The output from the meter was recorded with a pen recorder (BBC-Goertz Metrawatt). The oxygen meter was calibrated to 100% oxygen saturation with aerated seawater and to 0% with a solution of 0.01M sodium tetraborate with sodium sulphite. During early trials with this system, the jacket of the oxygen electrode was sealed through a rubber bung which was a tight fit in a port in the respirometer lid, but occasionally the electrode was short-circuited by salt water leaking past the bung. This problem was overcome by sealing the electrode jacket in an acrylic housing which screwed into the lid with an O-ring seal. Stratification of the water in the respirometer was prevented by a magnetic follower driven by a submersible magnetic stirring motor which kept the enclosed water in motion. The magnetic follower was enclosed in a perforated acrylic housing to prevent the crab interfering with its action.

Before each run, the respirometer, pump and tubing were disinfected with dilute hypochlorite solution. However, as micro-organisms are introduced with the animal (Sutcliffe *et al.*, 1975) and these consume oxygen, it was necessary to determine the rate of oxygen consumption of these micro-organisms in order to estimate the actual rate of oxygen consumption of the crabs. Measurements of the 'background' oxygen consumption within the respirometer were made over periods of 3-4 h before and after recordings of a crab's rate of oxygen consumption. The average of these two readings was used to correct the oxygen consumption estimates for each crab.

The rate of oxygen consumption (background or experimental) was calculated from the following formula.

$$\mathbf{Mo_2 = (P^io_2 - P^fo_2) \,.\, \propto wo_2 \,.\, V \,.\, T^{-1}}$$

where Mo_2 = oxygen uptake rate (μmol $O_2.min^{-1}$)

P^io_2 = initial partial pressure of oxygen in the chamber (Torr)

$P^f o_2$ = final partial pressure of oxygen in the chamber

$\propto wo_2$ = solubility coefficient for oxygen in sea water of 10°C, $32°/_{oo}$ *

V = volume of water in the chamber (l)

T = time over which the Po_2 change was monitored (min).

* $\propto wo_2$ was derived from the Bunsen Coefficient evaluated from the formula given by Weiss (1970). This gives a figure in l $O_2.l^{-1}.(760\ Torr)^{-1}$ which was converted to $\mu mol.l^{-1}.Torr^{-1}$ by the factor $10^6.(760)^{-1}.(22.393)^{-1}$ (1 µl $O_2 \equiv 22.393^{-1}$ µmol O_2, Radford (1964)).

Po_2 was estimated from the formula:

$$\mathbf{Po_2 = (BP - VP) \,.\, 0.20946}$$

where BP = Barometric pressure (mm Hg)

VP = Vapour pressure over water at 10°C (Hale, 1965)

0.20946 = The proportion of O_2 in dry atmospheric air (Hale, 1965)

The volume of water in the respirometer was determined by subtracting the volume of the crab from the capacity of the respirometer (1.6 l). The volumes of crabs were estimated by comparing their mass in air with that in water to determine the mass of water displaced. A known volume of water was weighed for each measurement to determine the density and therefore volume of water displaced by the crab. Crab volumes ranged from 2.9 - 6.8% of the capacity of the respirometer chamber.

All estimates of oxygen consumption are presented as mass specific rates (Mo_2) in $\mu mol\ O_2.min^{-1}.g^{-1}$.

5.2.3 Measurement of heart and scaphognathite rates

The heart and scaphognathite rates were measured using an impedance technique (Hogarth and Trueman, 1967; Ansell, 1973). Two small holes were drilled in each branchiostegite over the prebranchial chambers using a dental drill. Final penetration of the branchiostegite was achieved using a hypodermic needle. Electrodes were

prepared by removing the insulation from the last 2-3 mm of fine copper wire (gauge = 0.5 mm) and bending this section through 90°. Two electrodes were prepared for each scaphognathite. The bared ends of these wires were inserted into the holes and the wires were attached to the crab with cyanoacrylate adhesive, the setting of which was accelerated with dental cement hardener. The wires were attached near the drilled holes and were then led dorsally over the anterior margin of the crab and fixed to the carapace. Each pair of wires was connected to an impedance coupler (Strathkelvin Instruments), the output of which was displayed on an oscillograph (400 MD/2, George Washington Ltd., Sheerness). The heart rate was recorded using a similar technique, with electrodes inserted into holes drilled in the carapace dorsal to the pericardium. The electrical output from the oscillographs was connected via a voltage-reducing circuit to the analogue-to-digital converter of a BBC-B microcomputer (Acorn Computer Systems Ltd., Cambridge). The microcomputer was programmed to count the beats of the heart and scaphognathites during 30 s in each minute and these counts were recorded on magnetic disc. The microcomputer also provided a continuous display of the scaphognathite rate during measurements. The counts were later converted to rates (beats min^{-1}) and averaged over the periods of determination of oxygen consumption. All scaphognathite rates are expressed as the sum of the beat rates of both scaphognathites.

After electrode implantation, the crab was placed in the respirometer and the electrode wires were sealed through a rubber bung which was located in a port in the lid. The crab was allowed 24 h to acclimate to the experimental situation, during which time aerated sea water was periodically circulated from the reservoir through the respirometer. Simultaneous measurements of oxygen consumption, heart and scaphognathite rates were made.

5.2.4 Respiratory measurements from exercised crabs

After 24 h the crab was gently removed from the respirometer to a 10 l plastic tank containing aerated artificial seawater (10°C, 32‰). Suspending the crab in the water above the bottom of the tank resulted in it beating the swimming legs (5th pereiopods). When the crab stopped swimming it was tapped on the carapace with forceps to induce it to resume swimming. When the crab failed to respond to three such stimuli it was replaced in the respirometer and its oxygen consumption, heart and scaphognathite rates were monitored for a further 24 h. Replacing the crab in the

respirometer took c.5 minutes. It was therefore not possible to estimate oxygen consumption over the first few minutes of recovery from exercise. Results have been obtained from 10 individuals.

5.2.5 Measurement of scaphognathite rates during agonistic behaviour

Pairs of size-matched crabs were prepared for scaphognathite rate measurements as previously described. Following electrode implantation, they were transferred to individual holding tanks to recover for at least 24 h.

Observations of agonistic behaviour were made by placing the crabs in a 104 l glass tank with an arena of 64 x 42 cm and a substrate of 2 cm of gravel. They were allowed to settle for 16 h, while they were separated by a removable, opaque, vertical partition. The electrode wires were suspended from corks floating at the surface to minimise interference by the crabs. Counts of the scaphognathite beats were made with the micro-computer as before.

After the settling period, the partition was removed and agonistic behaviour was recorded. The partition was actuated by an electric motor and could be raised and lowered without the observer being detected by the crabs. The partition was elevated to 45 cm above the substratum, which took c.30 s. When one crab continually retreated in response to the other, they were again separated by the partition. The scaphognathite rates of the crabs were monitored for a further 24 h. The scaphognathite rates of the participants in 16 agonistic interactions have been monitored in this way. Due to equipment failure, for one of these pairs, scaphognathite recording was not possible during agonistic behaviour.

5.2.6 Haemolymph L-lactate estimation

The intensity of anaerobic metabolism during agonistic behaviour was investigated by assaying the concentration of haemolymph L-lactate at intervals after aggressive interactions. Crabs were maintained in similar conditions as before and interactions were conducted in the observation tank as previously described. Pairs of size-matched crabs were allowed a settling period of 4 h after transfer from their holding tanks before the partition separating them was raised and agonistic behaviour was recorded. After one crab consistently retreated from the other, they were again separated by the partition. Haemolymph samples were drawn with a hypodermic syringe by piercing the arthrodial membrane at the base of the right 4th pereiopod. Approximately 300 µl of haemolymph was withdrawn from the crab and placed in

an Eppendorf vial with an equal volume of Perchloric acid (0.6 M) and the sample was mixed thoroughly. After centrifuging at 10,000*g* for 10 minutes the solution was neutralised with a known volume of potassium carbonate (6 M). The mixture was again centrifuged at 10,000*g* and the supernatant withdrawn and stored at a temperature of -20°C until analyzed. The L-lactate concentration was assayed by the method of Gutmann and Wahlefield (1974) with the modification suggested by Engel and Jones (1978).

Haemolymph samples were taken at intervals of 0, 0.5, 1, 2, 4 and 12 hours after agonistic behaviour. The number of interactions sampled at each of these times was 5, 4, 4, 4, 5 and 4, respectively. No more than one haemolymph sample was taken from each crab. A control series of samples was taken by placing pairs of crabs in the observation tank for the same settling period and then raising and immediately lowering the partition. Haemolymph samples were taken from the control crabs at the same time intervals. Sample sizes were 4, 4, 3, 5, 4 and 4 pairs of crabs at each of the sampling intervals. In addition, the haemolymph lactate concentration was determined in 10 crabs after the settling period, but before removal of the partition.

5.3 RESULTS

5.3.1 Respiratory rates in undisturbed crabs

Simultaneous oxygen consumption (Mo_2), heart rate (F_h) and scaphognathite rate (F_{scs}) data were obtained from 10 individual crabs. The "resting" rates of these respiratory variables were estimated from measurements made over a period of 18 h when the crabs were not disturbed. These undisturbed rates were very variable (Table 5.1). It may be significant that the greatest variability was found in data from the smallest crab, which had most room to move around in the respirometer chamber. This variability is probably largely due to spontaneous activity by the crab. These rates will subsequently be referred to as "undisturbed rates".

The predominant mode of ventilation involved beating of only one scaphognathite (unilateral ventilation), with periodic cessation of all scaphognathite activity (spontaneous pausing) with simultaneous cardiac arrest. Periods of bilateral scaphognathite activity did occur, as did changes from use of one scaphognathite to the other during unilateral ventilation. This pattern of respiratory activity is characteristic of undisturbed crabs (McMahon and Wilkens, 1983).

5.3.2 Respiratory rates in exercised crabs

Male *Liocarcinus puber* fatigued quickly when made to swim by suspending them in the water. They became unresponsive to tactile stimulation after 3 - 8 minutes of exercise. The first measurements of oxygen consumption made after exercise were the highest in each case and ranged from 2.45 - 4.03 times the mean undisturbed rate (Table 5.2). Since these measurements were made c.5 minutes after the end of exercise (see section 5.2.4), they may not represent the maximum rates for these crabs under these conditions.

After exercise, the Mo_2 normally followed a logarithmic decline to undisturbed levels (Figure 5.1 a-d - four individual crabs chosen to illustrate the range of responses to exercise), although deviation from undisturbed rates after recovery obscured this pattern in a few cases. The Mo_2 of all crabs had recovered or was only slightly above resting rates within 8 h of the end of the exercise period. In order to compare the rates of recovery of individual crabs, the Mo_2 data for 0 - 8 h after

Table 5.1 Respiratory parameters for undisturbed *Liocarcinus puber* - data from ten males.

Crab mass (g)	Undisturbed oxygen cons. ± 95% c.l. ($\mu mol.min^{-1}.g^{-1} \times 10^{-2}$)	Undisturbed heart rate ($beats.min^{-1}$)	Undisturbed scaphognathite rate ($beats.min^{-1}$)
54	2.26 ± 0.238	40.4 ± 19.68	32.6 ± 48.12
83	1.20 ± 0.104	35.3 ± 15.48	64.1 ± 35.04
88	1.91 ± 0.104	44.6 ± 9.58	57.9 ± 28.69
93	1.78 ± 0.117	44.6 ± 17.76	84.8 ± 61.94
95	1.98 ± 0.040	45.7 ± 7.74	32.0 ± 16.33
97	1.41 ± 0.080	50.0 ± 13.17	76.0 ± 62.13
100	1.65 ± 0.096	42.9 ± 11.88	43.3 ± 20.36
105	1.59 ± 0.107	56.5 ± 11.64	50.6 ± 37.61
108	1.57 ± 0.090	28.2 ± 7.33	44.7 ± 29.29
127	1.53 ± 0.033	62.5 ± 9.07	74.3 ± 42.04

Table 5.2 Respiratory parameters for exercised Liocarcinus puber - data from ten males.

Mass (g)	Exercise period (mins)	Maximum[1] oxygen consumption (x rest)[2]	Maximum heart rate (x rest)	Maximum Scaphognathite rate (x rest)	Recovery time[3] (h)
54	3	3.69	2.04	11.02	6.47
83	8	2.45	1.45	2.77	6.55
88	3	3.10	1.87	5.30	4.60
93	3	2.64	1.52	3.96	2.40
95	3	2.65	1.70	4.58	10.23
97	6	3.08	1.51	4.16	11.16
100	5	2.64	1.46	2.82	4.40
105	3	3.08	1.48	5.59	13.89
108	3	4.03	2.54	5.53	5.44
127	3	3.37	1.16	2.85	5.86

1. Crabs were forced to exercise until they failed to respond to a tactile stimulus. Approximately 5 minutes elapsed between the end of exercise and the recommencement of recording. "Maximum" values recorded here therefore do not necessarily represent the maximum values achieved by crabs soon after exercise.

2. Maximum oxygen consumption and maximum heart and scaphognathite rates are expressed as multiples of the mean undisturbed rates.

3. Recovery time was estimated from a regression of oxygen consumption against time for the first 8 hours after exercise (see text).

Figure 5.1 The rate of oxygen consumption of *Liocarcinus puber* before and after exercise - exercise finished at time 0. Data from four males.

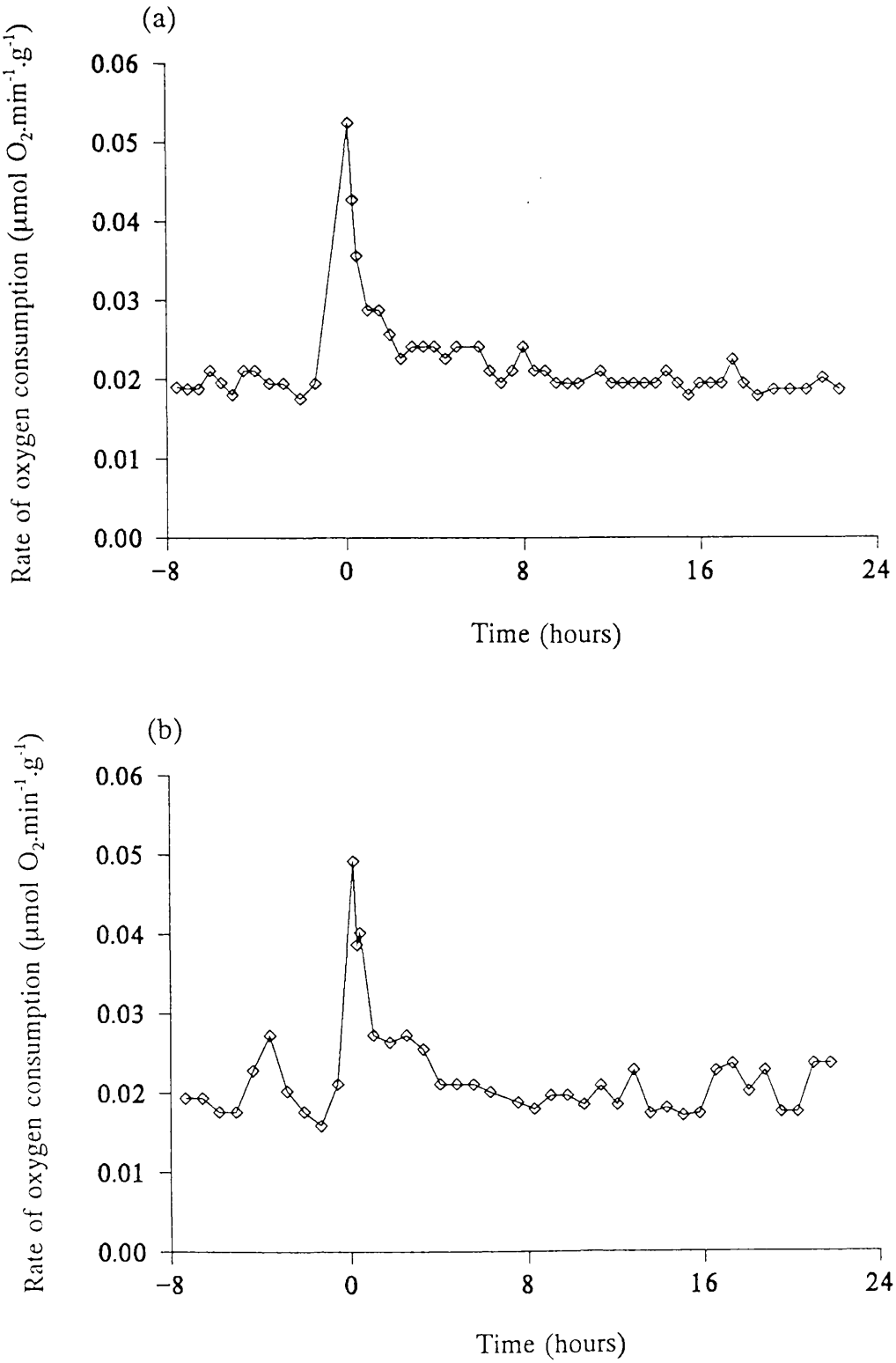
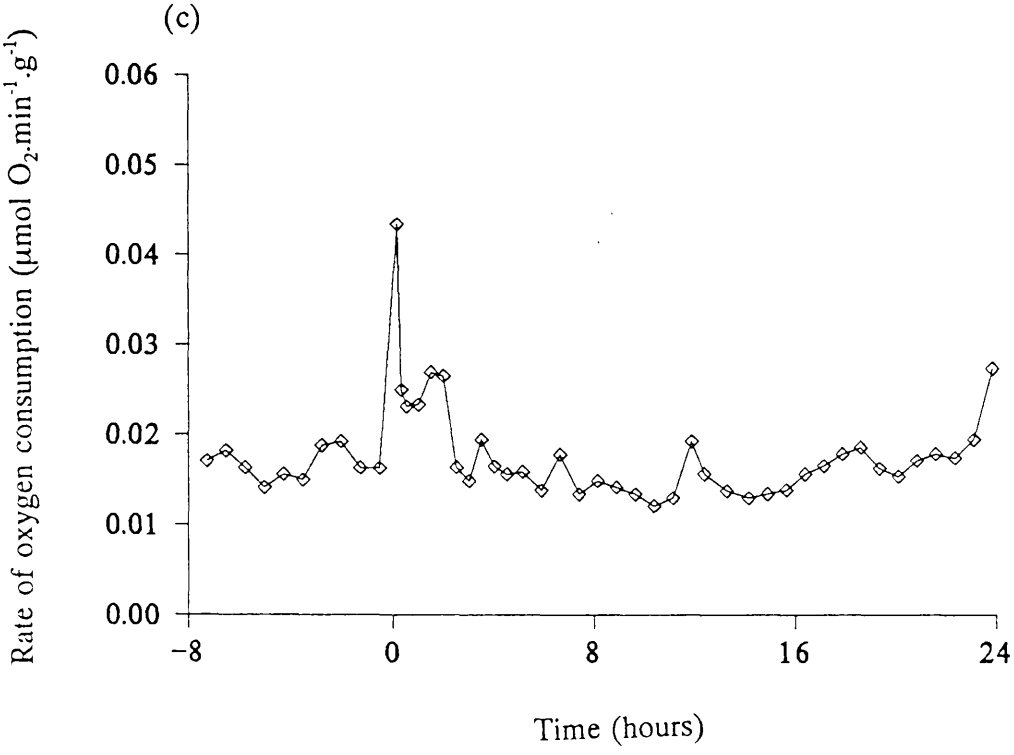
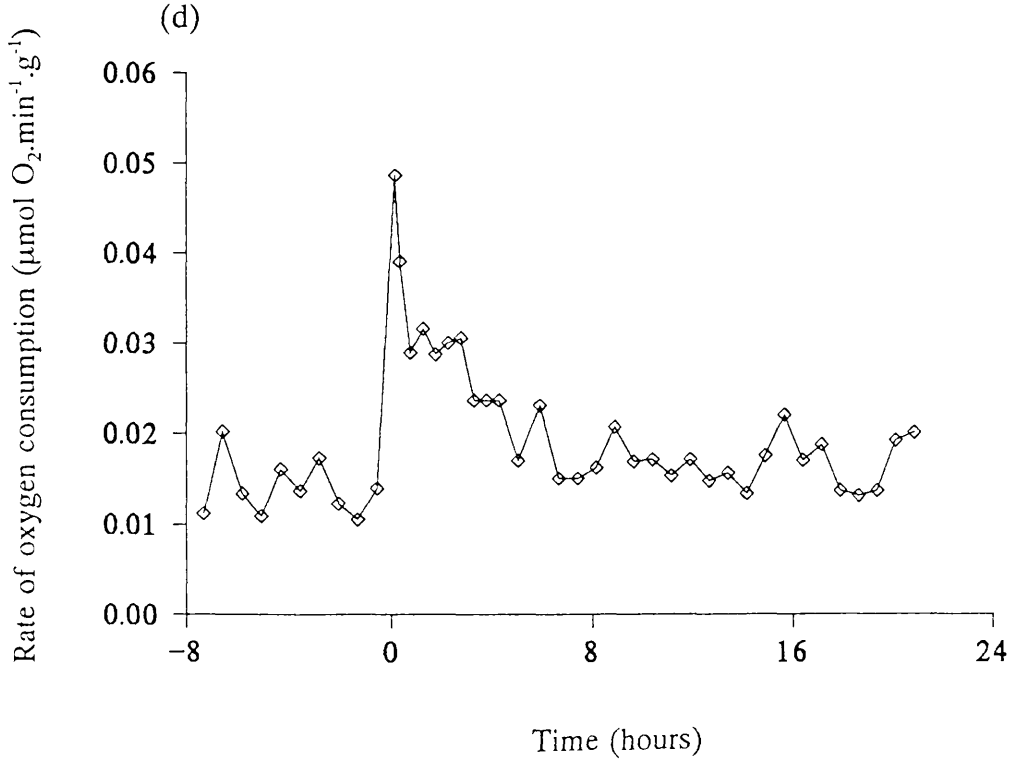


Figure 5.1 Continued





exercise were converted to multiples of the resting rate (Mo_2x) and these values were plotted against time after exercise, after logarithmic transformation (base 10) of both variables (Figure 5.2 a-d - same four crabs as in Figure 5.1). Highly significant linear relationships were found between these variables with Least Squares Regression (Table 5.3) and these were used to estimate the time at which Log Mo_2x = 0, i.e. when Mo_2x = 1, the resting rate of Mo_2. Estimated recovery times are given in Table 5.3. Analysis of Covariance (ANCOVA, Snedecor and Cochran, 1967) indicated that the regression coefficients of these regression equations for individual crabs were not significantly different ($F_{(9,125)}$ = 1.318, P>0.05), but that there were significant differences among the elevations ($F_{(9,134)}$ = 9.745, P<0.01). It is this variation in the elevations which largely accounts for variation in the estimates of recovery time (2.40 - 13.89 h). The elevations of these regression equations (a) are the estimates of Log Mo_2x when Log Time = 0 i.e. 1 h after exercise. Since the slopes did not vary significantly, estimates of the recovery time were highly correlated with Mo_2x at 1 h after exercise (10^a) (r = 0.916, P<0.01, df = 8), but recovery time was not correlated with the maximum Mo_2 recorded (r = 0.013, P>0.05, df = 8). Additionally, estimates of recovery time were not correlated with crab mass (r = 0.097, P>0.05, df=8), nor with the length of the exercise period (r = 0.074, P>0.05, df = 8).

Estimates of the excess post-exercise oxygen consumption (Herreid, 1980) were derived for each crab by integrating the derived functions describing Mo_2x recovery between 0 h and the estimated time to recover, and subtracting the product of the recovery time and the mean undisturbed Mo_2x (Table 5.3).

Figures 5.3 and 5.4 illustrate the time-course of the heart and scaphognathite rates respectively for the same four crabs as above. The heart rate did not increase by as great a factor as Mo_2 (1.16 - 2.54 times undisturbed rates) and took longer to return to resting levels. The change in scaphognathite rate, however, followed the time-course of Mo_2 closely. In all but one case, the maximum F_{scs} was higher than the undisturbed rate by a factor greater than that for Mo_2 (2.77 - 11.02 times). The maximum recorded F_{scs} of 11.02 times the undisturbed rate was achieved by the smallest crab (54 g) with a mean undisturbed rate of 32.6 beats.min^{-1} and a mean maximum rate of 359.3 beats.min^{-1}.

The relationship between F_{scs} (also as a multiple of the undisturbed rate) and time after exercise was best rectified by log transformation of the abscissa alone rather

Figure 5.2 The relationship between rate of oxygen consumption and time during 8 hours post-exercise. Data from four male *Liocarcinus puber*.

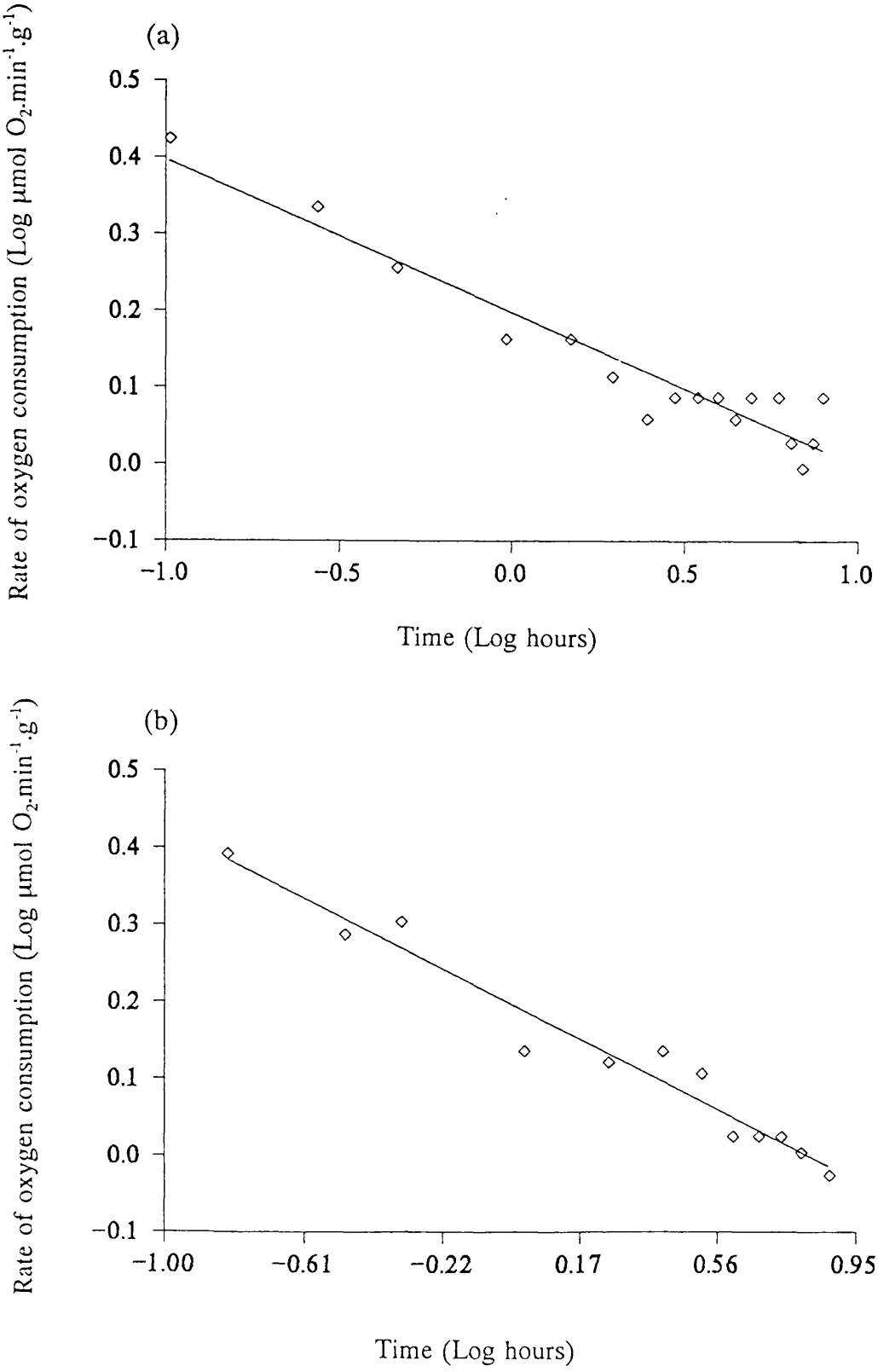
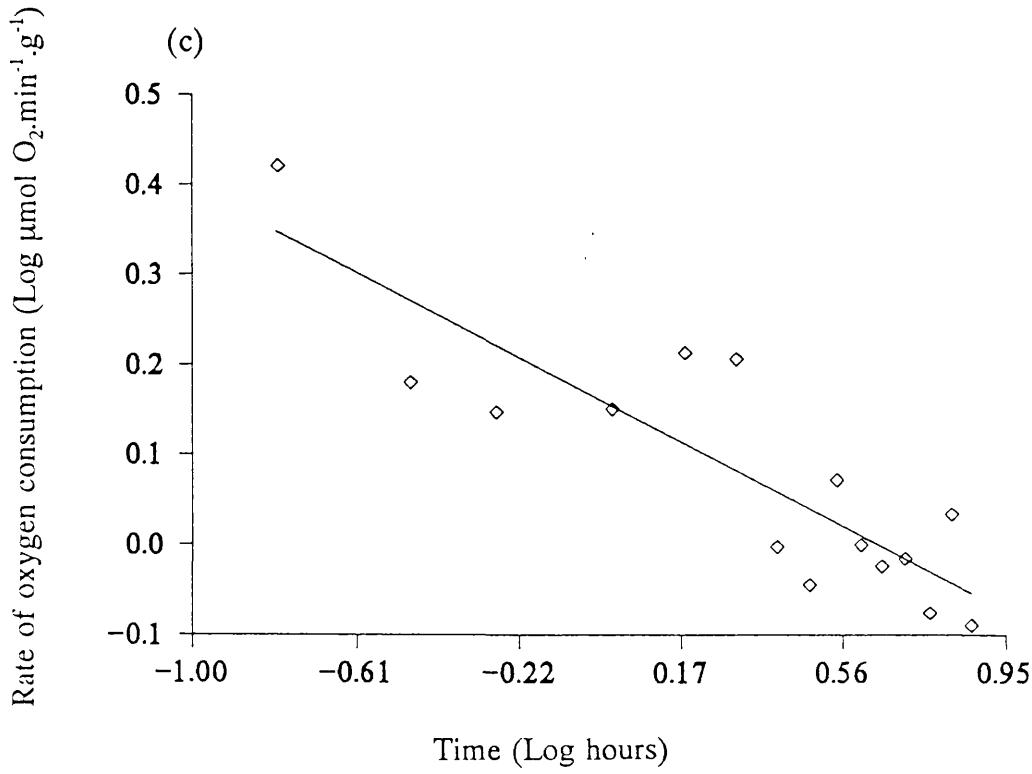


Figure 5.2 Continued



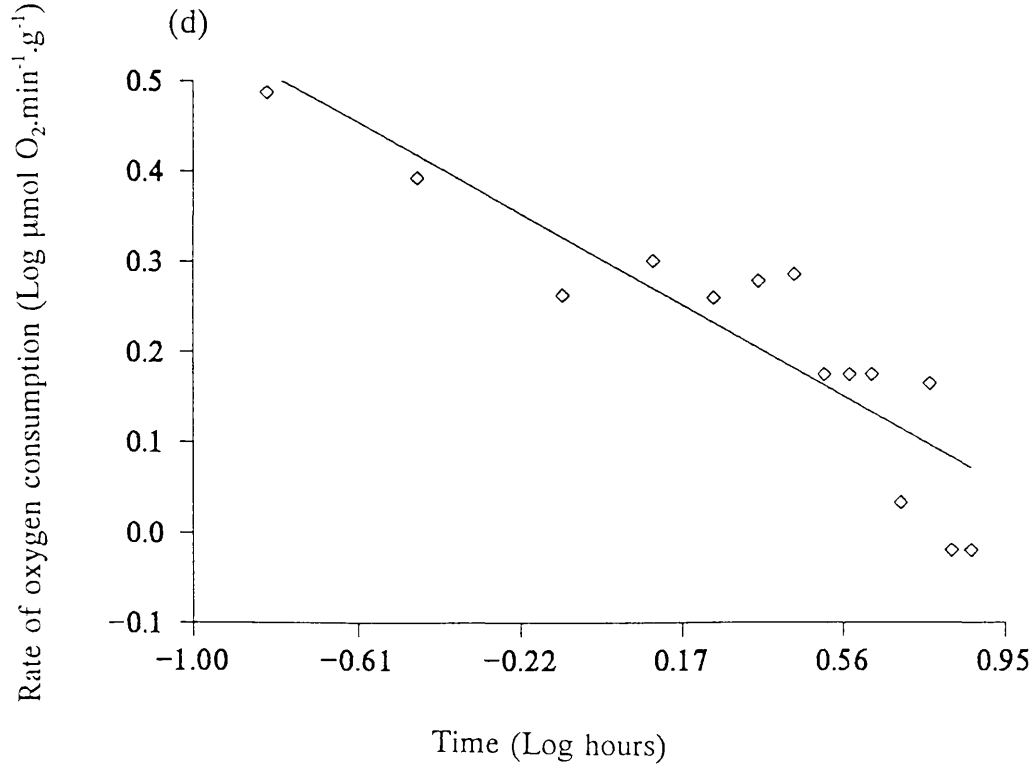


Table 5.3 Regressions of oxygen consumption against time during 8 h of recovery from exhaustive exercise. Data from ten male Liocarcinus puber.

Mass (g)	a[1]	b	F	degrees of freedom[2]	Recovery time (h)[3]	EPOC[4]
54	0.20	-0.24	21.03	1,11	6.47	2.08
83	0.19	-0.23	232.79	1,10	6.55	2.00
88	0.15	-0.23	24.80	1,13	4.60	1.40
93	0.11	-0.29	145.05	1,14	2.40	0.98
95	0.20	-0.20	171.77	1,13	9.46	2.55
97	0.26	-0.25	80.44	1,13	11.16	4.06
100	0.15	-0.24	39.26	1,13	4.40	1.40
105	0.30	-0.26	46.77	1,12	13.38	4.86
108	0.22	-0.29	20.27	1,11	5.44	2.29
127	0.21	-0.28	72.21	1,13	5.86	2.23

1. a and b are estimates of the Y-axis intercept and the slope respectively in the equation:

$$\log Mo_2x = a + b.\log Time$$

where Mo_2x = oxygen consumption as a multiple of the undisturbed rate (see Table 5.1)

and Time = time after exercise (h).

2. All regressions are significant at $P<0.001$

3. Recovery time has been estimated by evaluating these regressions for Time at $Mo_2x = 1$ (the undisturbed rate).

4. The excess post-exercise oxygen consumption (EPOC) has been estimated by the integral of each function between 0 h and the recovery time minus the product of the undisturbed rate of oxygen consumption ($Mo_2x = 1$) and the recovery time.

Figure 5.3 The heart rate of *Liocarcinus puber* before and after exercise - exercise finished at time 0. Data from four males.

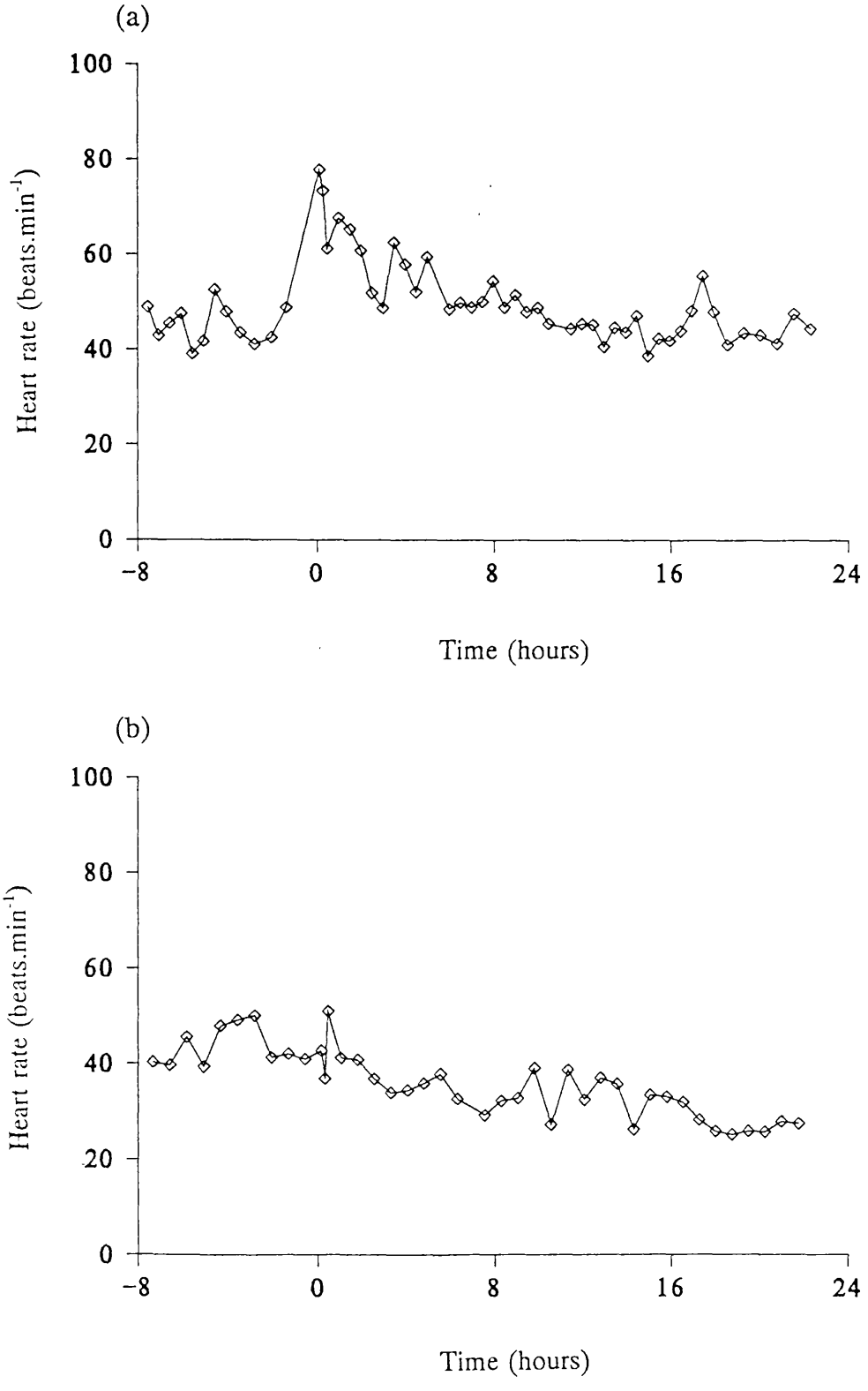
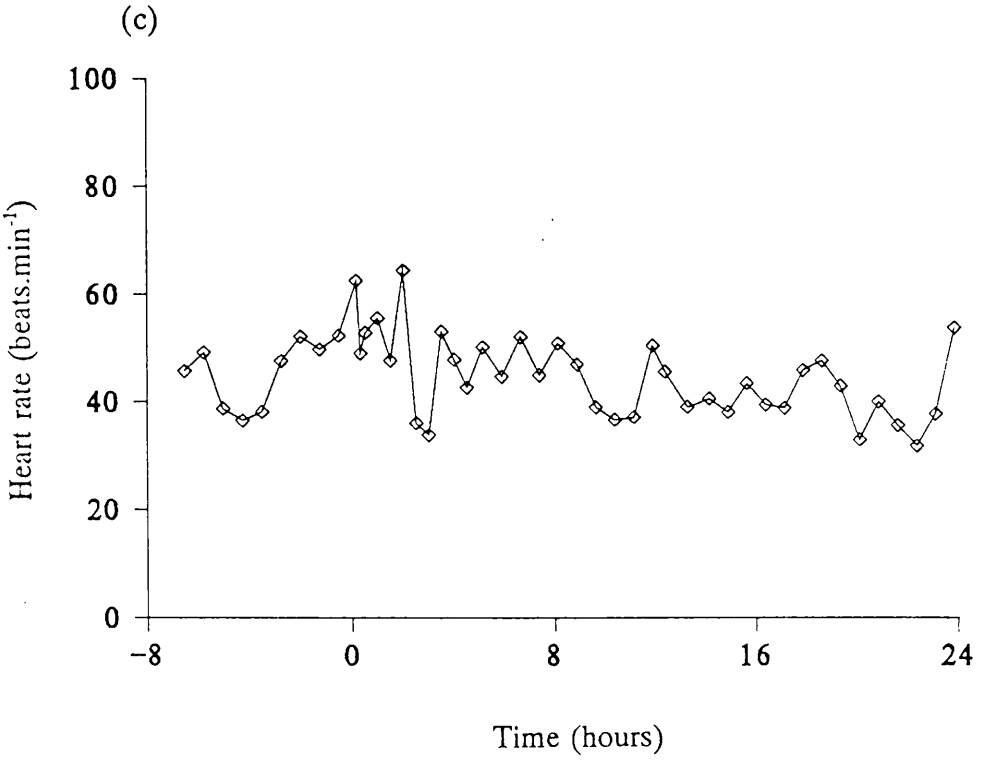


Figure 5.3 Continued



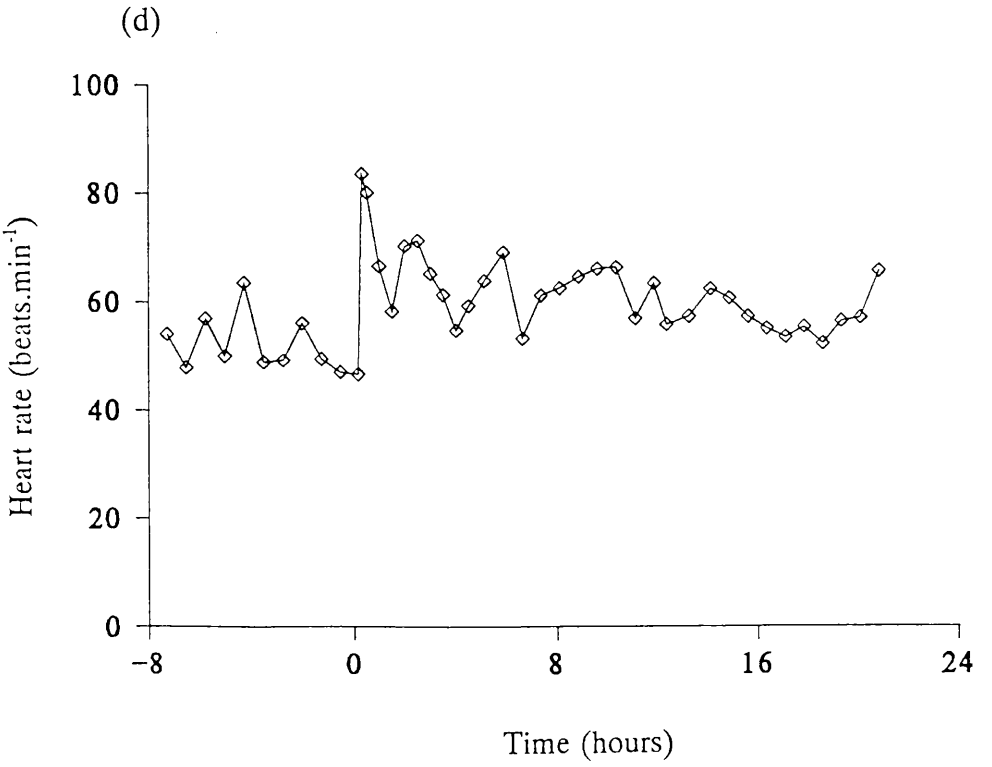


Figure 5.4 The scaphognathite rate of *Liocarcinus puber* before and after exercise - exercise finished at time 0. Data from four males.

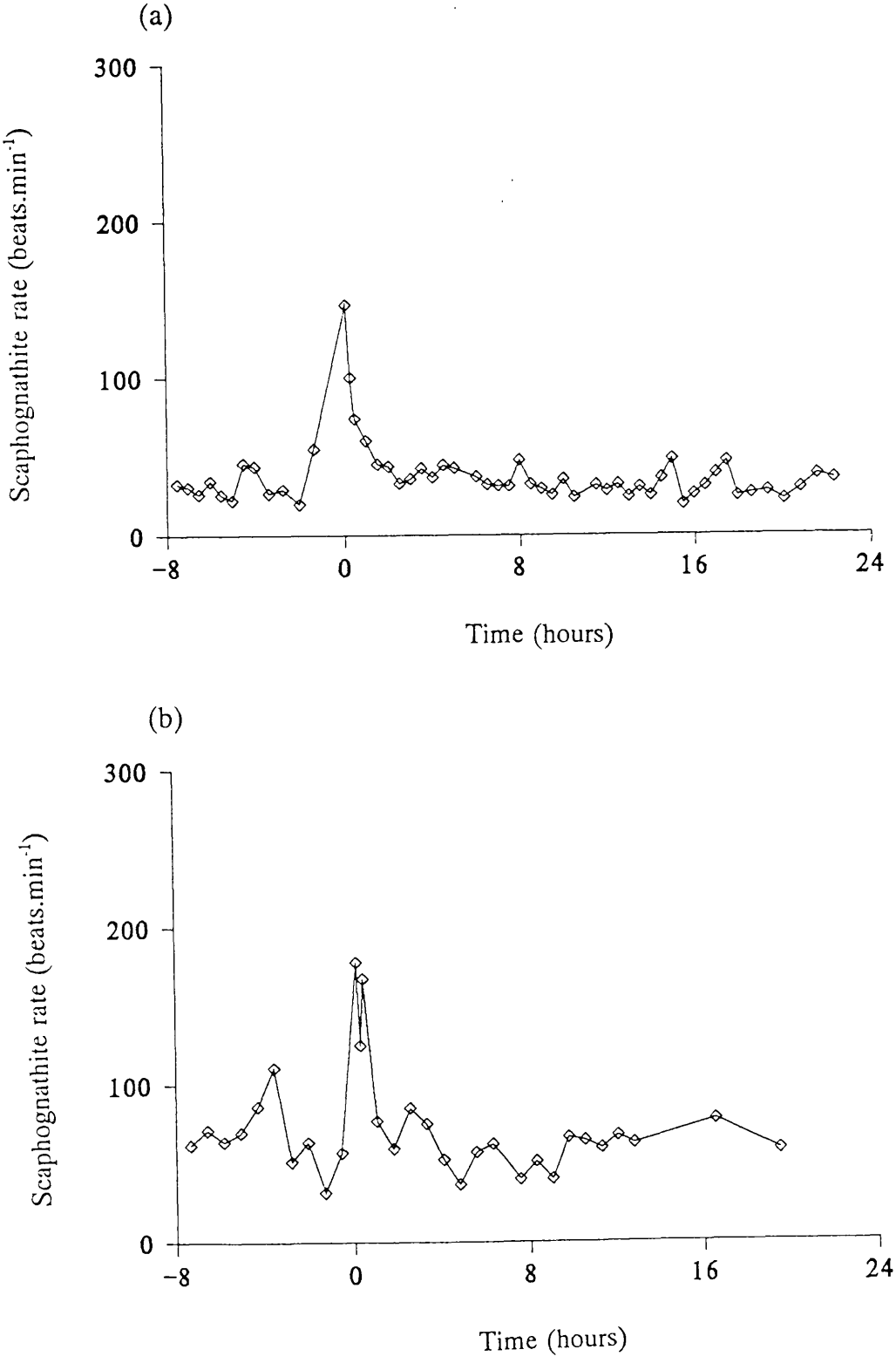
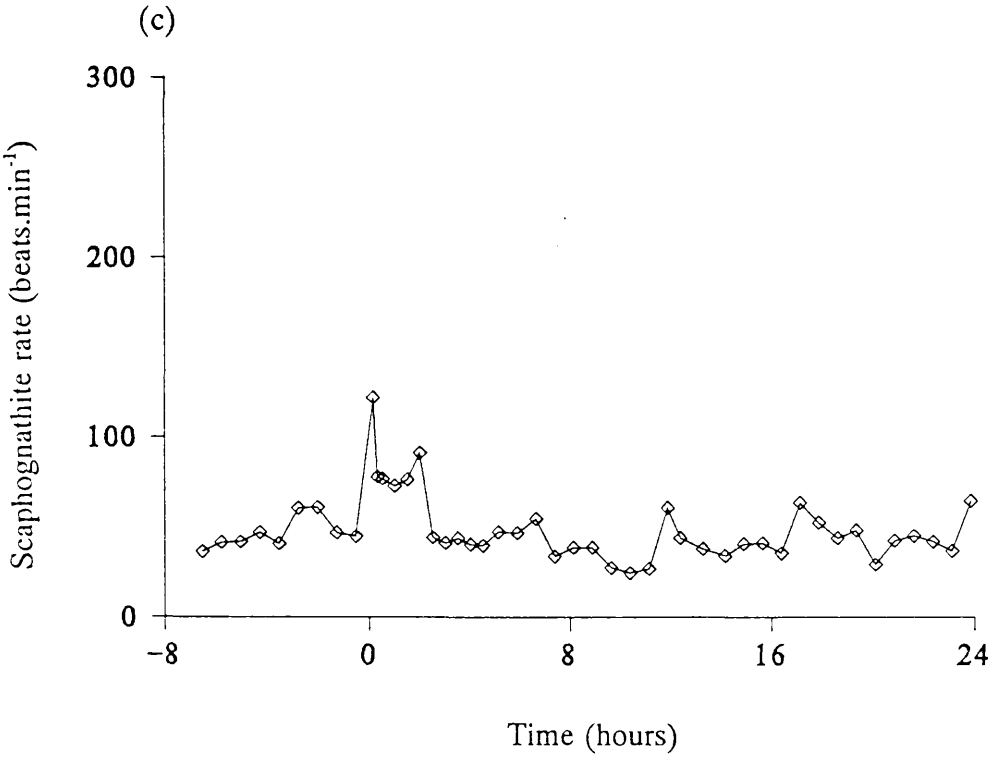
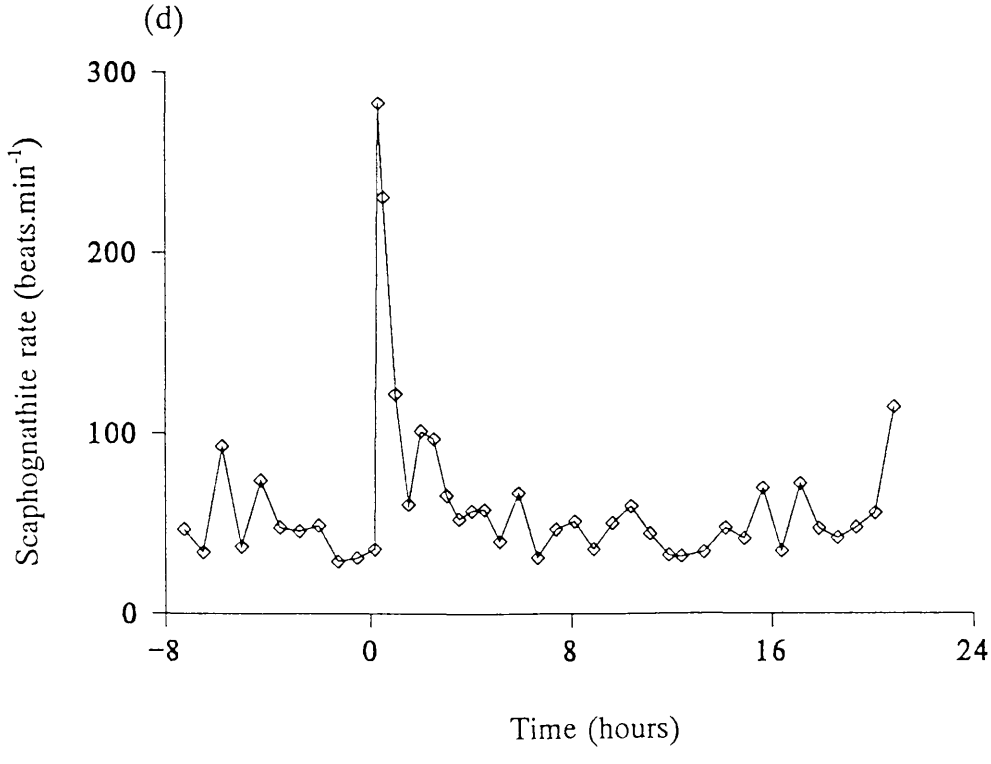


Figure 5.4 Continued





than the ordinate and abscissa as with the Mo_2 data. Significant linear relationships between these variables were obtained (Table 5.4). Estimates of F_{scs} recovery time and excess post-exercise scaphognathite activity were obtained from these regressions as with the Mo_2 data.

5.3.3 The relationship between oxygen consumption and scaphognathite and heart rates.

The rate at which crabs consumed oxygen was highly correlated with the beat rate of the scaphognathites (Figure 5.5 - same four crabs as above). Linear regressions of Mo_2 on F_{scs} were highly significant for each crab (Table 5.5). ANCOVA indicated that there were significant differences among the regression coefficients ($F_{(9,324)} = 25.853$, $P<0.01$).

Estimates of F_{scs} recovery time were not well correlated with Mo_2 recovery time, but estimates of the area under the Mo_2x recovery curve were significantly correlated with analogous estimates derived from the F_{scs} data ($r = 0.718$, $P<0.05$, $df=8$). In other words, during the recovery period, the oxygen consumed in excess of the amount that would have been used in the undisturbed state in this period of time, was correlated with the excess number of scaphognathite beats.

The heart rate also increased with the rate of oxygen consumption (Figure 5.6 - same four crabs as above), but as F_h in most cases took much longer to return to resting levels than Mo_2, there was not as clear a relationship as between Mo_2 and F_{scs}.

5.3.4 Scaphognathite rates during agonistic behaviour and subsequent recovery

5.3.4.1 Controls

Crabs undisturbed in the observation tank showed predominantly unilateral scaphognathite beating with occasional cessation of scaphognathite activity. The crabs were able to move around the tank and showed brief periods of rapid bilateral scaphognathite activity associated with locomotion. The scaphognathite rates of four individual crabs are illustrated in Figure 5.7 a-d. Scaphognathite rates are presented as means of five consecutive counts made over a period of 30 s, calculated at intervals of 30 minutes. These crabs did not exhibit prolonged periods of elevated scaphognathite rates.

The scaphognathite rates of four crabs subjected to raising and lowering of the partition are presented in Figure 5.8 a-d as the means of five consecutive 30 s counts.

Table 5.4 Regressions of scaphognathite rate against time during 8 h of recovery from exhaustive exercise. Data from 10 male Liocarcinus puber.

Mass (g)	a[1]	b	F	degrees of freedom[2]	Recovery time (h)[3]	EPSA[4]
54	1.733	-1.283	12.75	1,39	3.72	2.08
83	1.469	-1.018	57.60	1,39	2.89	1.28
88	2.043	-1.569	53.16	1,39	4.60	3.15
93	1.731	-1.818	131.65	1,39	2.52	1.99
95	1.897	-1.440	50.14	1,39	4.20	2.62
97	2.003	-1.103	17.86	1,39	8.11	3.89
100	1.455	-1.016	18.87	1,37	2.82	1.24
105	2.258	-2.444	66.02	1,39	3.28	4.04
108	1.748	-1.790	55.48	1,39	2.62	2.03
127	1.395	-0.917	56.15	1,39	2.70	1.07

1. a and b are the Y-axis intercept and the slope respectively in the equation

$$F_{SCS}x = a + b.\log \text{Time}$$

where $F_{SCS}x$ = the scaphognathite rate as a multiple of the undisturbed rate (see Table 5.1)

and Time = time after exercise (h).

2. All regressions are significant at $P<=0.001$.

3. The recovery time of the scaphognathite rate was estimated by evaluating these regressions for Time at $F_{SCS}x = 1$ (the undisturbed rate).

4. The excess post-exercise scaphognathite activity (EPSA) was estimated by the integral of each function between 0 h and the recovery time, minus the product of the undisturbed scaphognathite rate ($F_{SCS}x = 1$) and the recovery time.

Figure 5.5 The relationship between rate of oxygen consumption and scaphognathite rate during recovery from exercise. Data from four male *Liocarcinus puber*.

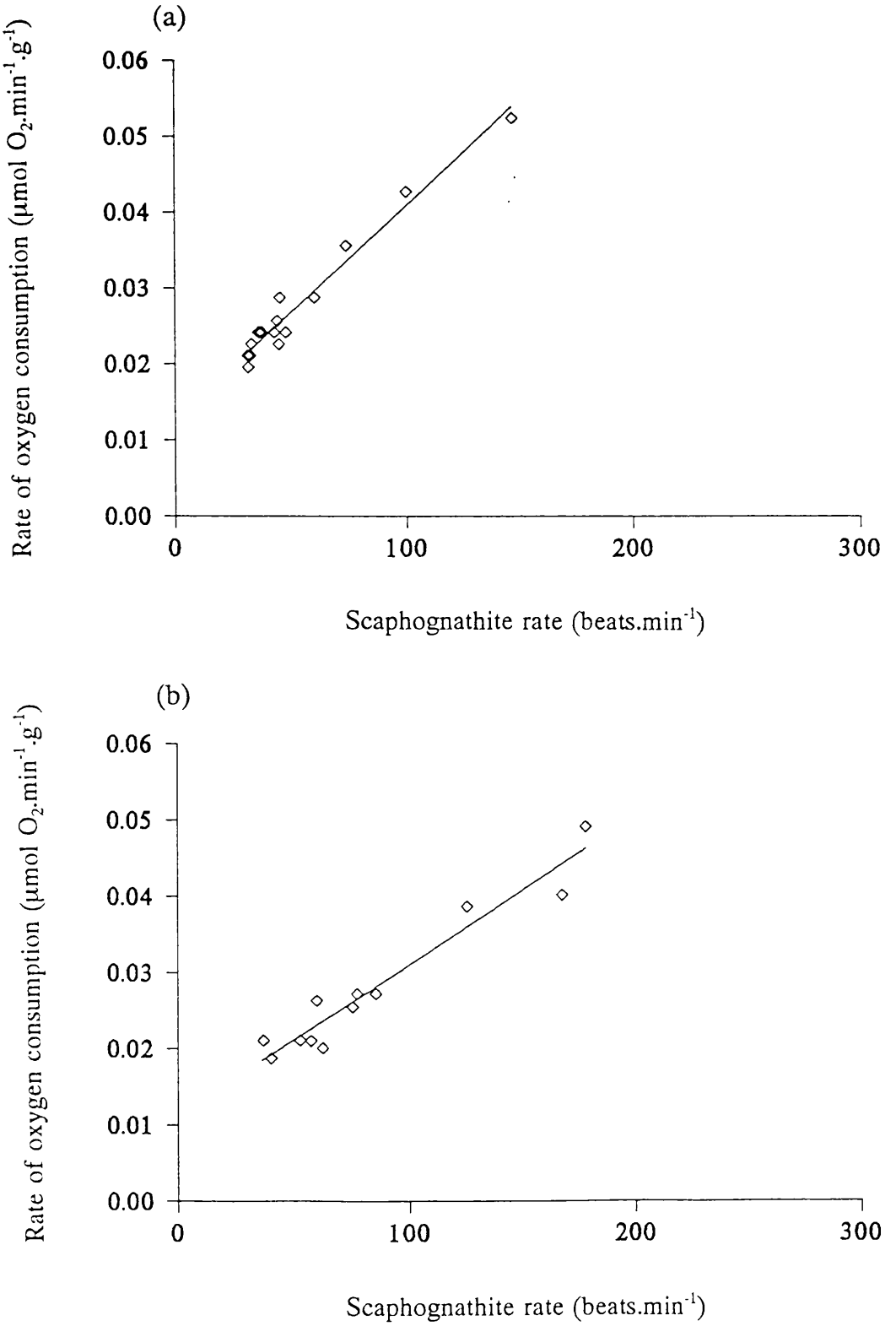
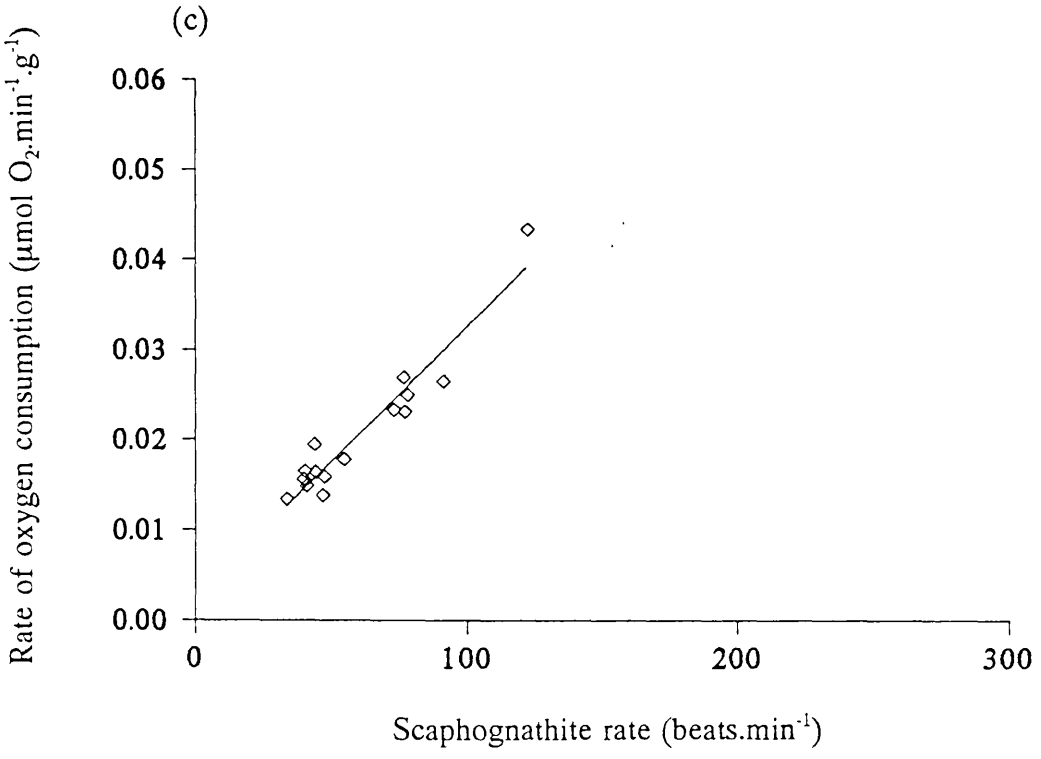


Figure 5.5 Continued



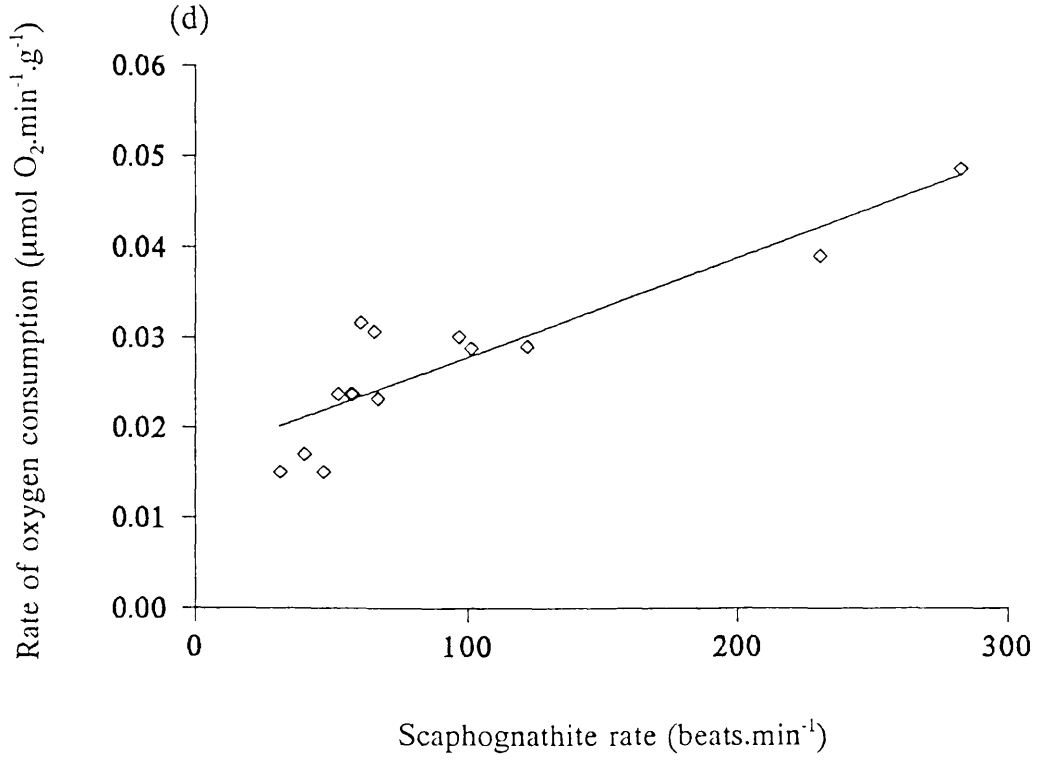


Table 5.5 Regressions of mass specific oxygen consumption of *Liocarcinus puber* against scaphognathite beat rate. Data from 0 - 24 h after exercise for ten males.

Mass (g)	a x 10^3	b x 10^4	F	degrees of freedom	P
54	16.58	1.90	447.33	1,34	<0.001
83	9.06	2.08	137.28	1,19	<0.001
88	10.87	1.48	190.62	1,35	<0.001
93	10.66	0.90	198.98	1,36	<0.001
95	11.41	2.88	468.92	1,40	<0.001
97	6.77	1.04	273.29	1,35	<0.001
100	4.52	2.73	190.14	1,35	<0.001
105	12.53	1.27	82.54	1,30	<0.001
108	5.97	2.38	173.34	1,25	<0.001
127	4.61	1.68	139.49	1,35	<0.001

a and b are estimates of the Y-axis intercept and the slope respectively in the equation:

$$Mo_2 = a + b.F_{SCS}$$

where Mo_2 = rate of mass specific oxygen consumption (μmol $O_2.min^{-1}.g^{-1}$ fresh wt.)

and F_{SCS} = scaphognathite beat rate (beats.min^{-1}).

Figure 5.6 The relationship between rate of oxygen consumption and heart rate during recovery from exercise. Data from four male *Liocarcinus puber*.

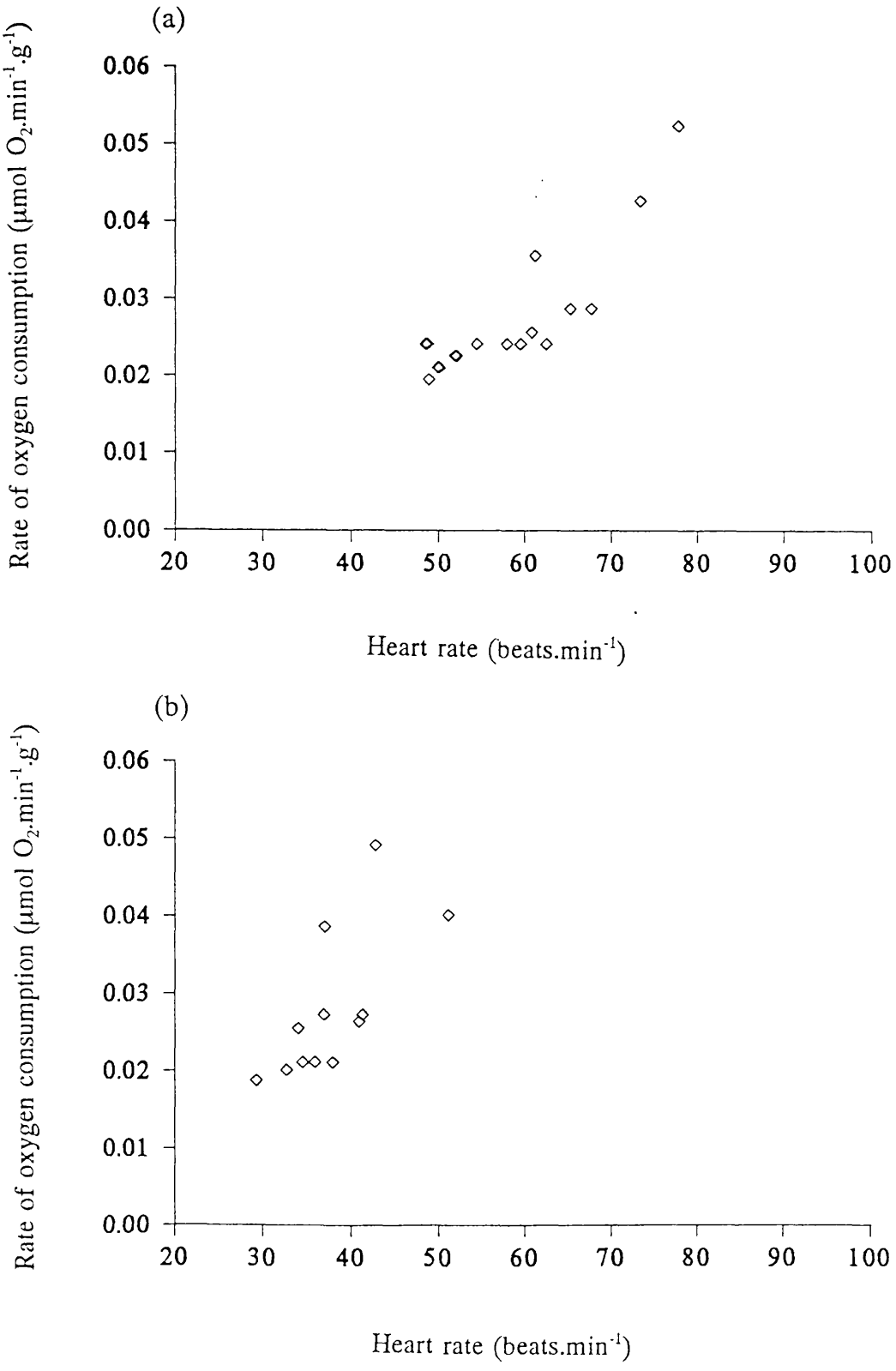
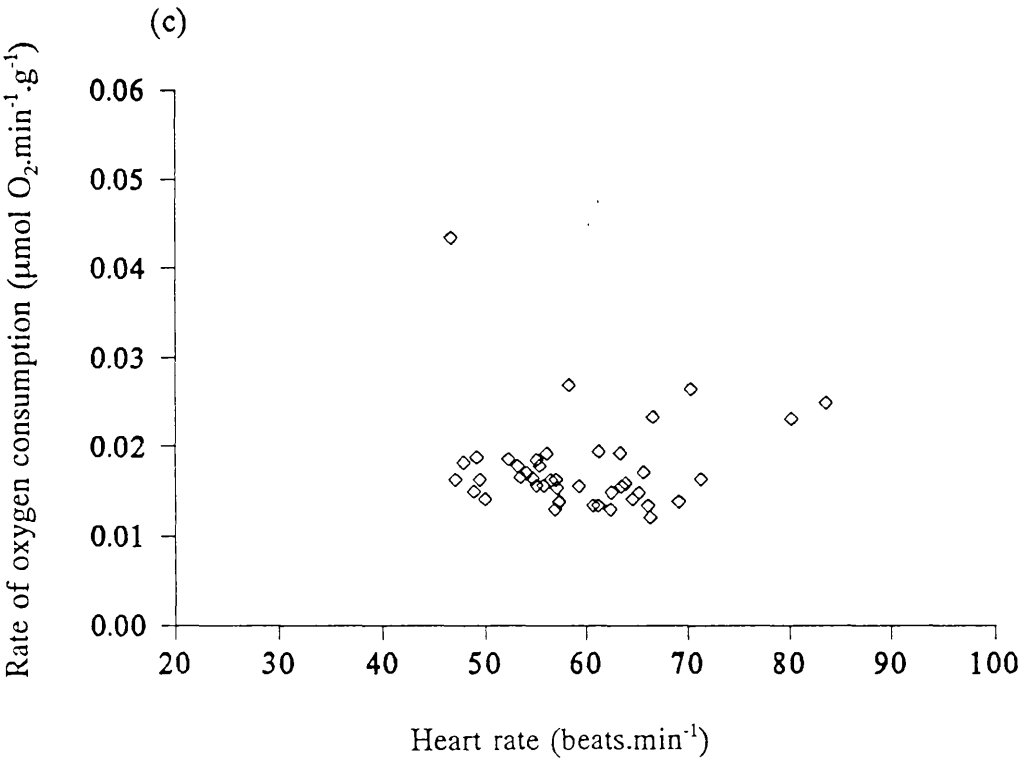


Figure 5.6 Continued



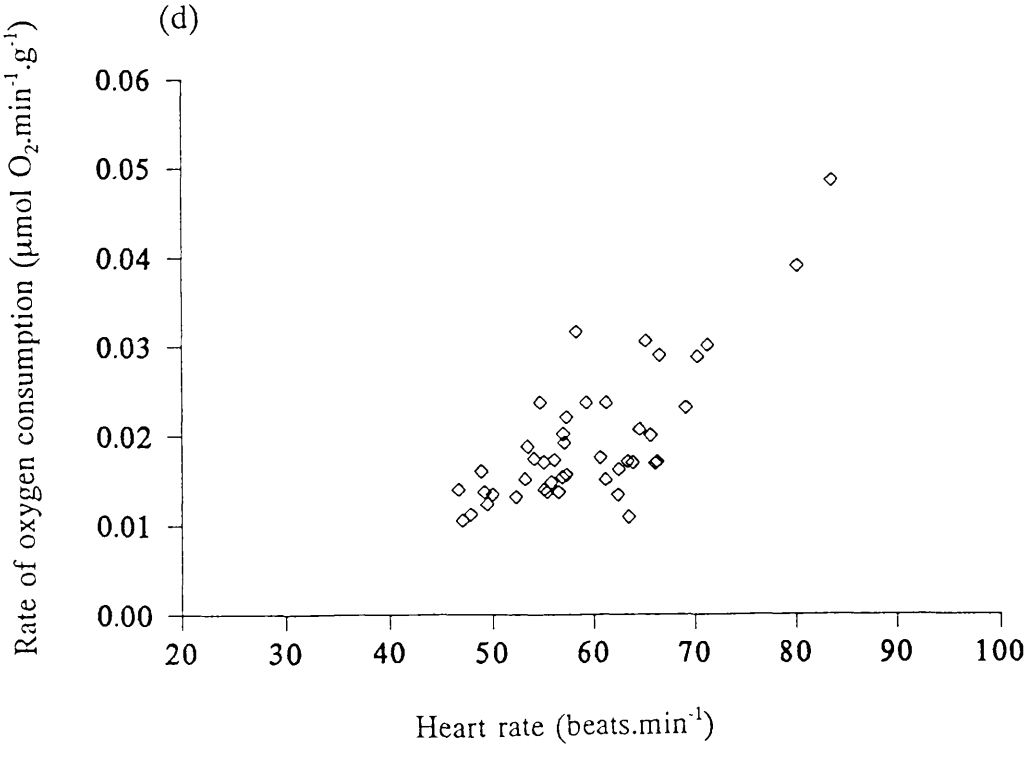


Figure 5.7 The scaphognathite rate of undisturbed *Liocarcinus puber* in the observation tank.

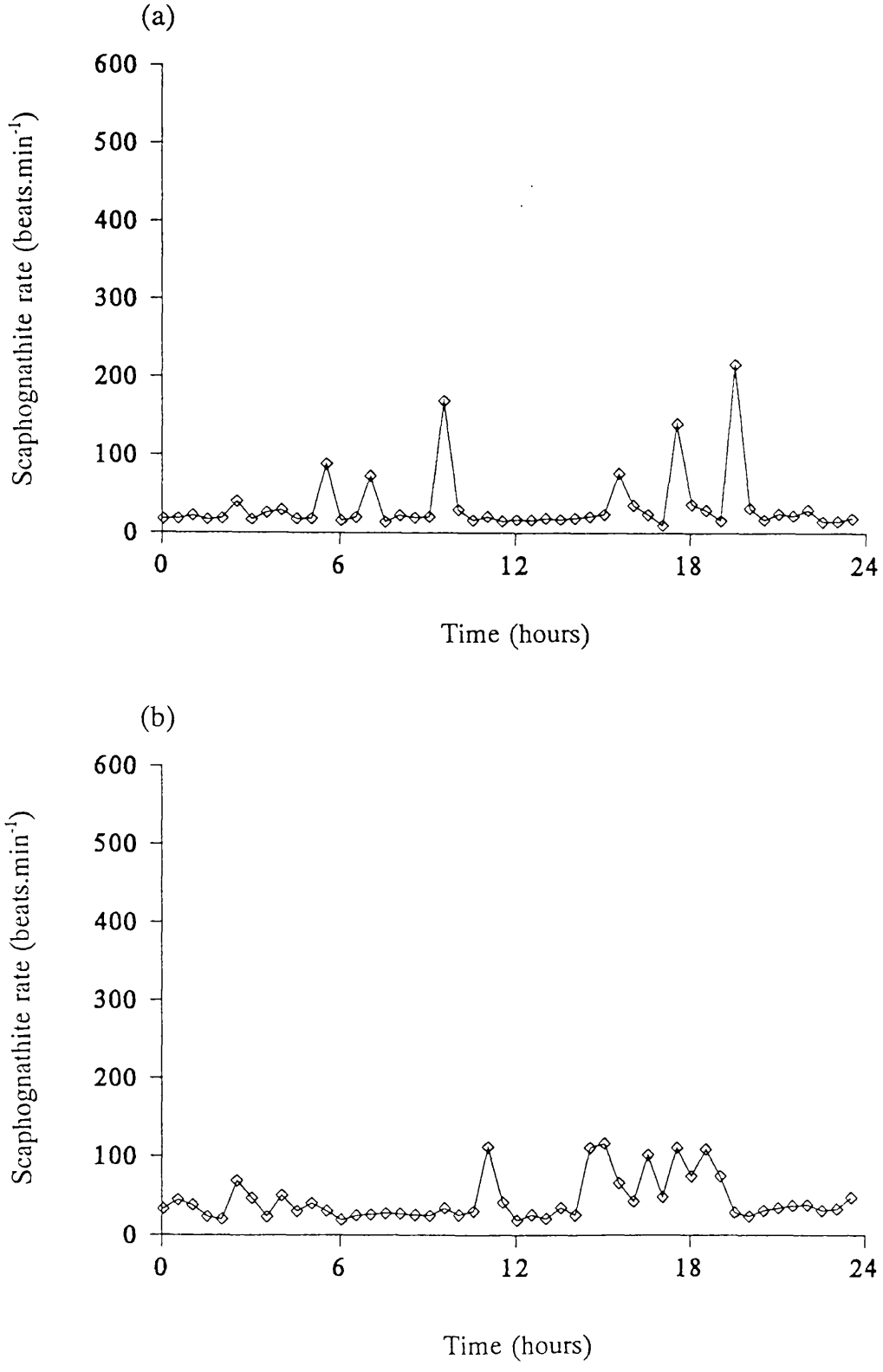
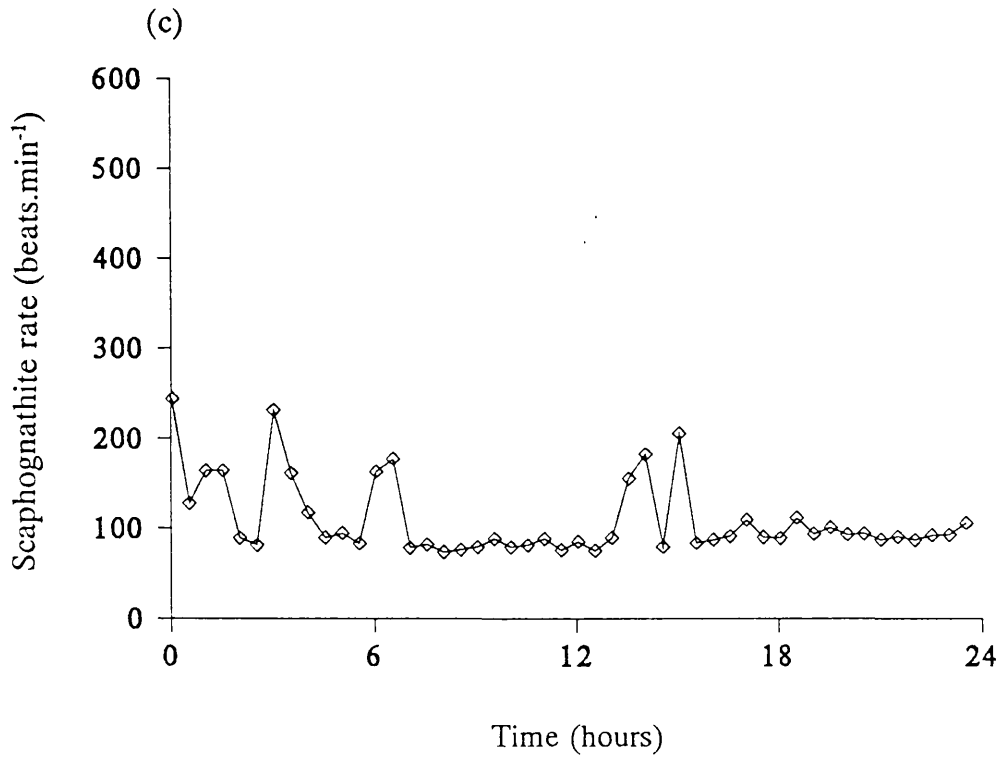


Figure 5.7 Continued



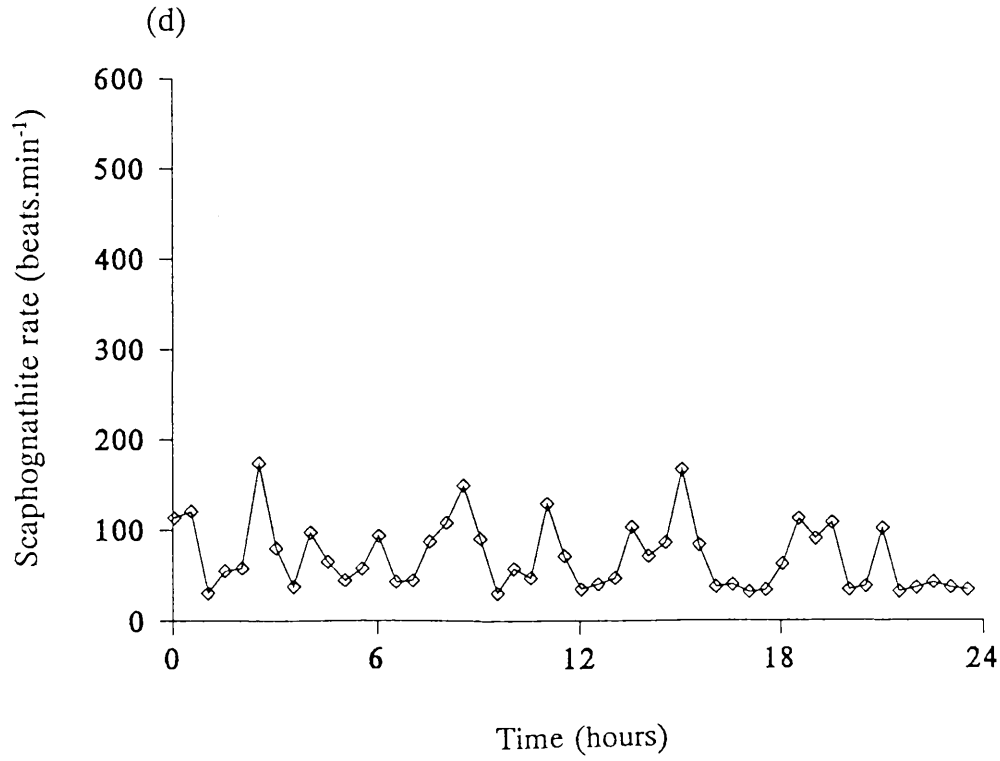


Figure 5.8 The scaphognathite rate of *Liocarcinus puber* in response to raising the partition.

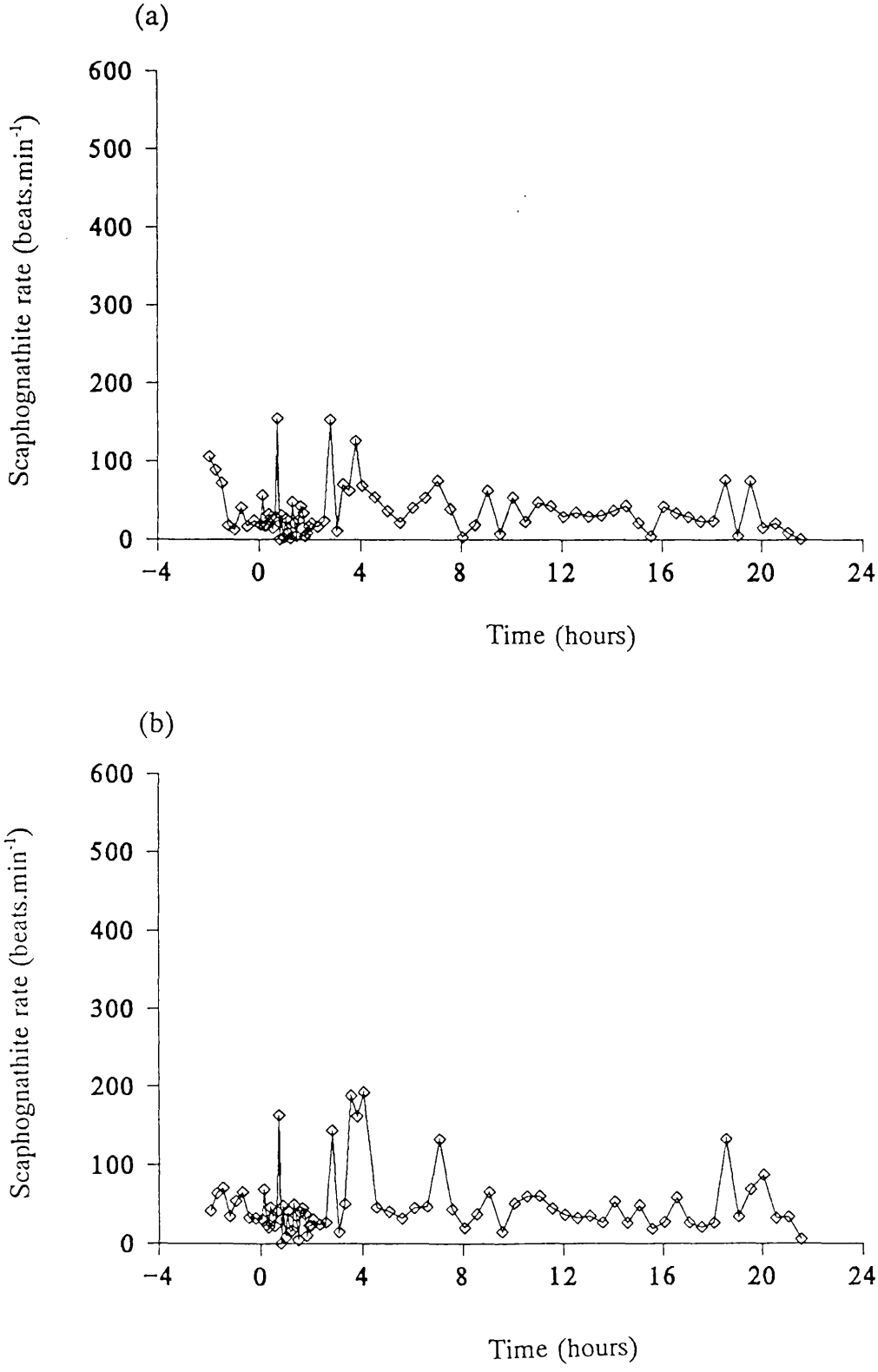
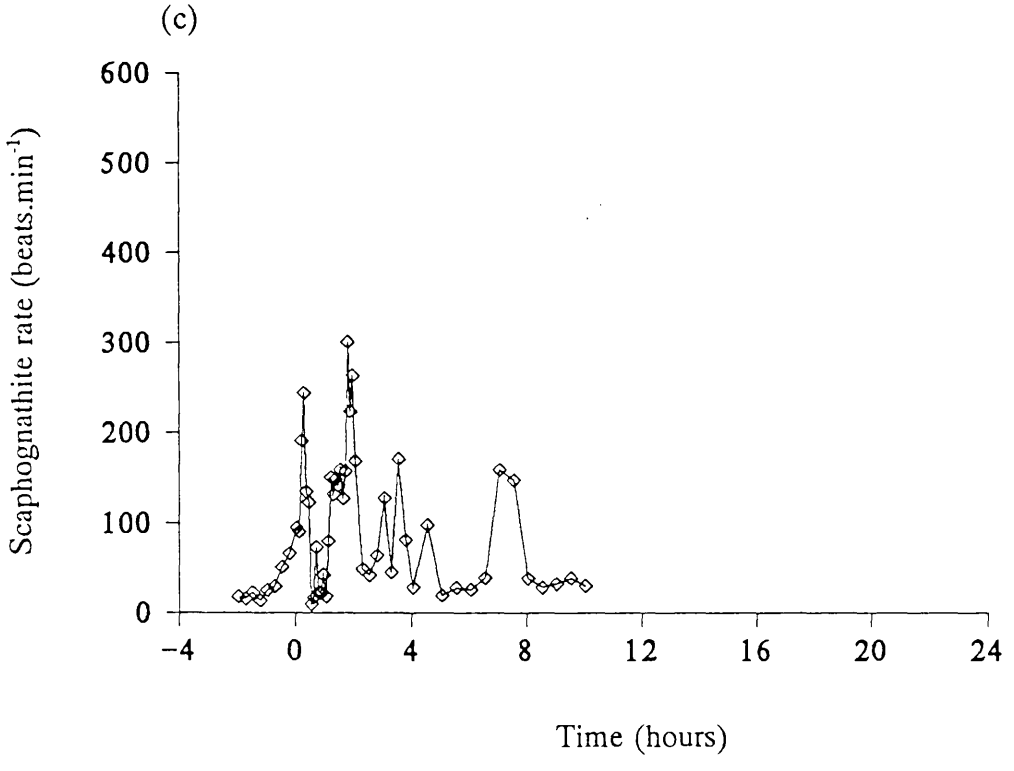
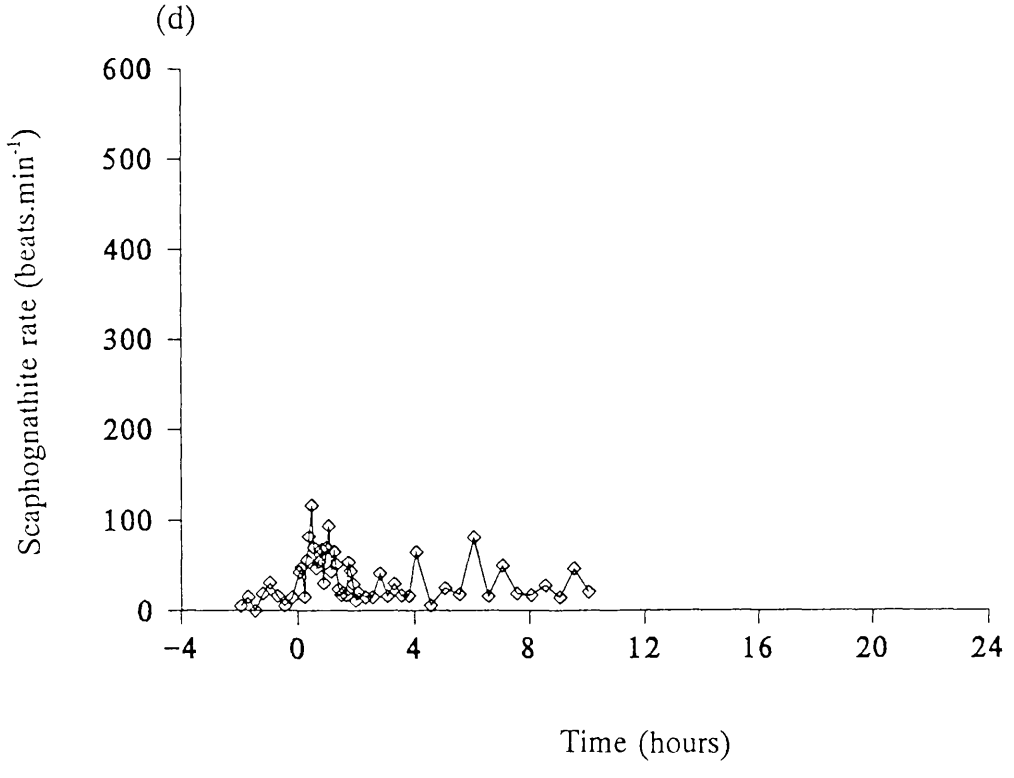


Figure 5.8 Continued





With "time-zero" taken as when the partition was lowered (raising and lowering took about 1 minute), these means were calculated every 15 minutes from -2 to 0 h, every 5 minutes from 0 to 2 h, every 15 minutes from 2 to 4 h and every 30 minutes from 4 h onward. This sampling regime was that used when monitoring scaphognathite rates in response to agonistic behaviour, to allow for rapid changes during interactions and shortly after (section 5.3.4.3). This regime was therefore used for controls also. Raising and lowering the partition resulted in cessation of scaphognathite beating for a period of between c.30 s and several minutes. This is the characteristic response to disturbance in crustaceans (Wilkens, 1981). Such apnoea was followed by hyperventilation resulting in a transitory increase in the mean scaphognathite rate.

5.3.4.2 Scaphognathite rates during agonistic behaviour

Scaphognathite activity during agonistic behaviour was characterized by periods of apnoea and hyperventilation. The rate of beating was therefore very variable (Figure 5.9). The scaphognathite rates of 30 crabs engaged in agonistic behaviour have been recorded (Table 5.6) and in all but 3 of these the rate during fighting was elevated. In these 3 exceptions apnoea predominated, resulting in lower mean rates. The maximum mean scaphognathite rates recorded during agonistic behaviour from the other crabs increased 2.18 to 20.34 fold over the undisturbed rates.

Certain behaviours were always associated with rapid scaphognathite beating. Bilateral display and striking with the chelae resulted in elevated rates in both interactants, while swimming retreats were associated with rapid beating in the retreating crab. Interactions involving bilateral display and striking were consequently associated with higher maximum scaphognathite rates than less intense forms of interaction (Median maximum F_{scs} of bilateral display, bilateral contact interactions = 509.1 beats.min^{-1}; Median maximum F_{scs} of less intense interactions = 208.2 beats.min^{-1}; Kruskal Wallis H_{adj} = 9.106, df = 1, $P<0.01$).

5.3.4.3 Scaphognathite rates during recovery from agonistic behaviour

Following agonistic behaviour, the shape of the scaphognathite recovery curve was similar to that recorded during recovery from swimming. The scaphognathite rates of four pairs of crabs prior to, during and after an interaction are illustrated in

Figure 5.9 A sample pen recording of the activity of the left and right scaphognathites of two *Liocarcinus puber* engaged in an agonistic interaction. (a) Initiation, displays and strikes.

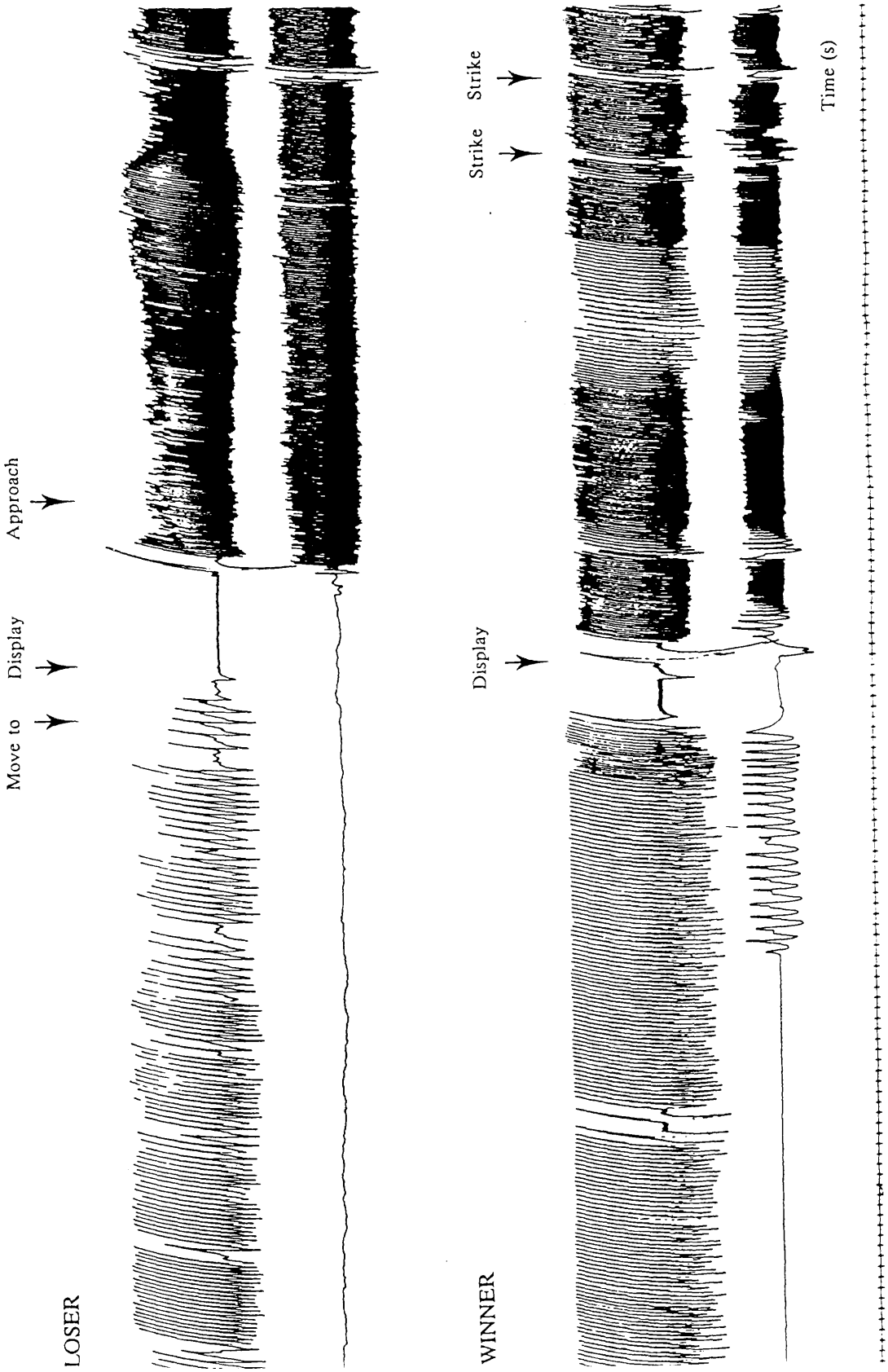


Figure 5.9 A sample pen recording of the activity of the left and right scaphognathites of two *Liocarcinus puber* engaged in an agonistic interaction. (b) Bilateral display and resolution.

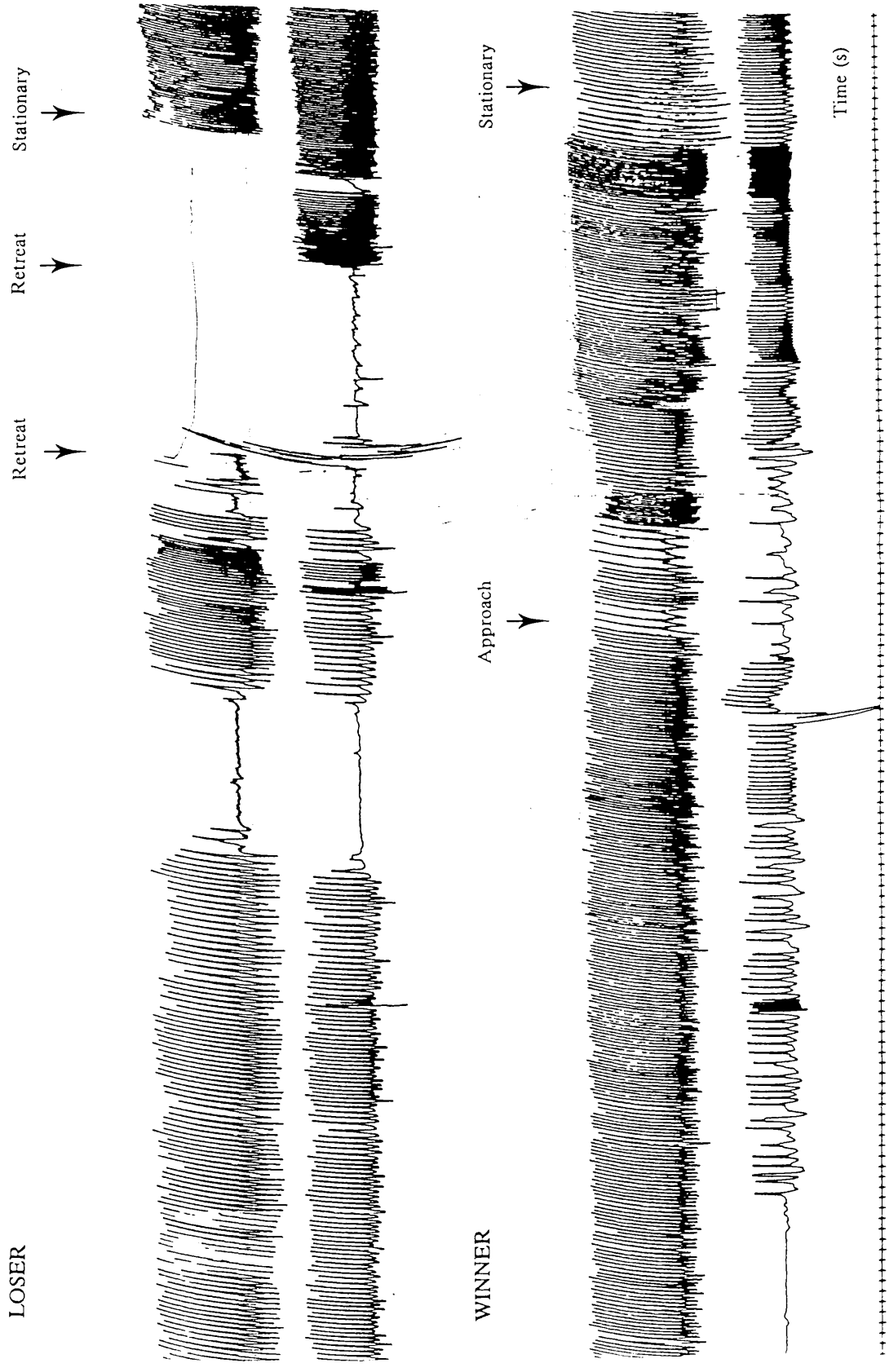


Table 5.6 Initiation, content and outcome of agonistic interactions between male Liocarcinus puber in which the scaphognathite rates of the crabs were monitored.

Test no.	Crab	Initiation[1]	Outcome[1]	Content[2]	Duration (min)
1	1	Initiator	Winner	UD/NC	2.13
	2	Responder	Loser		
2	1	Responder	Winner	BD/UC	7.20
	2	Initiator	Loser		
3	1	Responder	Winner	BD/BC	13.37
	2	Initiator	Loser		
4	1	Initiator	Winner	BD/BC	24.75
	2	Responder	Loser		
5	1	Initiator	Winner	BD/BC	37.77
	2	Responder	Loser		
6	1	Responder	Winner	BD/UC	20.15
	2	Initiator	Loser		
7	1	Initiator	Winner	BD/BC	37.77
	2	Responder	Loser		
8	1	Responder	Winner	BD/NC	4.82
	2	Initiator	Loser		
9	1	Responder	Loser	BD/NC	5.00
	2	Initiator	Winner		
10	1	Responder	Winner	BD/BC	11.32
	2	Initiator	Loser		
11	1	Responder	Winner	BD/BC	10.08
	2	Initiator	Loser		
12	1	-	Loser	BD/UC	4.07
	2	-	Winner		
13	1	Initiator	Loser	BD/BC	8.08
	2	Responder	Winner		
14	1	Initiator	Winner	BD/NC	7.53
	2	Responder	Loser		
15	1	Responder	Winner	BD/UC	4.55
	2	Initiator	Loser		
16	1	Initiator	Loser	BD/BC	3.86
	2	Responder	Winner		

Table 5.6 Continued.

1. See text for definitions of initiator, responder, winner and loser. The crabs in interaction 12 displayed simultaneously.

2. Content of the interaction in terms of the occurrence of display, strikes and grasps:

   UD - Unilateral display (by one crab only)

   BD - Bilateral display

   NC - No strikes or grasps by either crab

   UC - Unilateral striking or grasping

   BC - Bilateral striking or grasping

Figure 5.10 a-h, with the sampling regime as described in section 5.3.4.1. The relationship between F_{scs} (as a multiple of the undisturbed rate - $F_{scs}x$) and recovery time was best rectified in most cases by log transformation of the abscissa. Regressions of $F_{scs}x$ against Log Time were highly significant in all cases except for 5 crabs whose scaphognathite rates recovered within 5 minutes of the end of agonistic activity (Figure 5.11, Table 5.7). Recovery times have been estimated from these regressions as before (Table 5.8).

The regressions of scaphognathite rate against recovery period were consistently poorer fits for winners compared to losers (paired comparison of F values of regressions for winners and losers, Wilcoxon's T = 10.0, n = 12, P=0.025). The greater residual variation in the winner's scaphognathite rates appeared to be due to greater spontaneous activity by these crabs.

5.3.4.4 The respiratory demand of agonistic behaviour

The respiratory cost of this behaviour may be represented by the excess scaphognathite activity over undisturbed levels during the fight itself and during subsequent recovery (Table 5.8). The excess scaphognathite activity during the interaction (EFSA) has been estimated by the following formula:

$$\mathbf{EFSA = Duration.[F_{scs}(int) - F_{scs}(undist)]/F_{scs}(undist)}$$

where Duration = the duration of the agonistic interaction (hours)

$F_{scs}(int)$ = the mean scaphognathite rate during the interaction (beats.min^{-1})

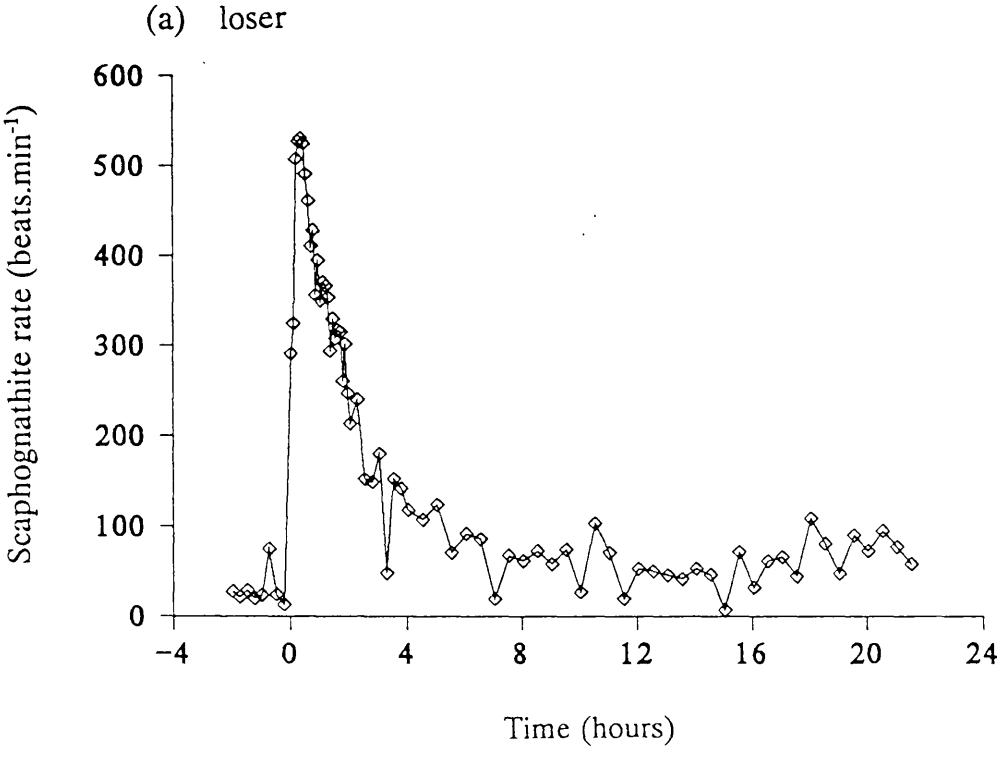
and

$F_{scs}(undist)$ = the mean undisturbed scaphognathite rate (beats.min^{-1})

The excess post-agonistic scaphognathite activity (EPSA) has been estimated by the following formula:

$$\mathbf{EPSA = A(Rec) - Rec.}$$

Figure 5.10 The scaphognathite rates of male *Liocarcinus puber* in response to agonistic behaviour. Data from four pairs of interactants.



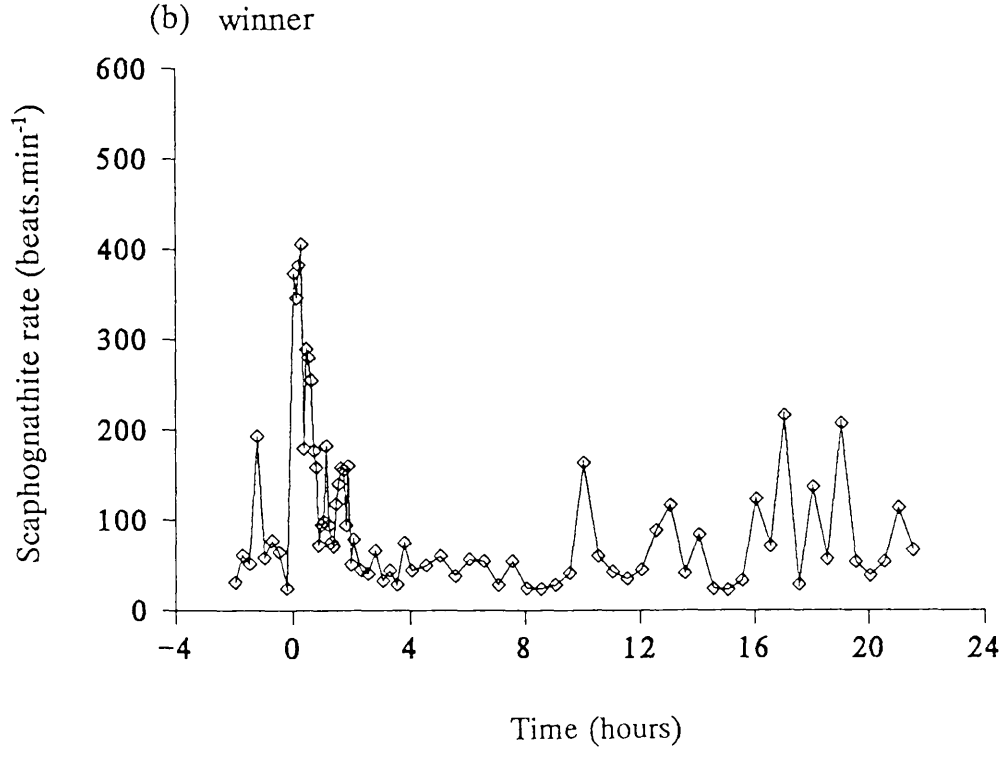
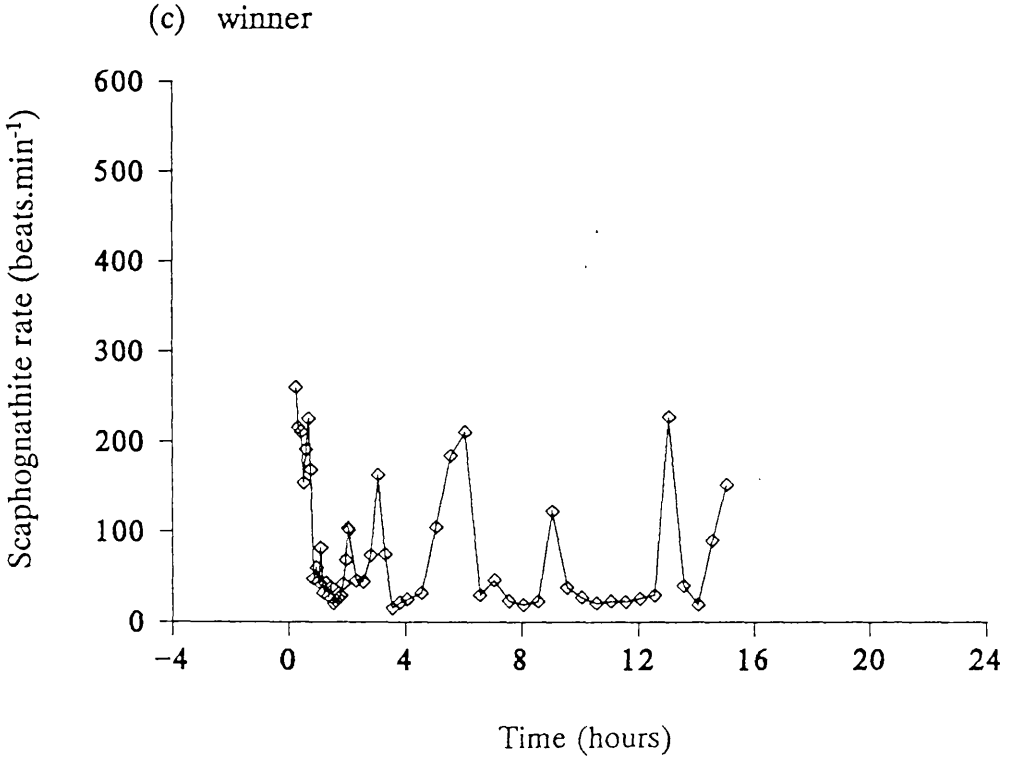


Figure 5.10 Continued



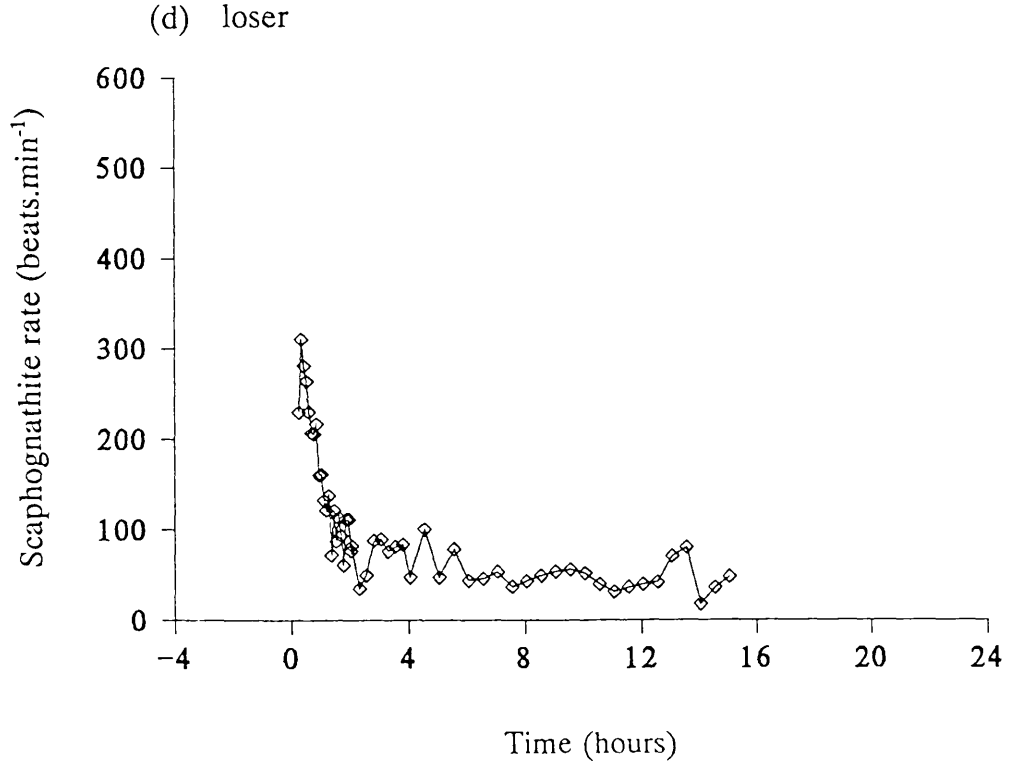
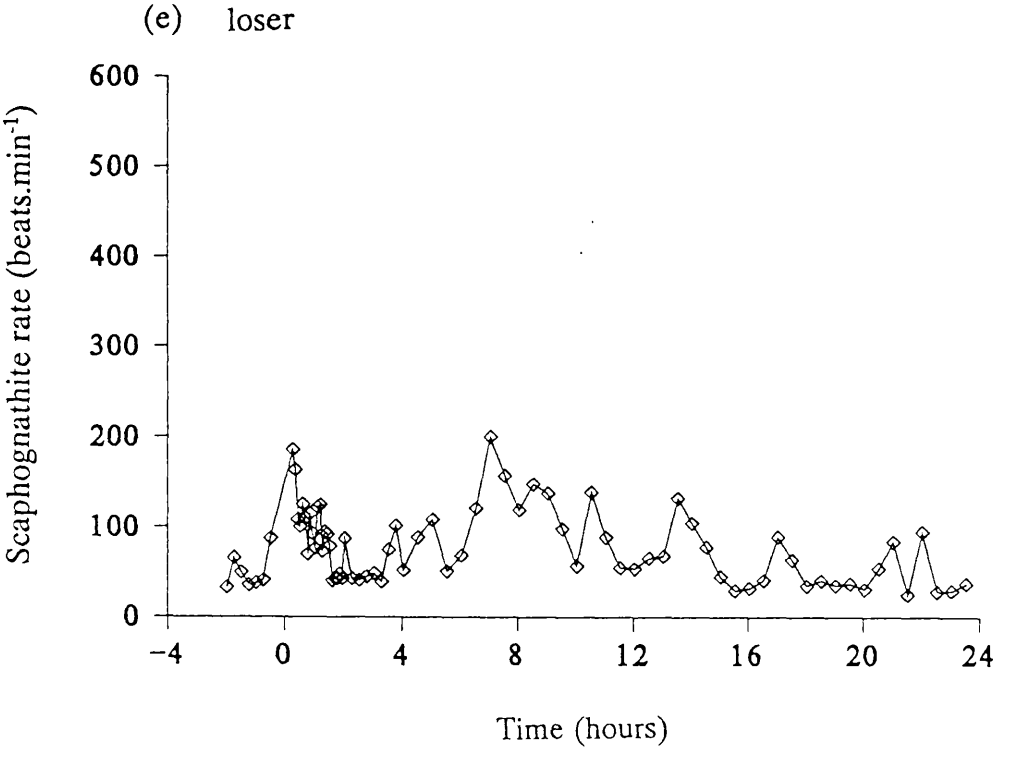


Figure 5.10 Continued



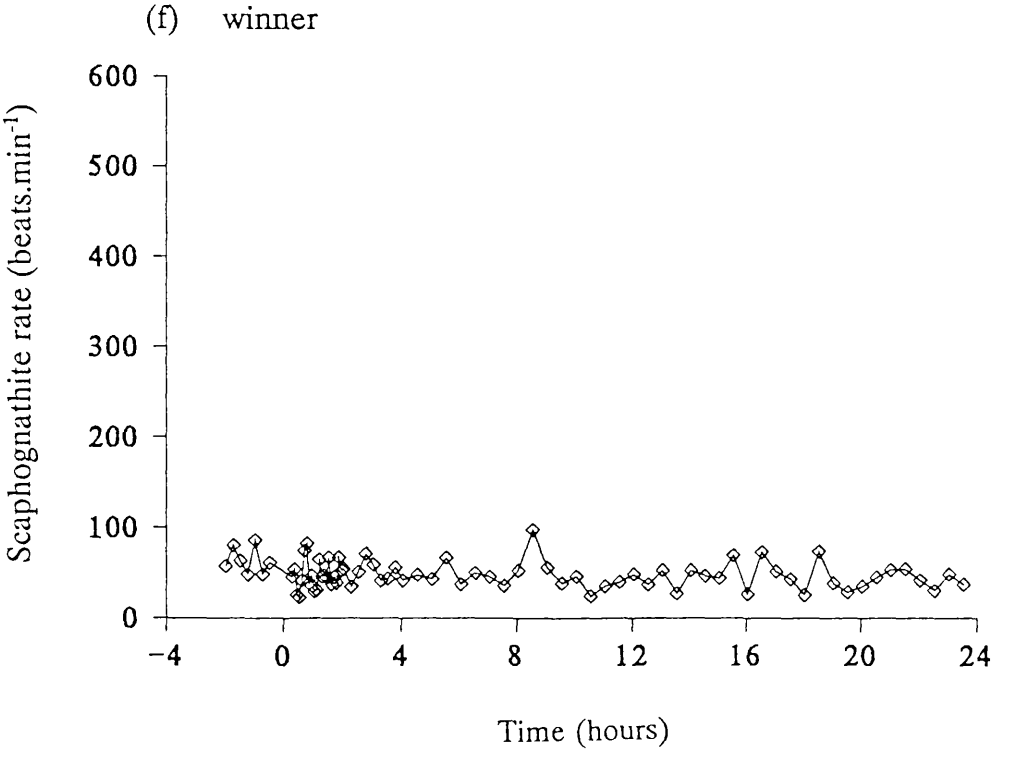
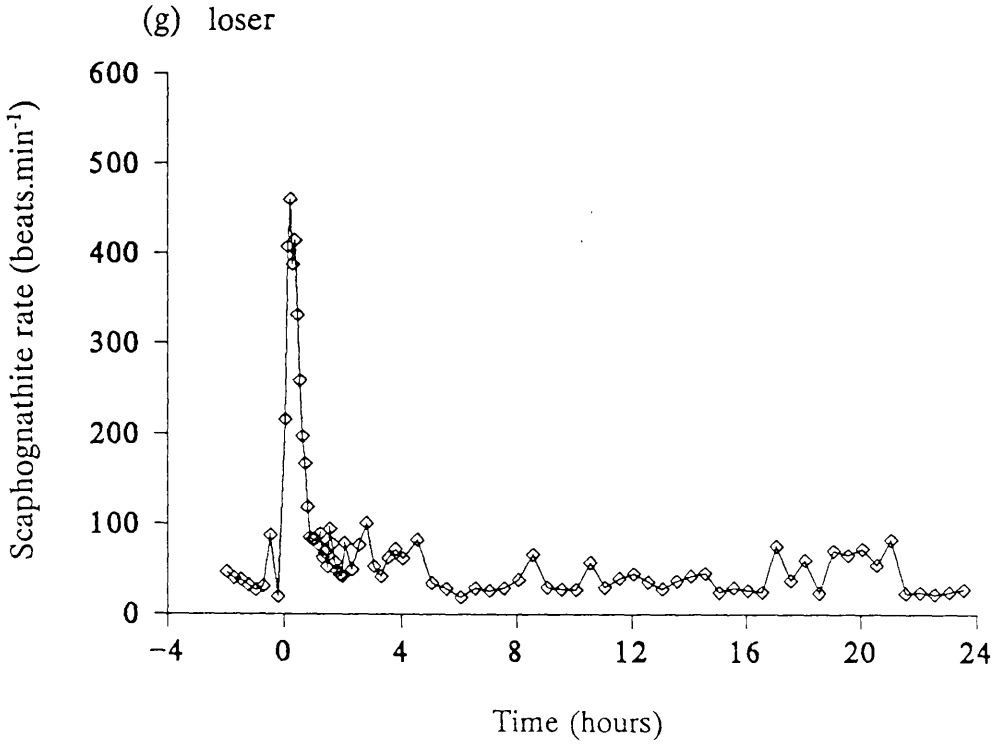


Figure 5.10 Continued



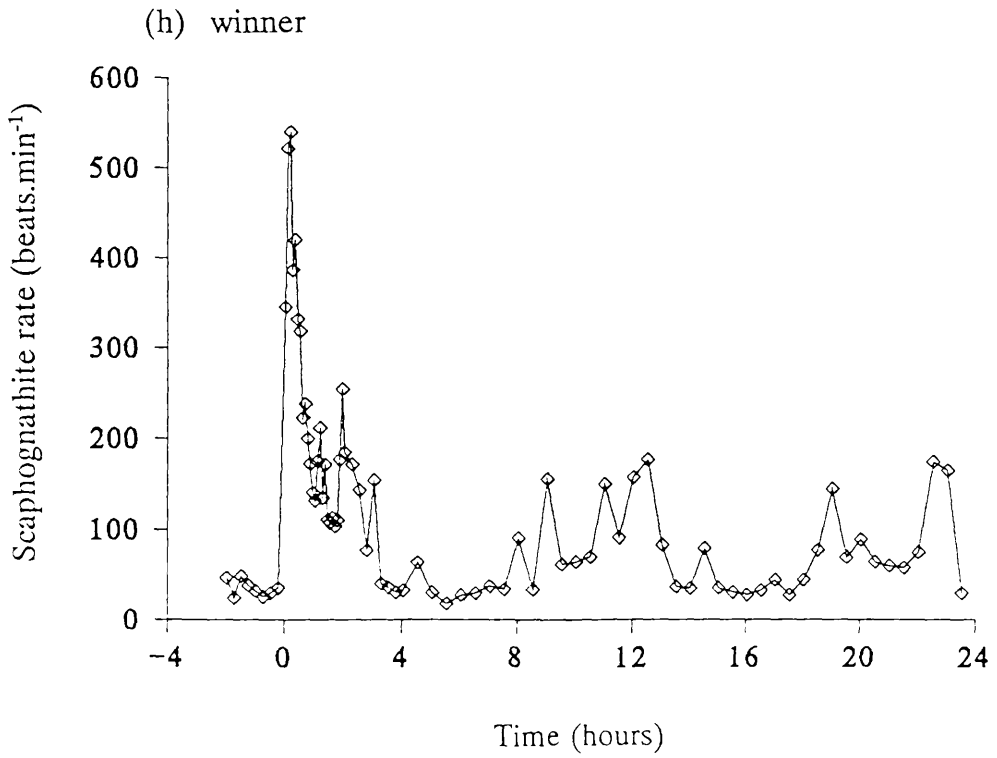
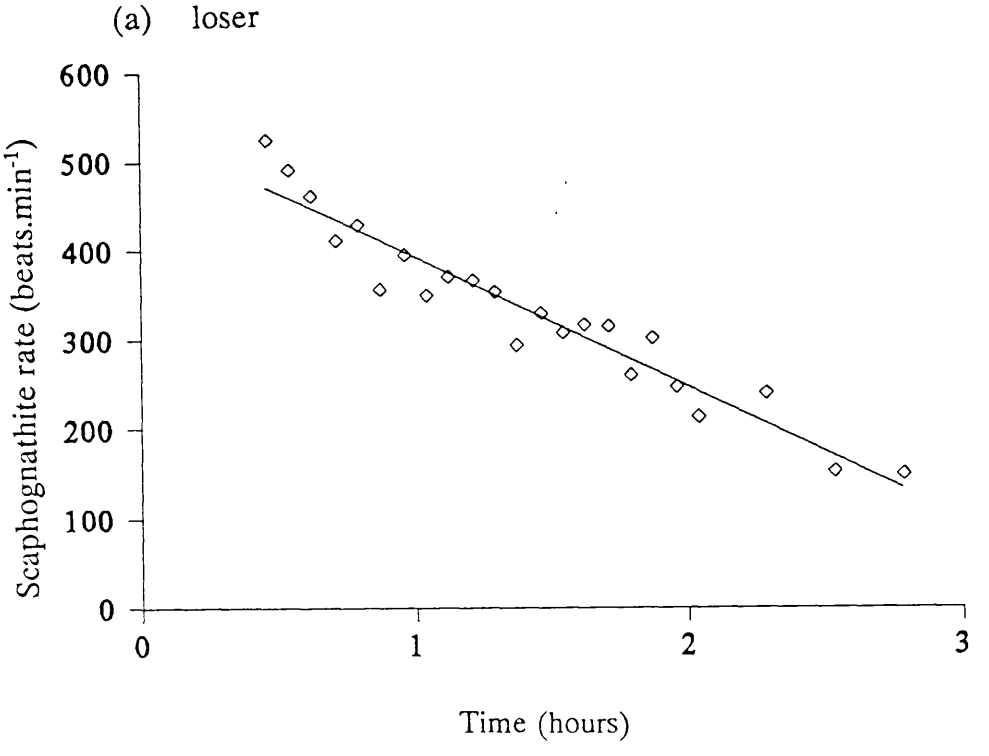


Figure 5.11 The relationship between scaphognathite rate and time during 3 hours after agonistic behaviour. Data from four pairs of interactants.



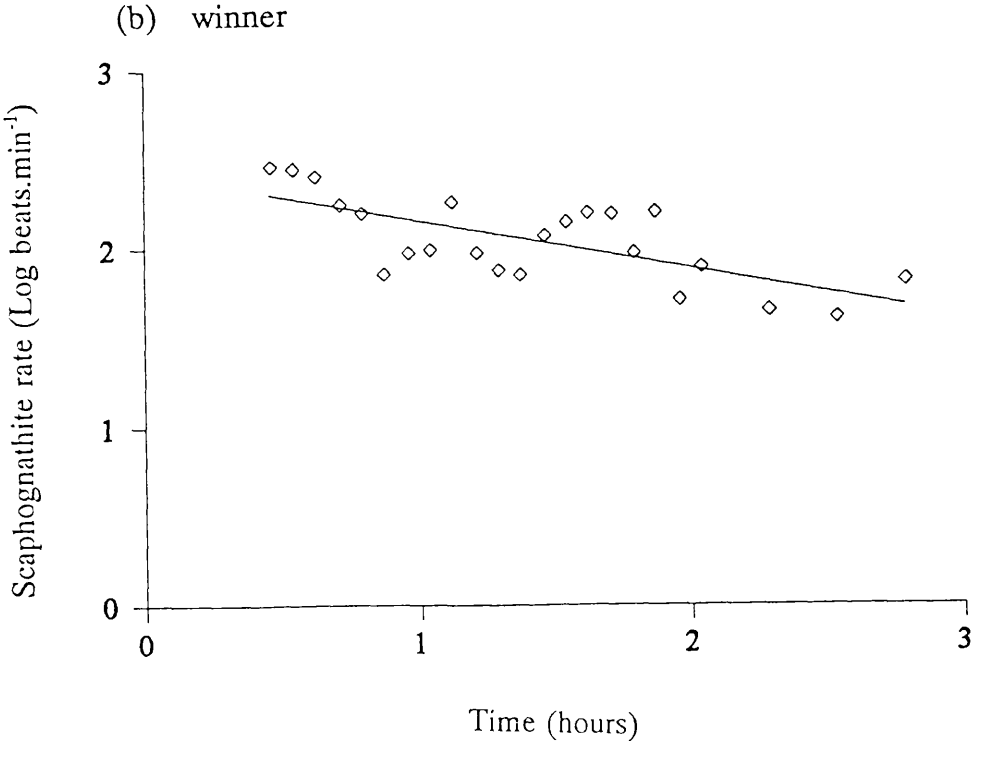
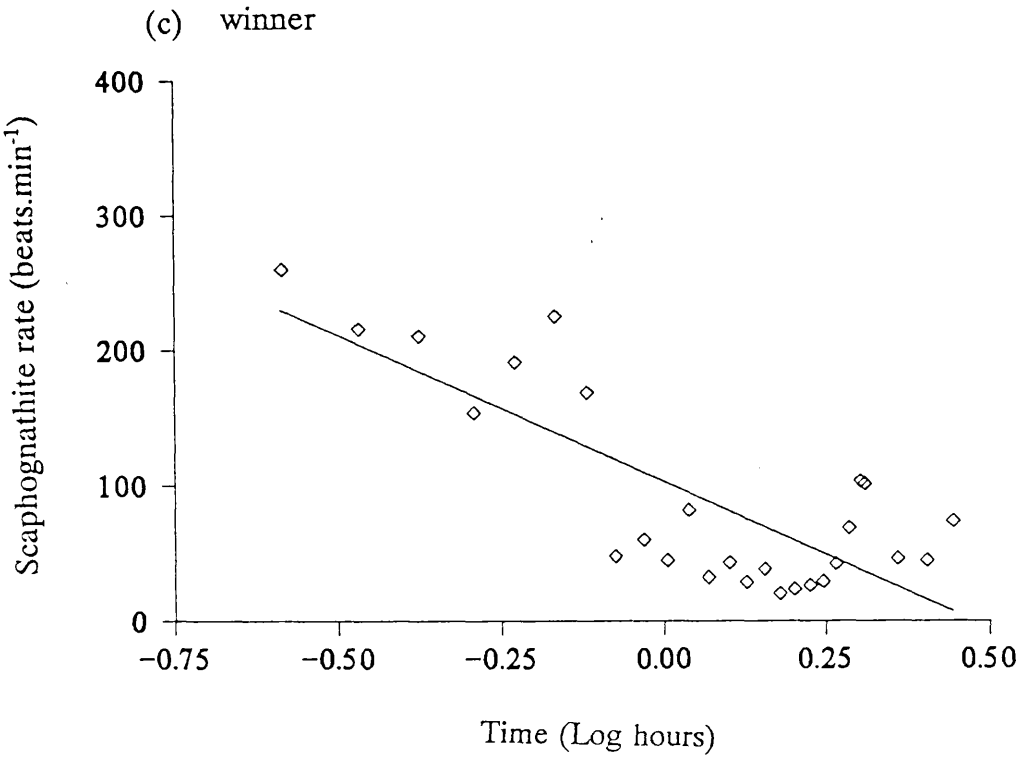


Figure 5.11 Continued



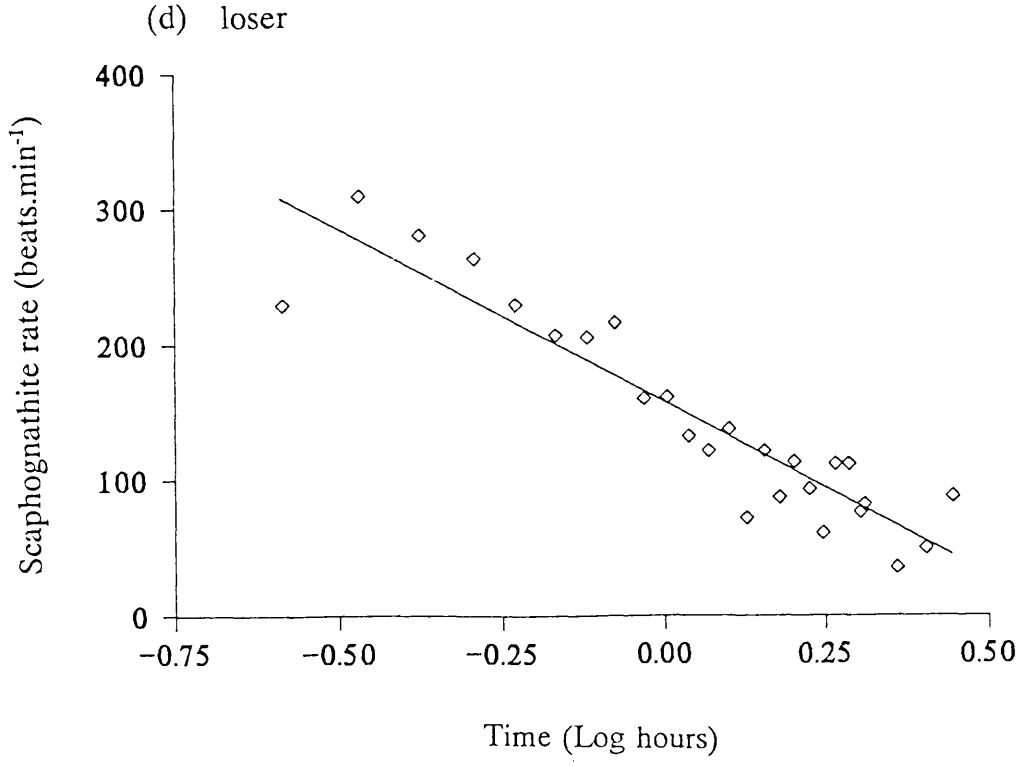
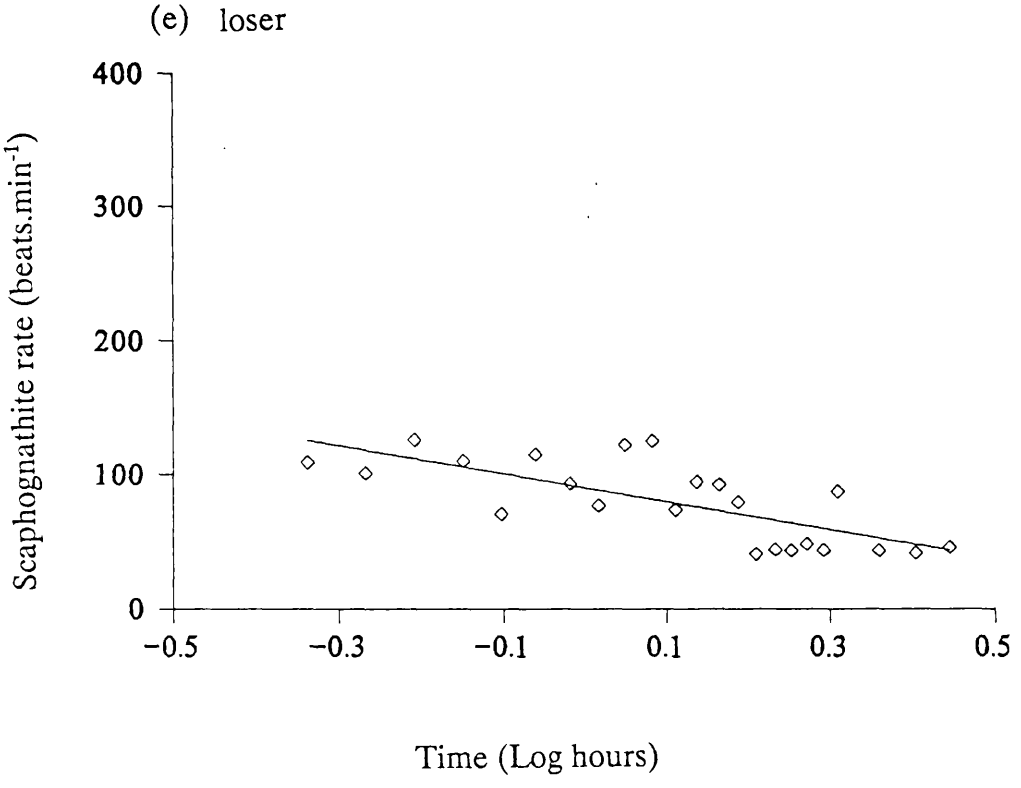


Figure 5.11 Continued



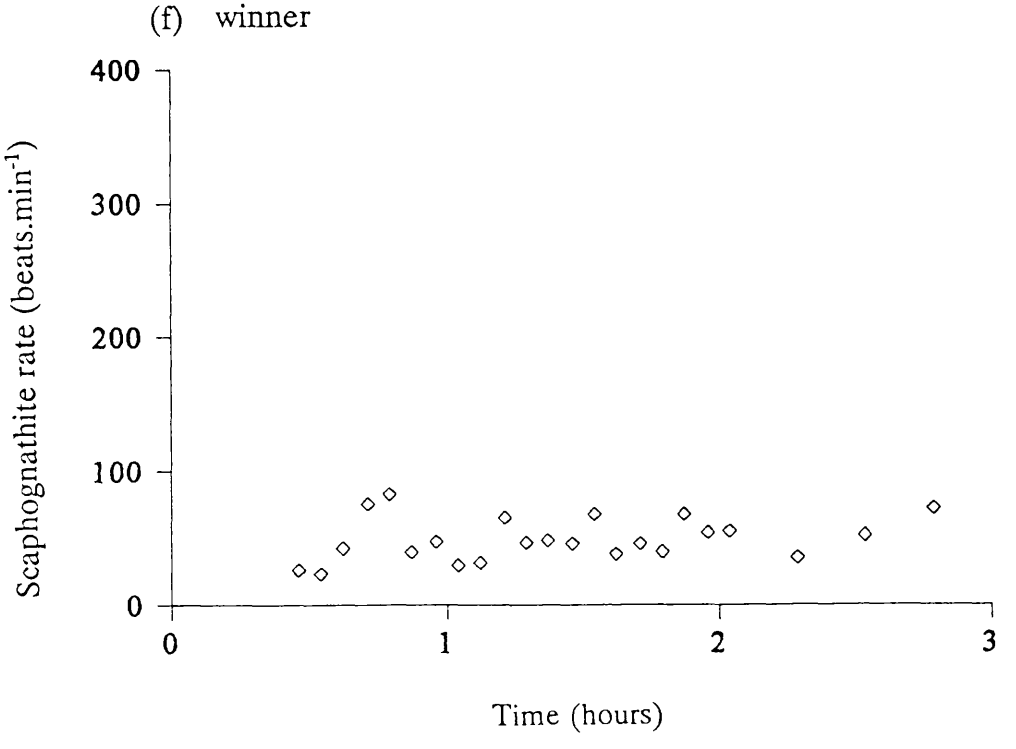
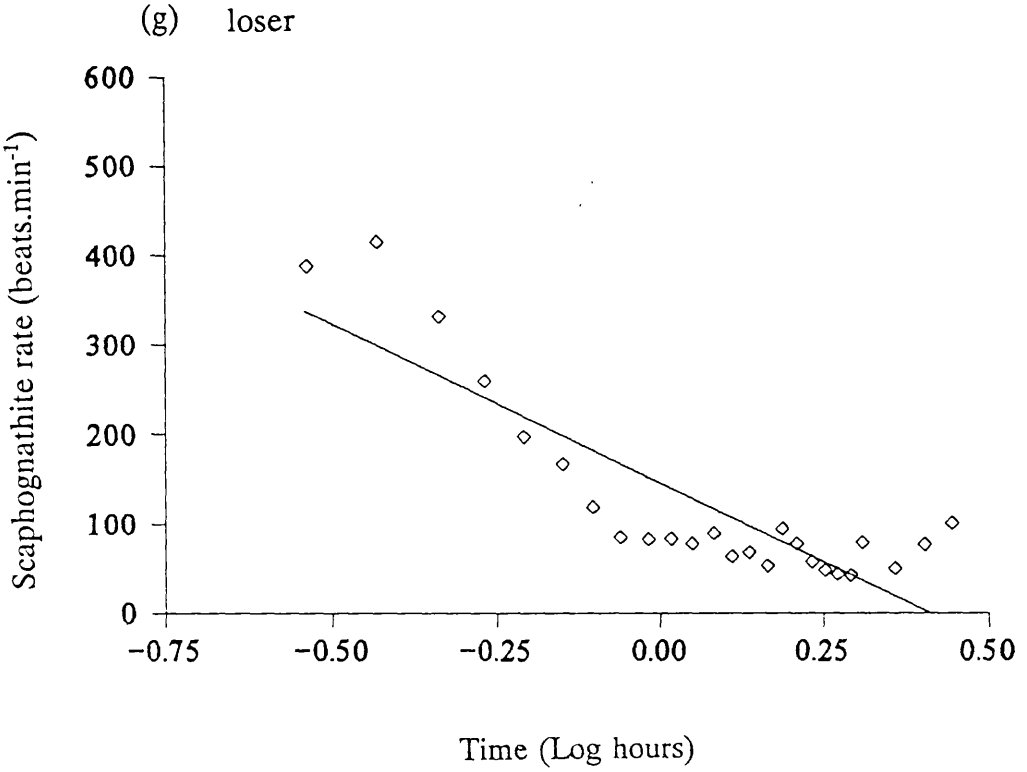


Figure 5.11 Continued



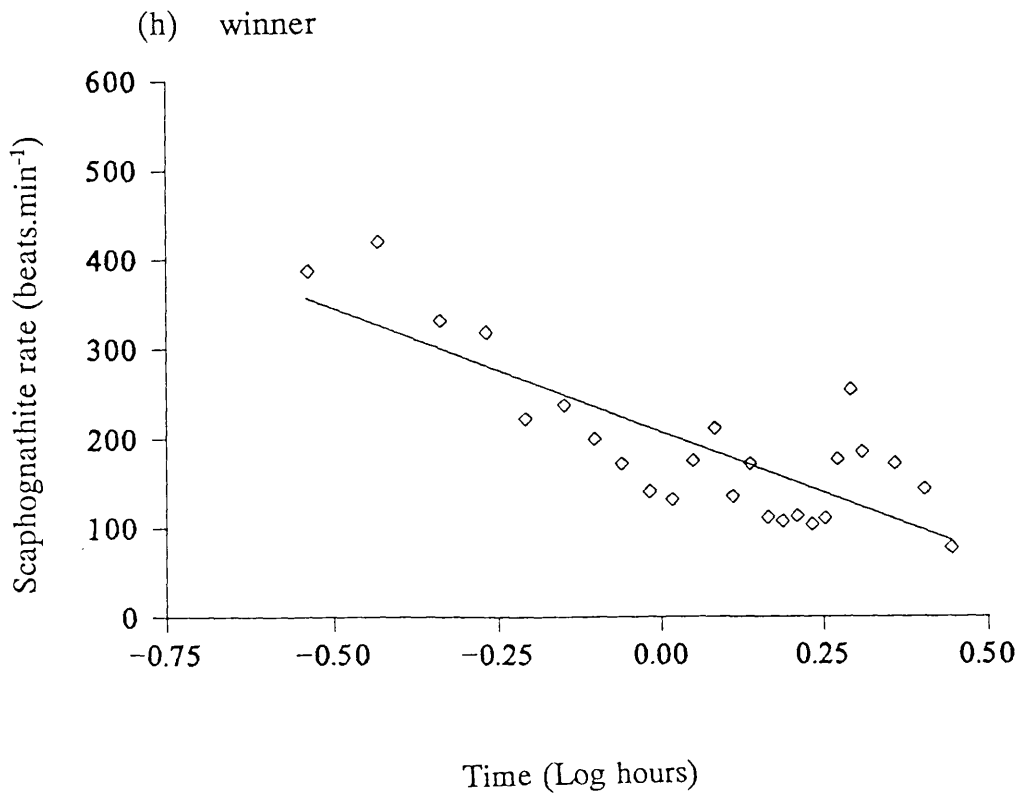


Table 5.7 Regressions of scaphognathite rate against time during the first three hours of recovery from agonistic interactions between male Liocarcinus puber.

Test no.	Crab	Regression type[1]	a	b	F	df	P
1	1	3	0.83	-1.96	113.67	1,26	<0.001
	2	-	-	-	-	-	-
2	1	-	-	-	-	-	-
	2	-	-	-	-	-	-
3	1	3	5.00	-4.99	53.79	1,24	<0.001
	2	3	2.61	-5.89	112.57	1,24	<0.001
4	1	3	0.81	-0.49	11.54	1,23	<0.01
	2	3	0.78	-0.68	8.86	1,23	<0.01
5	1	3	0.69	-0.74	10.28	1,21	<0.01
	2	3	0.81	-1.09	9.16	1,21	<0.01
6	1	3	1.55	-1.99	51.20	1,23	<0.001
	2	1	16.06	-4.69	288.35	1,23	<0.001
7	1	3	1.87	-0.86	8.30	1,21	<0.01
	2	3	3.77	-4.77	80.51	1,21	<0.001
8	1	3	1.92	-4.58	112.47	1,26	<0.001
	2	1	3.69	-1.14	64.64	1,26	<0.001
9	1	3	3.40	-7.29	134.26	1,25	<0.001
	2	3	2.96	-2.38	9.89	1,25	<0.01
10	1	2	0.30	-0.24	33.97	1,24	<0.001
	2	3	0.93	-0.85	43.79	1,24	<0.001
11	1	-	-	-	-	-	-
	2	3	1.30	-1.95	39.49	1,24	<0.001
12	1	3	0.97	-1.05	28.80	1,26	<0.001
	2	4	-0.05	-0.37	16.66	1,26	<0.001
13	1	3	3.38	-5.45	144.47	1,24	<0.001
	2	3	2.81	-5.89	41.63	1,24	<0.001
14	1	-	-	-	-	-	-
	2	3	1.67	-1.94	65.78	1,24	<0.001
15	1	3	1.25	-1.89	18.95	1,26	<0.001
	2	3	0.97	-1.41	20.33	1,26	<0.001
16	1	3	0.85	-1.29	75.02	1,26	<0.001
	2	3	1.27	-1.28	25.00	1,26	<0.001

Table 5.7 Continued.

1. Regression type refers to the transformation which gave the best linear fit to the data:

Type 1 - $F_{SCS}x = a + b.\text{Time}$

Type 2 - $\log F_{SCS}x = a + b.\text{Time}$

Type 3 - $F_{SCS}x = a + b.\log \text{Time}$

Type 4 - $\log F_{SCS}x = a + b.\log \text{Time}$

Table 5.8 The respiratory response of male *Liocarcinus puber* to agonistic behaviour and subsequent recovery, estimated from the scaphognathite rate.

Fight no.	Crab	Mass[1] (g)	F_{SCS}[2]. (undist)	EFSA[2]	Recovery time (h)	EPSA[3]	CNSA[3]
1	1	40	87.9	-0.03	0.82	0.69	0.66
	2	37	44.1	0.05	0.00	0.00	0.05
2	1	115	68.5	0.23	0.00	0.00	0.23
	2	115	118.9	0.03	0.00	0.00	0.03
3	1	130	35.4	2.68	6.32	13.71	16.39
	2	123	40.1	1.69	1.87	4.80	6.48
4	1	97	60.7	0.89	0.40	0.09	0.97
	2	93	103.3	0.80	0.47	0.14	0.94
5	1	130	68.8	0.05	0.38	0.12	0.17
	2	127	55.5	0.49	0.67	0.32	0.80
6	1	108	70.6	1.33	1.89	1.63	2.96
	2	111	29.4	4.03	3.21	24.17	28.20
7	1	64	45.7	3.07	10.30	3.86	6.93
	2	51	57.0	3.21	3.80	7.87	11.08
8	1	130	17.9	-0.01	1.59	3.16	3.15
	2	130	98.8	-0.08	2.36	3.18	3.09
9	1	33	16.8	0.81	2.14	6.76	7.57
	2	44	28.7	0.32	6.65	6.88	7.20
10	1	119	37.9	1.11	1.22	0.53	1.65
	2	123	61.0	0.41	0.82	0.31	0.72
11	1	93	53.7	0.41	0.00	0.00	0.41
	2	93	22.4	0.68	1.43	1.22	1.89
12	1	111	62.0	0.23	0.93	0.42	0.65
	2	111	48.2	0.26	0.74	0.43	0.69
13	1	100	46.8	0.91	2.73	6.47	7.38
	2	108	36.6	0.90	2.03	5.19	6.10
14	1	164	63.9	-	0.00	0.00	-
	2	220	50.2	-	2.21	1.87	-
15	1	111	33.0	0.01	1.35	1.11	1.12
	2	108	69.2	-0.06	0.95	0.59	0.53
16	1	134	84.4	0.15	0.77	0.43	0.58
	2	141	68.1	0.23	1.63	0.91	1.14

Table 5.8 Continued.

1. Mass was estimated from a regression of mass agaist carapace width determined from a seperate group of crabs.

$$\textbf{Mass} = 3.75\ \textbf{Carapace width} - 151.0 \quad F_{(1,22)} = 250.2,\ P<0.001$$

2. EFSA - the excess scaphognathite activity during the interaction:

$$\textbf{EFSA} = \textbf{Duration}.[F_{SCS}(\textbf{int}) - F_{SCS}(\textbf{undist})]/F_{SCS}(\textbf{undist})$$

where Duration = the duration of the agonistic interaction (hours)

F_{SCS}(int) = the mean scaphognathite rate during the interaction (beats.min^{-1})

and F_{SCS}(undist) = the mean undisturbed scaphognathite rate (beats.min^{-1})

Negative values occur where F_{SCS}(int) < F_{SCS}(undist) due to the predominance of apnoea during the interaction.

3. EPSA - the excess post-interaction scaphognathite activity

CNSA - the cumulative net scaphognathite activity.

$$\textbf{CNSA} = \textbf{EFSA} + \textbf{EPSA}$$

See text for detailed explanations of these terms.

where A(rec) = the area under the recovery curve, estimated from the integral of the function describing the recovery of $F_{scs}x$ between the end of agonistic behaviour and the estimated recovery time (beats.60^{-1}.F_{scs}(undist)$^{-1}$),

and Rec = the product of the estimated recovery time (hours) and $F_{scs}x$(undist) (=1).

The total respiratory demand of this behaviour (cumulative net scaphognathite activity, CNSA) has been estimated as the excess scaphognathite activity during the interaction itself plus that during recovery (CNSA = EFSA + EPSA).

The excess scaphognathite activity during fighting was correlated with the interaction duration for both winners (r_s = 0.682, df = 13, P<0.01) and losers (r_s = 0.698, df = 13, P<0.01). The excess scaphognathite activity during recovery (EPSA) was not correlated with interaction duration for winners (r_s = 0.003, df = 14, P>0.50) or losers (r_s = 0.277, df = 14, P>0.20). The cumulative net scaphognathite activity (CNSA) was correlated with interaction duration for losers (r_s = 0.573, df = 13, P<0.05), but not for winners (r_s = 0.130, df = 13, P>0.50). Despite this difference, there was no significant difference between winners and losers in terms of the excess scaphognathite activity during fighting (median EFSA of winners = 0.321, median EFSA of losers = 0.487; Wilcoxon's T = 62.0, n = 15, P>0.50), in terms of the excess scaphognathite activity during recovery (median EPSA of winners = 0.799, median EPSA of losers = 0.901; T = 71.0, P>0.50) or in terms of the total excess scaphognathite activity (median CNSA of winners = 1.136, median CNSA of losers = 0.937; T = 65.0, n = 15, P>0.50).

The intensity of interactions could be classified according to the occurrence of bilateral display and striking. The excess scaphognathite activity during fighting was greater for crabs engaged in interactions involving bilateral display and bilateral striking than those involved in less intense types of interaction (Kruskal Wallis H_{adj} = 7.63, df = 1, P<0.01). There was no significant relationship between interaction intensity and the CNSA (H_{adj} = 2.07, df = 1, P>0.10). However, the number of strikes received by the loser was significantly correlated with the excess scaphognathite activity during fighting for the winner (r_s = 0.827, n = 7, P<0.05) and loser (r_s = 0.869, n = 7, P<0.05) and with the cumulative net scaphognathite activity of the loser (r_s = 0.810, n = 7, P<0.05), but not the winner (r_s = 0.391, n = 7, P>0.05).

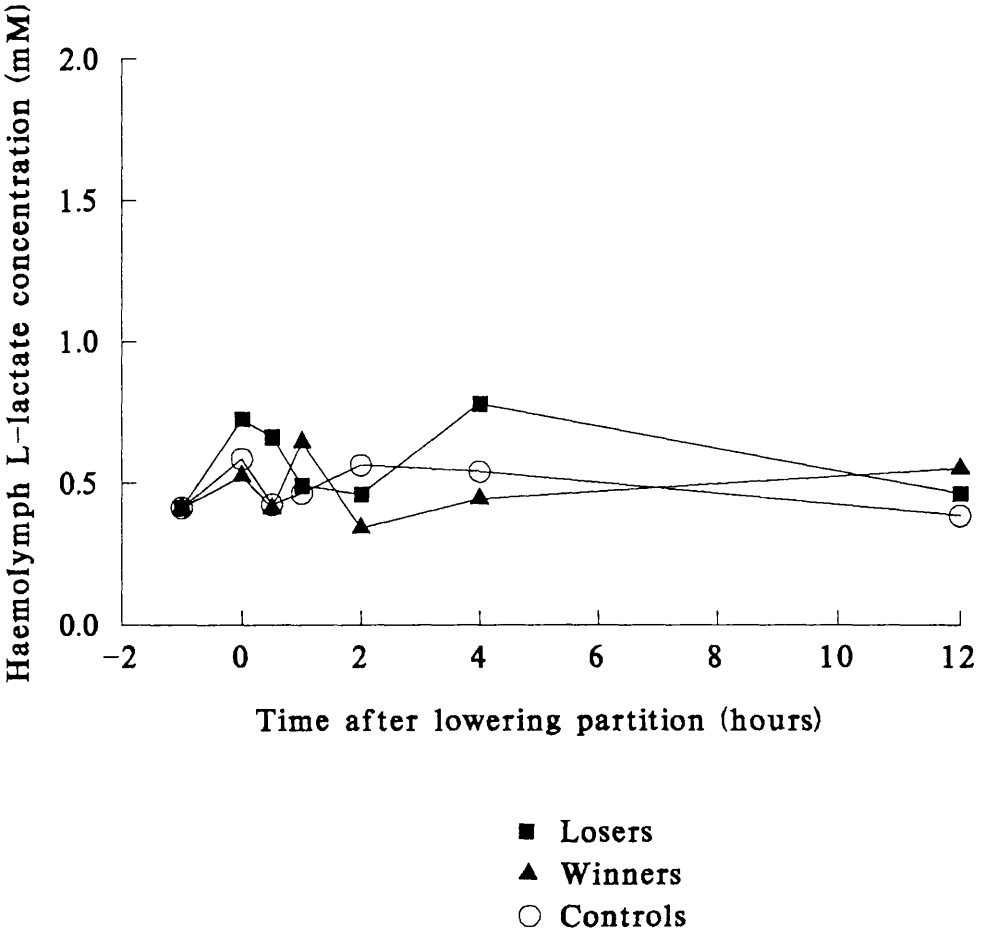
There was an indication that the number and total duration of swimming retreats by the loser was correlated with its excess scaphognathite activity during the interaction and with its cumulative net scaphognathite activity, but these correlations were not significant (EFSA: $r_s = 0.695$, $n = 7$, $P>0.05$; CNSA: $r_s = 0.689$, $n = 7$, $P>0.05$).

5.3.5 Haemolymph L-lactate concentrations after agonistic behaviour

The means of the measurements of haemolymph lactate concentration were significantly correlated with their variances. Estimation of means and analysis of variance were therefore carried out on these measurements after logarithmic transformation (base 10).

A two way ANOVA with recovery time (0-12 h) and category of crab (winner, loser or control) as factors indicated that mean haemolymph concentrations were not significantly different in crabs after different recovery periods ($F_{(5,10)} = 0.968$, $P>0.50$) or between any of the three categories of crab ($F_{(2,58)} = 2.14$, $P>0.10$). Since agonistic behaviour did not result in lactate levels significantly greater than in crabs only subjected to raising and lowering of the partition, energy production by anaerobic metabolism during interactions was presumably not important (Figure 5.12).

Figure 5.12 Mean haemolymph L-lactate concentrations in male *Liocarcinus puber* after agonistic behaviour.



5.4 DISCUSSION

5.4.1 Exercise performance of *Liocarcinus puber*

Liocarcinus puber could be induced to swim for 3 - 8 minutes by suspending them above the substratum, after which time they were unresponsive to tactile stimulation. This may have been because they were incapable of further exercise or because they habituated to the stimuli causing them to swim (loss of contact with the substratum and tapping on the carapace). During the course of the exercise bout, the beat rate of the swimming legs declined, until eventually the crab no longer generated noticeable propulsive force. The weak movements of the swimming legs which followed were interpreted as continued attempts to swim. At this stage, only one or two more bouts of swimming could be induced by tactile stimulation. It is unlikely that habituation to this stimulus occurred during the short duration of these trials. Observations of crabs during preliminary trials indicated that when they became unresponsive to gentle tactile stimulation, they would not respond to severe disturbance either. It is probable, therefore, that exercise ceased due to fatigue rather than habituation.

The short fatigue times of *Liocarcinus puber* when swimming contrast sharply with the capabilities of the related swimming crab, *Callinectes sapidus* (Booth *et al.*, 1982; Booth *et al.*, 1984; Houlihan *et al.*, 1985). *C. sapidus* was capable of swimming up to one hour in laboratory conditions and are known to undergo long breeding migrations (Spirito, 1972). The endurance of *L. puber* is similar to that of less active crabs such as *Cancer magister* (McMahon *et al.*, 1979) and *Carcinus maenas* (Burke, 1979) which can only sustain short periods of strenuous activity. Fatigue presumably occurs when the rate of ATP utilisation exceeds that of ATP formation and available ATP is depleted. The rate of ATP production may be impaired by acid-base disturbances affecting enzymes involved in ATP producing pathways or by depletion of the substrates of these enzymes. Anaerobic metabolism results in accumulation of acidic end products and inefficient - and therefore rapid - utilisation of substrates. Onset of fatigue is therefore more rapid when the supply of oxygen to the muscles is inadequate to sustain the energy demand aerobically. Aquatic crustaceans may be limited in their ability to supply oxygen to respiring tissues by the relative impermeability of the chitinous gills, the 'open' circulatory

system and the low oxygen carrying capacity of the blood (Taylor, 1982). These limitations may be compensated to some extent by stores of oxygen in the blood (the "venous reserve", McMahon and Wilkens (1983)).

The maximum rates of oxygen uptake recorded in this study were increases of 2.5 - 4.0 fold over the undisturbed rate. Since these measurements were made some minutes after the end of exercise, they are probably underestimates of the maximum factorial aerobic scope of *L. puber*. The rate of decline of the rate of oxygen consumption during the early part of recovery was very rapid. Therefore, although the crabs may have been subject to continued disturbance during the transfer from the exercise tank to the respirometer, it is likely that their rates of oxygen uptake were higher immediately after exercise. Published values for aerobic scope in other marine crustaceans have also been influenced by methodology. In some, the "resting" rate has been elevated due to experimental disturbance (McMahon *et al.*, 1979; Houlihan *et al.*, 1984,1985); in others, the mean "active" rate has underestimated the maximum rate due to inclusion of data from sub-maximal activity (Houlihan *et al.*, 1984,1985), or due to difficulty in quantifying the intensity of exercise (McMahon *et al.*, 1979).

After cessation of exercise, the rate of oxygen consumption of *L. puber* took between 2 to 14 hours to return to pre-exercise levels. A disproportionately long recovery period in comparison with the exercise bout has been found in all marine crabs subjected to strenuous activity and has been associated with significant accumulation and subsequent slow removal of lactate (McMahon *et al.*, 1979; Booth *et al.*, 1984). However, the magnitude of the oxygen debt has not always been clearly related to the duration or intensity of anaerobiosis, nor have the time-courses of oxygen consumption recovery and lactate removal always been closely coupled (Ellington, 1983). In this study the estimated excess post-exercise oxygen consumption was not related to the duration of the exercise period. This may have been because some components of excess post-exercise oxygen consumption are not directly related to energy expenditure (Herreid, 1980), because duration of swimming bout was not a good index of the energy expenditure of the crabs, or because a proportion of the oxygen debt was not measured.

It was apparent that there was variation in the intensity of exercise performed by different crabs. The duration of a swimming bout was therefore not necessarily well correlated with the energy expended by the crab. Further investigation of the relationship between energy expenditure and oxygen consumption in this species

requires the power output and oxygen consumption of crabs to be measured throughout the exercise and recovery periods. The power output of swimming crabs would be difficult to measure accurately due to the variety of thrust vectors that they develop during swimming. It is possible to measure the work rate of terrestrial crabs walking on a treadmill (Herreid and Full, 1988). A treadmill within a water-filled respirometer might allow control of the ambulatory exercise of an aquatic crab, while simultaneously monitoring oxygen consumption.

5.4.2 The relationship between heart and scaphognathite rates and oxygen consumption

Due to the restrictive nature of available techniques for direct measurement of oxygen consumption, the scaphognathite rate has been used as an indirect measure of aerobic metabolism. Assuming that most oxygen uptake occurs in the branchial chambers (Taylor, 1982), the amount of oxygen consumed per beat of the scaphognathites is a function of the oxygen content of the water, the stroke volume of the scaphognathites and the extraction efficiency of the branchial chambers. The positive Y-axis intercepts obtained for all regressions of rate of oxygen consumption against scaphognathite rate indicate that the quantity of oxygen consumed per scaphognathite beat decreased with increasing beat rate, but above around 60 beats.min^{-1} the rate of change was small. The change in oxygen consumption in relation to the scaphognathite rate may have been due to changes in the respiratory performance of crabs at different respiratory rates or to systematic changes in the error of measurement. Changes in the performance of the respiratory system that would lead to lower oxygen consumption per scaphognathite beat are a decrease in the stroke volume of the scaphognathites at high rates of beating, or an increase in the extraction efficiency of oxygen from the water by the branchial chambers at low respiratory rates. McDonald *et al.* (1980) found a marked increase in the extraction efficiency of the branchial chambers of *Cancer magister* at the onset of unilateral ventilation. The occurrence of this phenomenon in *L. puber* could explain at least part of the observed variation in oxygen uptake per beat. Systematic changes in the error of measurement may have resulted from the difficulty in accounting for oxygen consumption other than that by the crab. The "background" oxygen consumption within the respirometer increased during the course of measurements, as final background values were higher than initial background values. Since it was not

possible to estimate background consumption continuously, an average of the initial and final values was used. This average was necessarily an under-estimate of the actual background consumption towards the end of the period of measurements of any one crab. Such under-estimation of the background oxygen consumption would lead to over-estimation of consumption by the crab at a time when respiratory rates were low. Another reason for under-estimation of background consumption and consequent over-estimation of the oxygen consumption of the crab, was that the component of background consumption due to epibionts on the crab could not be accounted for, as they were introduced and removed with the crab. It is unknown in what way oxygen consumption by epibionts changed during the period of measurements.

As the relationship between oxygen uptake and scaphognathite rate differed between individuals it was not possible to predict the oxygen consumption of a different group of crabs accurately from their scaphognathite rates. All respiratory measurements were therefore standardised by expressing them as a multiple of the undisturbed rate of each crab.

The increase in oxygen uptake per beat at low scaphognathite frequencies resulted in the average recovery time of the scaphognathite rate being less than the recovery time of the rate of oxygen consumption. The 'cumulative net scaphognathite activity' has been calculated in an analogous way to the "cumulative net oxygen consumption" (Herreid, 1980). The cumulative net scaphognathite activity is the number of beats in excess of that which would have occurred in the undisturbed state, which are attributable to agonistic behaviour (standardised with respect to the undisturbed rates of individual crabs). Since the oxygen consumed per beat only varied significantly at very low beat rates, the cumulative net scaphognathite activity is a useful estimate of the cumulative net oxygen consumption. Respiratory measurements were not available during the swimming bout nor for the first five minutes of recovery. It was therefore not possible to compare the cumulative net oxygen consumption with the cumulative net scaphognathite activity incurred by this activity. However, the excess post-exercise oxygen consumption was correlated with the excess post-exercise scaphognathite activity. The heart rate was also elevated after exercise, but declined to undisturbed levels at a different rate from the oxygen consumption and scaphognathite rates. There was consequently not as close a relationship between heart rate and oxygen consumption as between scaphognathite

rate and oxygen consumption. It has been noted in other crustaceans that cardiac output increases during exercise, but that this is accomplished mainly by an increase in cardiac stroke volume rather than a proportional increase in heart rate (McMahon and Wilkens, 1983).

5.4.3 Respiratory activity during agonistic behaviour

In 90% of the crabs in which the scaphognathite rate was monitored during agonistic behaviour, mean rates during the interaction were elevated. This elevation was brought about by periods of extremely rapid scaphognathite beating, alternating with periods of apnoea. The scaphognathite rates obtained in this study are compared with published values for a variety of decapod crustaceans in Table 5.9. Useful comparison of the results of these studies is limited by the varied experimental conditions and procedures to which the animals were subjected. The highest rates reported were for *Callinectes sapidus* during sustained swimming. This study was carried out at 20°C, but the animals were not thought to be swimming maximally (Booth *et al.*, 1982). Apart from *C. sapidus*, *L. puber* has the highest recorded scaphognathite rate for the range of decapod crustaceans in Table 5.9. The maximum rate of 726.2 beats.min^{-1} (a 30 s average) was recorded from a 64 g crab which initiated and won an interaction involving bilateral display and bilateral striking. Certain behaviours were associated with greatly increased scaphognathite beat frequencies. Striking appeared to have the most marked effect on the scaphognathite rate. Often, one strike was followed by greatly elevated rates in both crabs. Bilateral display, particularly when the crabs pushed against each other, also resulted in high frequency beating. Interactions with bilateral display and strikes consequently involved higher rates of beating and greater excess scaphognathite activity than less intense interactions. It is not known whether these acts are highly energetic in themselves or if escalation of intensity results in elevation of respiratory rates in preparation for possible future acts. Rapid scaphognathite beating itself has an associated energetic cost, regardless of the activity that causes it. Wilkens *et al.* (1984) estimated the energetic efficiency of the scaphognathites of *Carcinus maenas* as 3.15% and they suggested that the oxygen consumed by the scaphognathite muscles at high beat frequencies might limit the animal's aerobic capacity for exercise.

The production of strong respiratory currents during agonistic behaviour has been

Table 5.9 Scaphognathite rates of decapod crustaceans: a comparison of published values with the results of the present study.

Species	Mass (g)	Temp. (°C)	F_{SCS} max.[1] (bpm)	n[2]	Comments	Reference
Cancer productus	226-460	12	254 ± 9	10	5-10 mins after apnoea	McMahon & Wilkens (1977)
Cancer magister	551-960	8 ± 1	302 ± 10	9	After 20 mins prodding	McMahon et al (1979)
Callinectes sapidus	90-190	20	624 ± 38.8	11	During sustained swimming	Booth et al (1982)
Liocarcinus depurator	-	16 ± 0.5	100 (mean)	-	During hypoxia[3]	Uglow (1973)
Liocarcinus holsatus	-	16 ± 0.5	190 (mean)	-	" "	" "
Carcinus maenas	83-105	12-13	330 ± 66.7	12	After 1 min. tactile stimulation	Mercier & Wilkens (1984)
" "	71-133	12-13	500 (max)	-	Recovery from operation	Wilkens et al (1984)
Procambarus clarkii	-	10	344 ± 34	-	"Strenuous activity"	C.D. Hassal & B.R. McMahon[4]
Pacifastacus leniusculus	26.3 ± 3.7	10	157.0 ± 8.0	6	After prodding with a glass rod for 10 minutes	Rutledge (1981)
		20	273.7 ± 14.9	6		" "
		25	282.0 ± 14.5	6		" "
Liocarcinus puber	33-141	10	372.6 ± 37.9 (12.1-726.2)	30	During agonistic behaviour	Present study

Table 5.9 continued

1. Scaphognathite rates are means ± standard errors of the sum of the frequencies of both scaphognathites, unless otherwise stated.

2. Number of animals used to determine mean.

3. Hypoxia data included for comparison of congeners.

4. Unpublished data cited by McMahon and Wilkens (1983).

noted in some other crustaceans. Jachowski (1974) observed that the blue crab, *C. sapidus*, produced a strong jet of water directed at the opponent during agonistic encounters and he suggested that this might be a tactile or olfactory stimulus. The same phenomenon has been noted in the river crab, *Potamon potamios* (Erpenbeck and Altevogt, 1966), the intertidal crab, *Grapsus* (Kramer, 1967), the crayfish, *Orconectes virilis* (Rubenstein and Hazlett, 1974) and several hermit crab species (Barron and Hazlett, 1989). In the last-named study, hermit crabs produced currents directed downwards during agonistic interactions, compared with the normally upwardly directed respiratory current. This, and the fact that production of a downwards current by a hermit crab often resulted in the retreat of its opponent, led Barron and Hazlett (1989) to suggest that these currents were hydrodynamic displays. When *Liocarcinus puber* engage in bilateral display and push each other, the exhalant channels and the antennules - which have a chemosensory function (Gleeson, 1980) - of the two crabs are in close proximity. It is therefore likely that crabs are able to detect the current produced by their opponents. If the strength of ventilatory currents reflects the size and fitness of crabs, then it is possible that these are used to assess "resource holding power" (Parker, 1974). In addition, it is probable that any olfactory stimulus carried in the ventilatory current of one crab would be detected by its opponent. These suggestions remains speculative, however. A rapid respiratory rate in response to intense activity would inevitably result in a strong jet of water from the scaphognathites.

5.4.4 Recovery from agonistic behaviour

The mean recovery time from agonistic behaviour estimated from the scaphognathite rate was 1.8 ± 0.80 hours (mean ± 95% C.L.) compared with 3.7 ± 1.21 hours to recover from exhaustive swimming. Due to the apparent increase in oxygen uptake per beat at low scaphognathite rates, these figures are probably underestimates of the recovery time of the rate of oxygen consumption. While it is evident that agonistic behaviour is not exhausting, the respiratory consequences of fighting last much longer than the duration of the interaction itself. There was no significant accumulation of haemolymph lactate during agonistic behaviour, in contrast to the marked elevations of lactate measured in decapod crustaceans subjected to a variety of stresses (Table 5.10). The prolonged post-agonistic period of elevated respiratory rate did not therefore represent an "oxygen debt", where

Table 5.10 Haemolymph L-lactate concentrations in aquatic decapod crustaceans: a comparison of published values with the results of the present study.

Species	Temp. (°C)	Lactate concentration (mM) rest	post-exercise	Comments	Reference
Cherax destructor	10	0.5	4.1	≈1 h after 30 tail flips	Phillips *et al* (1977)
Homarus gammarus	7	0.1	1.3	≈20 mins after 30 tail flips	" " " "
Nephrops norvegicus	7	0.14	0.5	2 min after exercise	" " " "
Carcinus maenas	7	0.30	4.00	6 min after exercise	" " " "
Cancer pagurus	7	0.14	2.10	8 min after exercise	" " " "
Liocarcinus puber	7	0.34	1.10	7 min after exercise	" " " "
Maia lithodes	7	0.15	0.47	7 min after exercise	" " " "
Carcinus maenas	15	2.44	13.22	after 15 min activity in air	Burke (1979)
" "	22.5	2.78	7.11	after 15 min activity in water	" "
Callinectes sapidus	20	0.7	2.4	after 2 min swimming	Booth *et al* (1982)
	-	-	9.8	after 25 min swimming	" " " "
Liocarcinus puber	15	0.4	11.1	after 24 h aerial exposure (RH=75-80%)	Johnson & Uglow (1985)
" "	10	0.27	0.72	losers 0 h after agonistic behaviour	Present study
" "			0.64	winners 1 h after agonistic behaviour	" "

excess oxygen was consumed during recovery as a consequence of lactate metabolism (Herreid, 1980). The periods of hyperventilation and the oxygen and phosphagen stores within the animals appear to be sufficient to support agonistic activity and associated periods of apnoea without recourse to anaerobic metabolism. The respiratory and metabolic responses of aquatic crustaceans to sub-maximal exercise have received relatively little attention (McMahon and Wilkens, 1983). The components of excess post-exercise oxygen consumption in response to such activity have therefore not been identified. Although part of the post-agonistic elevation of respiratory rate may be attributed to spontaneous activity in some crabs, in those which remained quiescent after the interaction, it was presumably associated with recharging of oxygen and phosphagen stores. The rôle of hormones in regulating energy production during agonistic behaviour in crustaceans is not known. Some hormones, such as 5-Hydroxytryptamine, cause large increases in heart and scaphognathite rates and their effects have been shown to persist for up to 2 hours (Wilkens, 1981).

Unsystematic observations during this study suggested that winners were more likely to move around the observation tank after an agonistic interaction than losers, which tended to remain quiescent. This was reflected in the poorer mathematical descriptions of the recovery data which were possible for winners. This phenomenon has not been noticed before in *L. puber*, because post-agonistic activity has not been studied. Post-agonistic activity would lead to increased estimates of energetic expenditure. Whether these should be considered overestimates depends on whether this activity is a result of agonistic behaviour, in which case it represents part of the energetic expenditure associated with fighting. Inhibition of activity in losers may also represent a cost in terms of lost opportunities for resource acquisition. Realistic interpretation of this phenomenon awaits information on post-agonistic activity of crabs in natural conditions.

5.4.5 Energetic cost of agonistic behaviour

As the energy requirement of agonistic behaviour was met primarily by aerobic metabolism, the energetic cost of this activity should be closely related to the oxygen consumption (Eckert *et al.*, 1988) - and therefore also to the scaphognathite rates - of the interactants.

The energetic expenditure of crabs during agonistic behaviour must be a function of the duration of the interaction and the acts involved. Agonistic interactions of *L. puber* are variable in their content and duration (chapter 2). An attempt to reduce this variation was made by pairing size-matched crabs to produce a high proportion of intense interactions, which were assumed to be the most energetically expensive. Although most interactions in this study were relatively intense, involving bilateral display and striking, there remained considerable variation in their content.

The duration of agonistic encounters was found to be related to the estimated energetic costs of losers but not winners. However, there was no significant difference in estimated energy expenditure between losers and winners. During most interactions, eventual winners and losers performed similar activities. Major differences did not occur until near the resolution of an encounter, when winners tended to strike more and losers retreated from their opponents by swimming (winners did not swim in any of the interactions in this study). These differences do not seem to have been sufficient to cause disparity of energy expenditure between winners and losers.

The data only permitted analysis of the relationship between interaction intensity and energetic cost on the basis of a coarse classification of intensity. This analysis indicated that while more intense interactions involved greater respiratory rates during the interaction itself, there was no significant relationship between intensity and total energetic cost as estimated by the cumulative net scaphognathite activity. The content of interactions seemed to have some bearing on the energetic costs to interactants however, as the energetic cost of losers was related to the number of strikes they received. The nature of the relationship between interaction content and energetic cost is likely to be complex due to the permutations of different types of acts which may be involved.

More detailed analysis of the relationship between the content of interactions and the energetic costs of participants requires data from interactions of a greater range of intensities. The present results indicate that different acts have different energetic consequences. The energetic requirements of particular behaviours may be inferred from the relative energetic costs of interactions involving different proportions of these acts, but a considerable data set is required for this type of analysis. If it were possible to induce agonistic displays in a respirometer, instantaneous measurements of oxygen uptake rate could be used to determine the energetic cost of individual

components of agonistic behaviour, as has been done for the social behaviour of some amphibians (e.g. Butcher *et al.*, 1982; Bennett and Houk, 1983; Taigen and Wells, 1985; Ryan *et al.*, 1983; Prestwich *et al.*, 1989). Such information is necessary to determine whether agonistic strategies employed by crabs are related to their energetic consequences. If the behaviour of crabs is influenced by energetic considerations, then the magnitude of costs of competition for resources of different value may be examined. Several game theory models predict that on average animals will incur greater costs when competing for resources of higher value (Hammerstein and Parker, 1982; Maynard Smith, 1982; Enquist and Leimar, 1987). Testing of such predictions requires quantifiable costs that have a bearing on the behaviour of the animal. The results of this study indicate that energetic cost is quantifiable. The relative costs of interactions over a range of intensities, between size-mismatched crabs and over different resources should be examined.

At present, the respiratory consequences of agonistic behaviour can only be compared with those of exhausting activity and the undisturbed state. Estimates of the energetic costs of a range of activities are required so that the exertion of crabs during fighting may be better interpreted.

6. FIELD STUDIES OF THE AGONISTIC BEHAVIOUR OF *LIOCARCINUS PUBER*

6.1 INTRODUCTION

6.1.1 Field studies of agonistic behaviour in Crustacea

In the preceding chapters, laboratory studies of the agonistic behaviour of *L. puber* have been described, where controlled conditions were necessary to allow manipulation of the factors under investigation. Most existing information about crustacean agonistic behaviour has been gained from such laboratory or aquarium studies. Many species of Crustacea are suitable for such work, as they readily behave in artificial conditions as they do in their natural environment (Dingle, 1983). This chapter presents the results of two field studies of the behaviour of *L. puber* (a diving survey and a video study) and describes some additional field observations of the behaviour and ecology of this species.

While laboratory and aquarium studies are valuable for detailed descriptions of behaviour and controlled investigation of the factors that influence it, they can at best, provide only indirect evidence about the incidence of agonistic behaviour in natural conditions, the circumstances in which it occurs and its ecological relevance. However, the preponderance of studies in artificial conditions reflects the difficulties involved in observing crustaceans in their natural environment. Most field studies of crustacean agonistic behaviour have been of intertidal or semi-terrestrial species that are active out of water in daylight and are therefore easily observed (e.g. Warner, 1970; Hazlett, 1974; Hyatt, 1977; Hyatt and Salmon, 1978,1979; Lindberg, 1980; Salmon, 1984; Abele *et al.*, 1986; Christy, 1988). Aquatic crustaceans, many of which are nocturnal, are more difficult to observe, and there are fewer behavioural field studies of such species. Most studies of the agonistic behaviour of aquatic marine crustaceans have used divers with self-contained underwater breathing apparatus (SCUBA) to make direct observations. Sinclair (1977) used SCUBA to observe staged agonistic interactions between stone crabs, *Menippe mercenaria.* O'Neill and Cobb (1979) used divers to observe both spontaneous and staged competitive interactions for shelter between American lobsters, *Homarus americanus.* Glass (1985) recorded few spontaneous agonistic interactions between swimming

crabs, *Liocarcinus depurator*, by diving, but observed several interactions between crabs retreating from divers and conspecifics encountered during their retreat. Diving is often the only method of making direct underwater observations of aquatic species, but behavioural observations by the diving techniques that are cheapest and most easily available - using open-circuit, self-contained apparatus with compressed air as the breathing mixture - are limited by the noise of the breathing apparatus, weather, underwater visibility, air supply, decompression time and thermal tolerance (Gamble, 1984). Video techniques allow long periods of observation without disturbance, if a static camera is used and artificial lighting is not required (Holme, 1984), but such a system is also limited by underwater visibility and by a fixed field of view. The cost of operating submersibles or remotely operated vehicles is usually prohibitive for behavioural studies, but some observations have been made by these means. The agonistic behaviour of a deep sea crab, *Macroregonia macrochira*, has been recorded around hydrothermal vents at 1600-2000 m depth, using visual and video observations from a submersible and by remote photography (Tunnicliffe and Jensen, 1987). Such work was only feasible as part of a larger study and the disturbance caused to the subjects by the equipment limited its use in detailed behavioural investigation. The most comprehensive field study to date is that of Karnofsky *et al.* (1989a,b), who circumvented some of the limitations of SCUBA diving by using snorkel divers to study the activity of lobsters, *H. americanus*, in a shallow cove. They accumulated 333 hours of mainly nocturnal observation over a three year period and in that time observed 71 intraspecific agonis tic interactions.

6.1.2 Distribution and movements in the field

The frequency of intraspecific agonistic interactions and their ecological significance depend on the distribution and movements (in terms of spatial displacement) of individuals in a population. As these variables are relatively easy to quantify and are of direct relevance to commercial exploitation, there are numerous studies of the distribution and movement of crustaceans. Movement of groups of individuals has been inferred from short term changes in abundance in adjacent localities (e.g. Naylor, 1962; Smith and Jamieson, 1989) and from direct observations (Dare and Edwards, 1981). Monitoring the movements of individuals requires them to be uniquely marked. Mark and recapture methods have been used to study large scale (e.g. Edwards, 1979; Diamond and Hankin, 1985; Campbell, 1989) and small

scale displacement of crustaceans (e.g. Edwards, 1958; Crothers, 1968; Hazlett, 1984; Wilber, 1986; Norman, 1989). Others have marked individuals to allow repeated visual records of their location and activity (Hazlett and Rittschoff, 1975; Salmon, 1984; Glass, 1985; Glaholt, 1990). In addition, crustaceans have been tracked using ultrasonic transmitters (Lund and Lockwood, 1970; Monan and Thorne, 1973; Chapman *et al.*, 1975; Hill, 1978; Herrnkind, 1980; Maynard and Webber, 1987). Recently, a method has been developed for telemetering the electrical activity of individual muscle groups in large crustaceans over a range of up to 500 m, allowing the frequency of specific behaviours to be determined from free ranging individuals (Wolcott and Hines, 1989).

Some field studies of activity in crustaceans have used several techniques, in order to study different types of activity or to study activity in different habitats. Muntz *et al.* (1965) studied the predatory activity of several species of crabs using ground bait, traps and divers. Chapman *et al.* (1975) studied various aspects of the burrow-related behaviour of the Norway lobster, *Nephrops norvegicus*, in the field, using remote photography, underwater television, diving and acoustic tracking. McMillan *et al.* (1988) investigated the habitat preferences of Dungeness crabs, *Cancer magister*, by sampling with beam trawls, traps, diver transects and intertidal quadrats.

6.1.3 Agonistic behaviour and the efficiency of commercial traps

Agonistic behaviour has important consequences for the commercial exploitation of some species of Crustacea. The capture rate of traps decreases with time after deployment (Miller, 1978,1979; Brown, 1982; Bjordal, 1986; Robertson, 1989; Smith and Jamieson, 1989). This "gear saturation" may be due to any one or a combination of reduced local density of the target species, reduced attractiveness of the bait, increased escapement from the trap and reduced entry to the trap. The last-named may be due to the presence of individuals inside the creel, to interactions between animals attempting to enter and those inside, or to interactions between individuals outside the trap. Observations of traps have revealed that agonistic interactions, involving individuals both inside and outside, are significant in reducing the rate of entry to a trap (Miller, 1978; Bjordal, 1986; Karnofsky and Price, 1989).

6.1.4 Field observations of *Liocarcinus puber*

The aims of the present study were to investigate the abundance and distribution of *L. puber* in its natural habitat, to determine the frequency of spontaneous agonistic interactions and to determine whether agonistic behaviour in the laboratory is representative of that in the field. In addition, the influence of agonistic behaviour on the capture efficiency of creels has been investigated.

6.2 MATERIALS AND METHODS

6.2.1 Surveys of the abundance and activity of *L. puber*

6.2.1.1 Selection and description of study site

One site was selected for a quantitative survey of the abundance and activity of *L. puber*. Selection criteria were an abundance of *L. puber*, shelter from prevailing winds, shallow depth, easy access and proximity to Glasgow. No site completely satisfied these criteria, mainly because *L. puber* is not abundant in very sheltered areas (Kitching *et al.*, 1959). The site selected was at Routenburn in the Firth of Clyde (55° 49.1'N, 4° 53.1'W; Figure 6.1). A high number of *L. puber* had been noted there during preliminary site assessment. The site receives some shelter from the prevailing south-westerly wind, being in the lee of Great Cumbrae Island. The degree of exposure is greater to the west and north-west. Access is easy as the A78 runs close to the shore at this point. The site is 56 km from Glasgow by road. Street lighting in Routenburn facilitated diving operations at night.

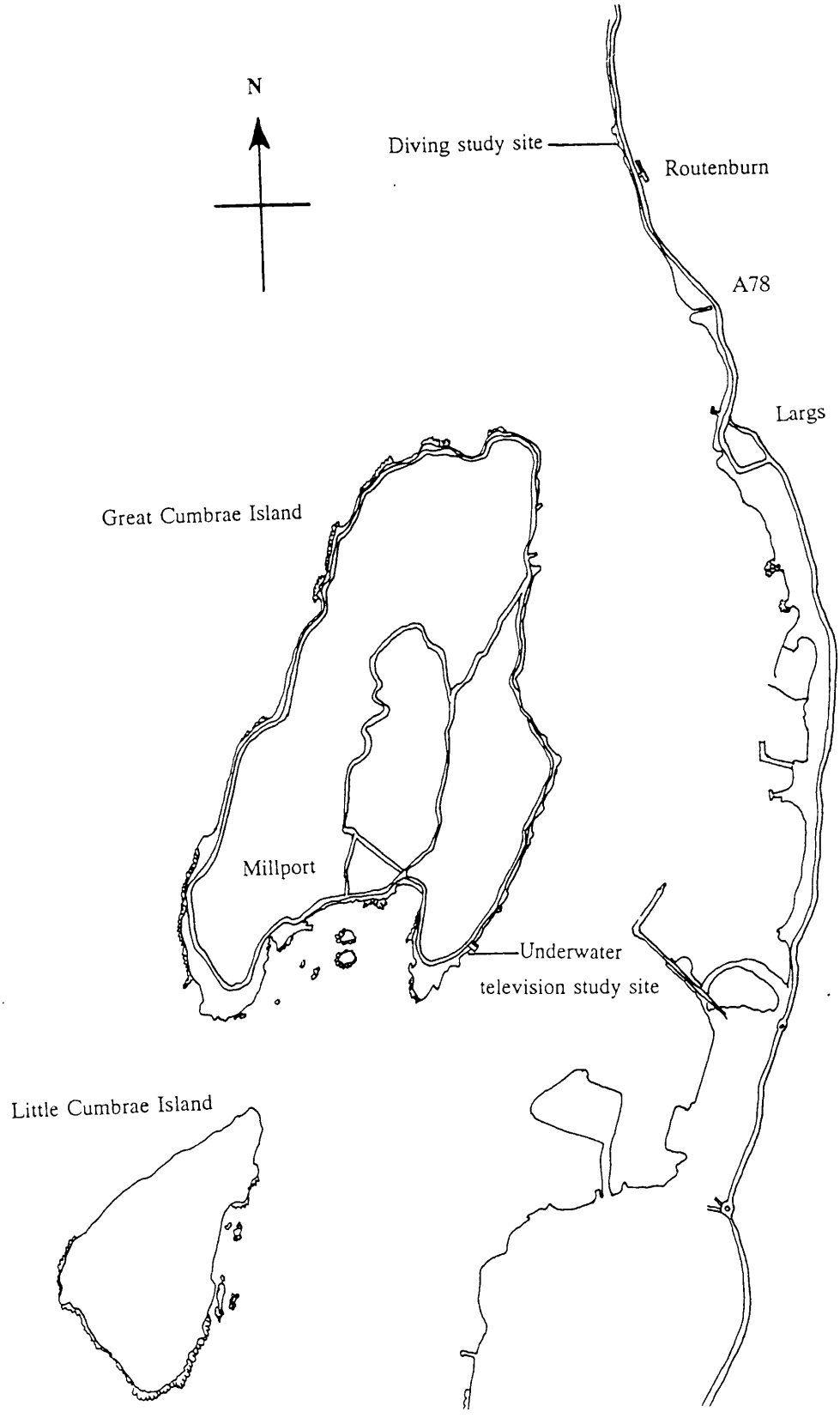
The site consisted of a boulder shore which sloped gently into the sublittoral zone, falling 6 m over a distance of about 100 m. Boulders of about 0.5 m diameter predominated from the upper shore to 4 - 5 m below chart datum (b.c.d.), where boulders and cobbles were scattered on sand. Sand with few boulders or cobbles extended from about 6 m b.c.d. Chart datum in this area is 1.26 m below Ordnance Datum (Newlyn).

There were few algae higher than approximately 0.5 m above chart datum: barnacles (*Semibalanus balanoides*) dominated the substratum with patches of small mussels (*Mytilus edulis*). An extensive mussel bed lay to the north of the site. From 0.5 m above chart datum to 1 m b.c.d. the kelps *Laminaria digitata* and *L. hyperborea* were common. *L. saccharina* and the brown alga *Desmerestia aculeata* were abundant from 1 m b.c.d. to the extent of the rocks at 4 - 5 m b.c.d. The kelp *Saccorhiza polyschides* was common from 2 - 5 m b.c.d. The dense kelp and crevices between boulders provided much shelter for *L. puber* and other crustaceans.

6.2.1.2 Survey technique

The site was surveyed by divers swimming along one of four transects at right angles to the shore. These transects were directed by a compass bearing (250°) from starting points 5 m apart, marked on rocks at approximately the level of mean high

Figure 6.1 Location of the study sites for diving surveys and underwater television studies.



water of spring tides (MHWS). Transects were surveyed by performing 5 circular searches (see below) along them at distances of 40, 50, 60, 80 and 90 m ground distance from MHWS. These distances corresponded to levels of 0.5 m above chart datum and 0.0, 1.0, 3.0 and 4.0 m below chart datum. These positions were chosen to fall in different habitat types. The 40 m search area was on the barnacle dominated mid-shore, the 50 m area was in the *Laminaria hyperborea* zone, the 60 m area was in the transition from *L. hyperborea* to a predominance of *L. saccharina*, the 80 m area was on a slightly steeper part of the seabed with large boulders and a dense cover of *L. saccharina* and *Saccorhiza polyschides* and the 90 m search area was close to the limit of the rocks. Distances were measured with a marked polyester cord. Circular search areas were defined by a 2 m radius line of polyester cord, weighted at both ends and attached to the transect line at one end. The radius of these circles was chosen to allow five areas to be searched in one dive. Dive duration was potentially limited by air supply and battery charge in the torches on night dives. Preliminary trials indicated that it was not possible to complete five circular searches of 4 m radius in one dive.

First, causing as little disturbance as possible, divers visually scanned the search area for crabs not sheltering under rocks or algae. The area was then searched thoroughly by moving the radius line sector by sector and looking for crabs sheltering under rocks or algae. The behaviour of *L. puber* was obviously affected by the presence of divers. Usually, active crabs became inactive, but they would adopt a cheliped extend display or attempt to escape if a move was made to capture them. It was therefore only possible to classify the location and behaviour of each crab broadly, based on its activity when first seen. Location was classified as 'in the open' (standing on rocks or weed), or 'under cover' (crouching under rocks or weed). Activity was recorded as 'doing nothing', 'feeding', 'mating' or 'paired', where 'mating' refers to crabs in copula and 'paired' refers to crabs in pre- or post-copulatory pairs. Each crab was captured and sexed, their carapace width was measured and notes were made of any missing limbs. Crabs of less than 40 mm carapace width could not be sexed reliably underwater and were therefore recorded as juveniles. A pencil mark was made on the sternum and distinguishing features were noted before releasing crabs to avoid recording individuals more than once in each dive.

This sampling method was biased against small crabs which were difficult to find

and capture. It was also biased against crabs in some form of shelter, as it was not possible to search for crabs in all crevices and under large rocks, or to capture all crabs in such locations.

Transects were surveyed at times of 0100, 0300, 0500, 0900, 1300, 1700, 2100 and 2300 h Greenwich Mean Time (GMT). All times in this chapter are given in Greenwich Mean Time. Sampling effort was greater at night because previous studies have indicated a nocturnal peak of activity in *L. puber* (Kitching *et al.*, 1959; Ebling *et al.*, 1964; Choy, 1986). One of the four transects was surveyed at each of these eight times during a period of 3 days when there were high tides at around midnight and midday GMT. Such tides occurred at new and full moons. At night, waterproof torches were used. Initially, red filters were used on torches, in order to reduce disturbance to crabs. Crabs have low sensitivity to red light (Cronin, 1986). However, crabs responded to filtered light and the filters seriously reduced the utility of the torches. Unfiltered torchlight was therefore used on most night surveys.

The four transects were similar in depth profile and nature of the bottom and the abundance of *L. puber* was equivalent in each (see section 6.3.1). A maximum of four dives was carried out in one outing. Consequently, each of the four transects was surveyed no more than once in each outing and there was at least 36 hours between replicate surveys of one transect.

It was originally intended to perform these surveys at intervals throughout the year to monitor seasonal variations in the activity of *L. puber*. However, limitations imposed by the weather and by the availability of transport and personnel did not allow this. The dates on which surveys were carried out are given in Table 6.1.

6.2.2 Additional diving observations

Unsystematic observations of *L. puber* have been made over the period April, 1987 to October, 1990 at different sites and times of day. These dives were not made at specific times and did not follow specific routes. Crabs were not captured or measured on these dives. In late autumn and winter there were few dives in areas where *L. puber* were abundant, due to adverse weather conditions.

6.2.3 Underwater television studies

An underwater television system was used to record the behaviour of *L. puber* in shallow water near the University Marine Biological Station, Millport (55°45.0'N,

Table 6.1 Dates and times of surveys of the activity and abundance of *Liocarcinus puber* at Routenburn (55°49.1'N, 4°53.1'W).

	Survey Number						
GMT	1	2	3	4	5	6	7
01:00	13/8/88	25/8/88	11/9/88	29/10/88	21/3/89	20/5/89	3/7/89
03:00	12/8/88	24/8/88	10/9/88	29/10/88	20/3/89	19/5/89	2/7/89
05:00	12/8/88	-	11/9/88	29/10/88	21/3/89	20/5/89	-
09:00	10/8/88	22/8/88	8/9/88	26/10/88	-	17/5/89	-
13:00	10/8/88	22/8/88	8/9/88	26/10/88	-	-	18/6/89
17:00	10/8/88	22/8/88	8/9/88	26/10/88	-	-	18/6/89
21:00	10/8/88	22/8/88	8/9/88	26/10/88	-	-	3/7/89
23:00	12/8/88	24/8/88	10/9/88	29/10/88	20/3/89	19/5/89	2/7/89

4°54.3'W; Figure 6.1). A silicon diode array camera (TC-125-SDA, Hydro Products Inc., San Diego, California) was mounted at an angle of 40° from horizontal on a steel frame (Figure 6.2). It viewed an area of approximately 4.5 m^2, depending on underwater visibility. At night the camera view was illuminated by two 250 watt quartz iodide lights (HQ-250, Hydro Products) mounted on the steel frame, filtered with red acrylic. The combined control unit and power supply for the camera and lights (TP110, Hydro Products) was located with a time lapse video cassette recorder (Panasonic NV-8051, Matsushita Electric Industrial Co. Ltd., Osaka, Japan), in a building onshore. Power and video images were relayed by 174 m of cable (NC134, Hydro Marine Systems Ltd., Dyce, Aberdeen).

The camera frame was lowered by winch from the Marine Station pier and positioned by divers with the aid of buoyancy bags. The frame was placed 20 - 30 m south-east of the pier on sand, 4 m below chart datum. The frame was oriented towards the shore. The rocky shore shelved steeply at this point, with a boulder slope continuing to about 2 m b.c.d., where the substratum became predominantly sand. Large timbers lay in an irregular array on the sand, with a dense covering of *Laminaria saccharina*. *L. puber* sheltered among the rocks below the shore and beneath the timbers.

The behaviour of *L. puber* in three situations was recorded with this apparatus: at discrete food items, at a creel and in the vicinity of a sexually receptive female.

6.2.3.1 Discrete food items

Carcasses of flounder (*Platichthys flesus*) were placed in a weighted container of plastic mesh ('Netlon'), which prevented dispersal of the bait by crabs and other animals. The container was placed in view of the camera and was filmed for 24 hours, after which the bait was renewed and filmed for a further 24 hours. This was carried out in two 24 hour sessions from 31/8 - 2/8/88.

6.2.3.2 Creels

One creel of a type commonly used commercially to catch *L. puber* (Figure 6.3), was baited with whitefish, placed in view of the camera between 10:00 and 14:00 and was recorded for 24 hours. After this period the creel was emptied and re-baited. Captured *L. puber* were retained in holding tanks until the camera frame was removed, after which they were returned to the sea. Other captured animals were

Figure 6.2 The underwater television camera and frame.

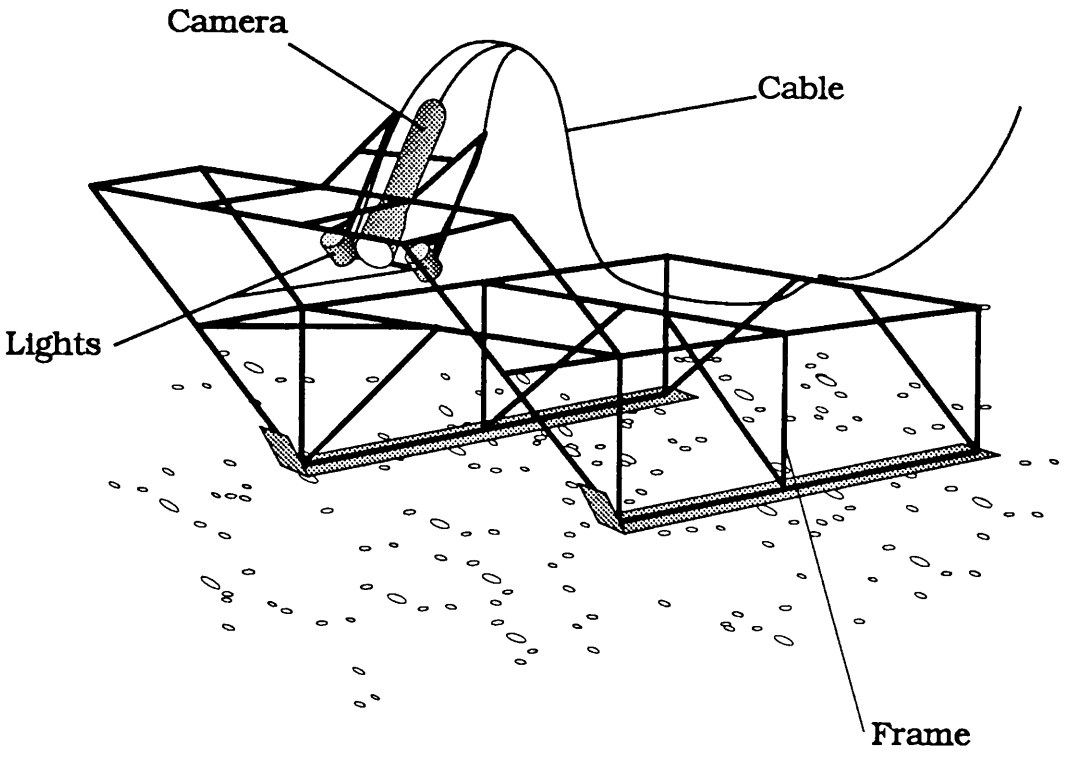
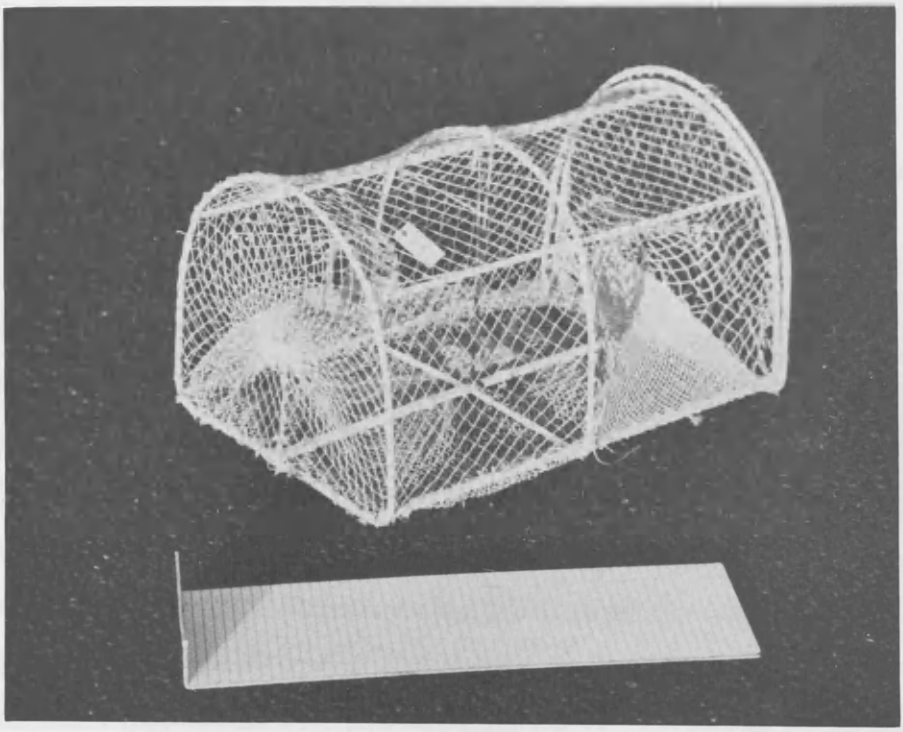


Figure 6.3 The type of creel used in underwater television studies of the capture of *L. puber* by creels. Scale = 55 cm, increments = 1 cm.



released immediately. It was periodically necessary for divers to clear the area of starfish (*Asterias rubens*), which were very abundant and sometimes smothered the bait.

This procedure was followed for three periods of four days. However, due to poor underwater visibility, the results presented here are from only one of these periods: from 3 - 7/10/89.

6.2.3.3 Receptive females

During August and September 1989, females were collected that were in pre-copulatory pairs with males. Individual females were tethered to a 1 kg weight with 1 m of monofilament nylon and were placed in view of the camera. Shelter was provided by a group of adjacent rocks. Recordings were made for 24 hours and then the female was replaced. This was carried out from 2 - 5/9/88.

6.2.4 Statistical Methods

The density of crabs recorded during diving surveys, the carapace widths of these crabs and the durations of agonistic interactions observed with the underwater television system have been analyzed with multi-factor analysis of variance. Unequal cell sizes necessitated the use of General Linear Models (GLM, Zar, 1984).

Two factor analysis of frequencies has been carried out with the log-likelihood ratio test with William's correction (Sokal and Rohlf, 1981). Where more than 20% of the expected frequencies were less than 5, or any of the expected frequencies were less than 1, Fisher's exact test has been used (Zar, 1984). Multi-factor analysis of the frequencies of crabs in various categories in the diving surveys has been performed with a log-linear model (Zar, 1984), using backward elimination to arrive at the simplest model (Norušis/SPSS Inc., 1988).

6.3 RESULTS

6.3.1 Diving surveys

6.3.1.1 Abundance and activity of *Liocarcinus puber*

Counts of crabs per circle (12.6 m^2) approximately followed a Poisson distribution and were therefore transformed to $\sqrt{(count+^3/_8)}$ before analysis (Zar, 1984). A multi-factor ANOVA of the transformed densities of crabs, with the factors survey number (1-7), transect number (1-4), time of dive (01:00-23:00 GMT) and ground distance from MHWS (40-90 m), indicated that crab density varied significantly with distance from the shore (Figure 6.4; $F_{(4,213)} = 42.07$, $P<0.001$), but not with survey number ($F_{(6,213)} = 0.16$, $P>0.50$), transect number ($F_{(3,213)} = 0.50$, $P>0.50$) or time of dive ($F_{(7,213)} = 1.24$, $P>0.20$) (Table 6.2). There were no significant interactions between these factors. Crab density was least at the 40 m search area on the shore and highest at the 90 m area, the furthest from the shore.

Interactions between the following factors in relation to crab numbers have been investigated with log-linear analysis: ground distance from MHWS (40-90 m), time of dive (01:00-23:00 GMT), gender (male, female or juvenile), location (in the open or under cover), activity (doing nothing, feeding, mating or pairing) and injury (none, one limb missing or more than one limb missing). The significant effects in a model with, and one without juveniles, are listed in Table 6.3.

Although there was an overall predominance of males (61.4% of crabs of determinate sex were male, significantly greater than 50%, $G_{adj} = 24.56$, df = 1, $P<0.001$), the proportion of females increased towards the shore (Table 6.4). Males appeared to be more active, as a greater proportion of them was observed in the open (34.4%) than females (19.5%) or juveniles (22.4%). Overall, 27.1% of the crabs were observed in the open, but all crabs at 40 m from MHWS and 36.5% of those at 80 m from MHWS were seen in the open. The 40 m search area was on the mid-shore, where crabs were only found during high tides at night. As there was no cover there, all crabs were in the open. The reason for the above average proportion of crabs in the open at the 80 m sweep is not known. It may be that the nature of the substratum at this location resulted in a greater proportion of the crabs hiding in crevices being missed than at the other stations.

Crabs were found in the open most often at night (Figure 6.5), indicating predominantly nocturnal locomotor activity. The analysis excluding juveniles

Figure 6.4 The density of *L. puber* at different ground distances from mean high water of spring tides (MHWS) at Routenburn. Means and 95% confidence intervals were calculated from square root-transformed data.

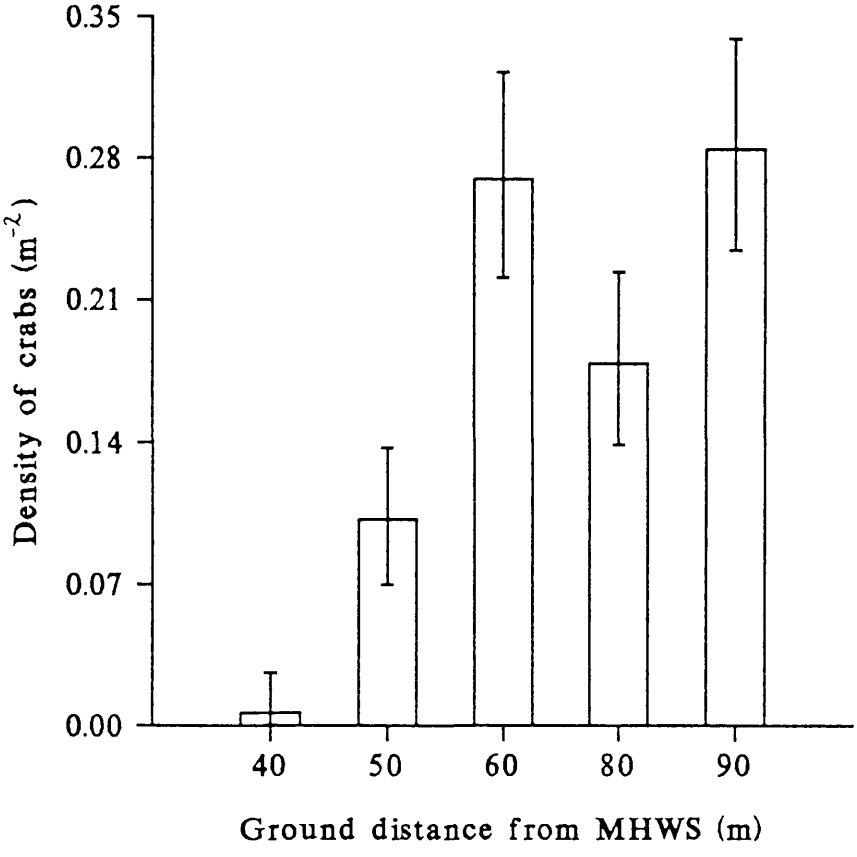


Table 6.2 Mean densities of crabs recorded during diving surveys, classified with respect to survey number, transect number and time of dive. Means and 95% confidence intervals were calculated from square root-transformed counts in areas of 12.6 m^2 and are presented as density (m^{-2}).

Classification		Mean density (m^{-2})	95% confidence limits	
			Upper	Lower
Survey no.[1]	1	0.15	0.201	0.114
	2	0.13	0.178	0.090
	3	0.16	0.207	0.119
	4	0.15	0.194	0.109
	5	0.15	0.213	0.093
	6	0.15	0.191	0.106
	7	0.15	0.221	0.099
Transect no.[2]	1	0.14	0.171	0.108
	2	0.15	0.188	0.112
	3	0.15	0.186	0.110
	4	0.17	0.203	0.133
Time of dive (GMT)	01:00	0.17	0.220	0.124
	03:00	0.11	0.154	0.073
	05:00	0.14	0.197	0.092
	09:00	0.14	0.198	0.092
	13:00	0.17	0.229	0.115
	17:00	0.14	0.200	0.094
	21:00	0.13	0.183	0.089
	23:00	0.19	0.248	0.144

1. The dates of surveys are given in Table 6.1.

2. Four transects were surveyed at the study site, numbered 1 to 4 from south to north.

Table 6.3 Results of Log-Linear analysis of numbers of crabs recorded in diving surveys. Significant effects remaining after backwards elimination to arrive at simplest model.

(a) Juveniles included

Effect	df	^{2}Change in G	P
Distance * Activity	12	36.568	0.0003
Gender * Location	3	14.501	0.0023
Time * Activity	21	47.352	0.0008
Location * Activity	3	32.814	<0.0001
Distance * Location	4	25.204	<0.0001
Time * Location	7	93.982	<0.0001
Injury	3	816.224	<0.0001

Fit of the model to the data: G = 591.027 df = 5048, P>0.99

(b) Juveniles excluded.

Effect	df	^{2}Change in G	P
Distance * Time * Location	28	42.584	0.0382
Activity * Injury	9	18.599	0.0288
Distance * Activity	12	34.029	0.0007
Distance * Gender	8	16.272	0.0386
Time * Activity	21	45.702	0.0014
Gender * Location	2	13.834	0.0010
Location * Activity	3	28.578	<0.0001

Fit of the model to the data: G = 357.165, df = 3697, P>0.99

1. The symbol "*" represents interaction effects between the indicated factors.

2. The change in the Goodness of Fit of the model to the data if the indicated effect is eliminated.

Table 6.4 The proportions of Liocarcinus puber of different gender found at different ground distances from the shore.

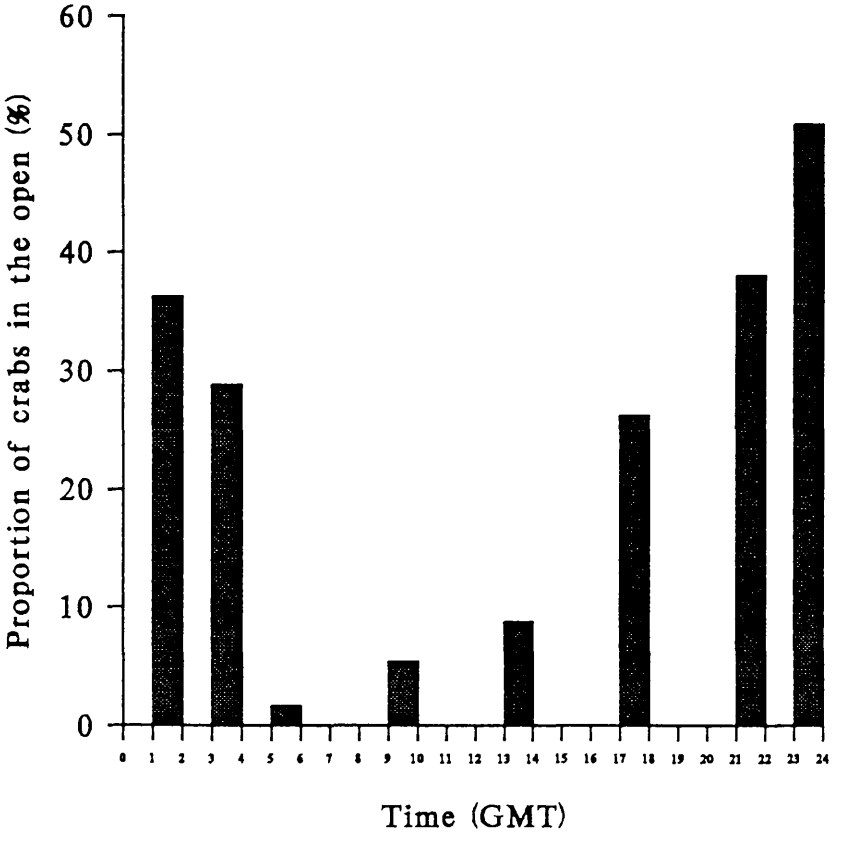
Gender	Ground distance (m) 40	50	60	80	90
Male	33.33	42.47	44.69	53.97	60.54
Female	66.67	39.73	39.66	28.57	24.86
Juvenile[2]	-	15.07	12.29	15.08	12.97
Indeterminate[3]	-	2.74	3.35	2.38	1.62
Totals	6	73	179	126	185

1. Table contents are percentages of the number of crabs found at each distance.

2. Crabs less than 40 mm carapace width were classified as juveniles.

3. Crabs of indeterminate gender were those it was not possible to capture.

Figure 6.5 The proportion of crabs found in the open at different times of day.



indicated a third order interaction between distance, time and location (Table 6.3). This seemed to be due to a large proportion of the adults found in the open being at the 40 m and 80 m search areas at night (Figure 6.6). Crabs were observed feeding mainly at night (Table 6.5) and most feeding crabs were found in the open (Table 6.6). In contrast, crabs engaged in reproductive activity (pairing or mating) were usually found under cover (Table 6.6). Pre- or post-copulatory pairs were found during the day and night, but the small number of copulating pairs observed were found in daylight (Table 6.5). Nocturnal copulation has been observed at other sites (personal observations).

A significant interaction between ground distance from MHWS and activity (Table 6.3) was mainly due to a large proportion of the reproductive activity being observed at the 60 m sweep (Table 6.7). The ratio of females to males was not greatest at this position (Table 6.4), but those positions with higher ratios occurred on the mid-shore (40 m area) and lower shore (50 m area). There may not have been sufficient cover in these locations for such activity.

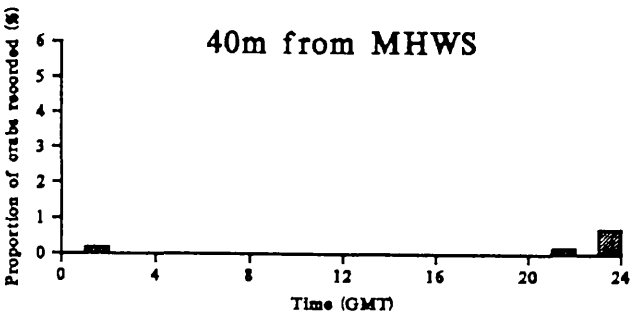
The patterns of limb loss for males, females and juveniles are indicated in Figure 6.7. The number of missing limbs was positively correlated with carapace width (r_s = 0.152, df = 553, P<0.001). The proportion of injured crabs observed feeding was similar to that of uninjured crabs, but no injured crab was observed engaged in any reproductive activity (Table 6.8).

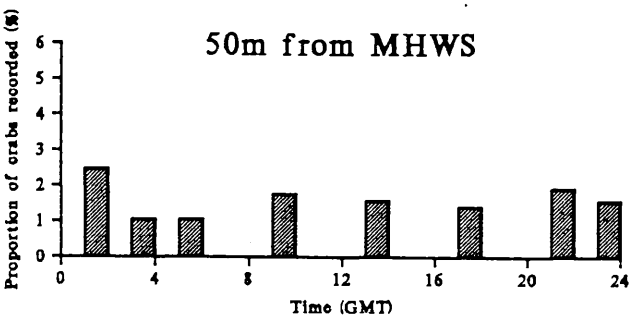
6.3.1.2 Crab sizes

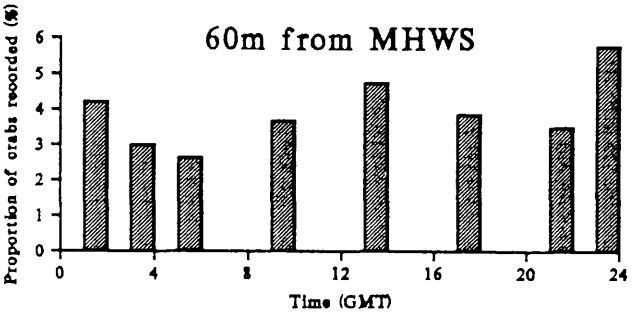
The carapace widths of crabs have been analyzed by a three factor, mixed effects, general linear model (Zar, 1984), with survey number as a fixed effect factor and gender and location as random effects factors. Inspection of the data indicated that other factors were not important with respect to carapace width. Juveniles were classified as such on the basis of size and were therefore excluded from this analysis. Males were significantly larger than females (Figure 6.8; $F_{(1,1)}$ = 1571.32, P<0.025), but carapace width did not vary significantly between surveys (Table 6.9; $F_{(6,1.05)}$ = 4.40, P>0.05) or between crabs in the open (62 ± 3.7 mm) and those under cover (59 ± 2.3 mm) ($F_{(1,1)}$ = 108.67, P>0.05). There were no significant interactions between these factors in relation to carapace width.

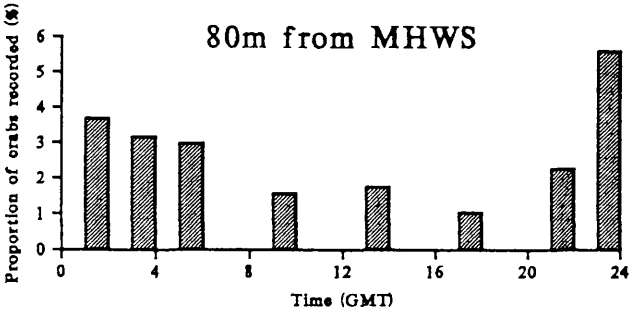
Separate analyses have been performed to compare the mean carapace widths of single crabs with those engaged in reproductive activity (pre- or post-copulatory pairs

Figure 6.6 The relative abundance of adult *L. puber* in relation to ground distance from the shore and time of day. Relative abundance is illustrated as a percentage of the total number of adults (crabs with a carapace width greater than 40 mm) observed during diving surveys (n = 479).


40m from MHWS
Proportion of crabs recorded (%)
0
1
2
3
4
5
6
0
4
8
12
16
20
24
Time (GMT)


50m from MHWS
Proportion of crabs recorded (%)
0
1
2
3
4
5
6
0
4
8
12
16
20
24
Time (GMT)


60m from MHWS
Proportion of crabs recorded (%)
0
1
2
3
4
5
6
0
4
8
12
16
20
24
Time (GMT)


80m from MHWS
Proportion of crabs recorded (%)
0
1
2
3
4
5
6
0
4
8
12
16
20
24
Time (GMT)

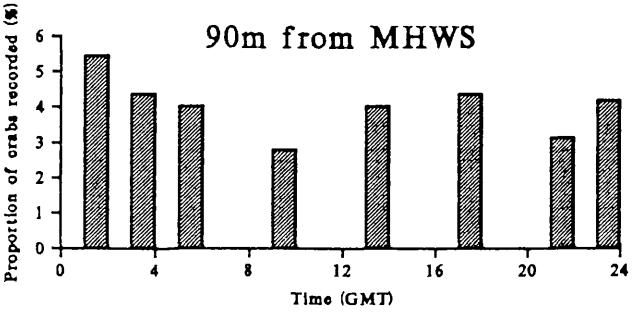

90m from MHWS
Proportion of crabs recorded (%)
0
1
2
3
4
5
6
0
4
8
12
16
20
24
Time (GMT)

Table 6.5 The proportions of Liocarcinus puber engaged in different activities at different times of day.

Activity	Time (GMT) 01:00	03:00	05:00	09:00	13:00	17:00	21:00	23:00
Nothing	96.70	87.88	93.44	91.07	86.96	88.52	92.06	92.16
Feeding	3.30	3.03	-	5.36	1.45	1.64	4.76	3.92
Mating	-	-	6.56	-	-	3.28	-	-
Paired[2]	-	9.09	-	3.57	11.59	6.56	3.17	3.92
Totals	91	66	61	56	69	61	63	102

1. Table contents are percentages of the numbers of crabs found at different times

2. "Paired" refers to crabs in pre- or post-copulatory pairs.

Table 6.6 The activity of Liocarcinus puber in different locations.

Activity	Location In the open	Under cover
Nothing	23.73	67.66
Feeding	2.46	0.35
Mating	-	1.05
Paired	0.70	3.87

1. Table contents are percentages of the total number of crabs recorded (569).

Table 6.7 The proportions of Liocarcinus puber found at different ground distances from the shore engaged in various activities.

	Ground distance (m)				
Activity	40	50	60	80	90
Nothing	100.00	100.00	83.80	92.06	94.59
Feeding	-	-	3.91	4.76	2.16
Mating	-	-	3.35	-	-
Paired	-	-	8.94	3.17	3.24
Totals	6	73	179	126	185

1. Table contents are percentages of the crabs found at each distance.

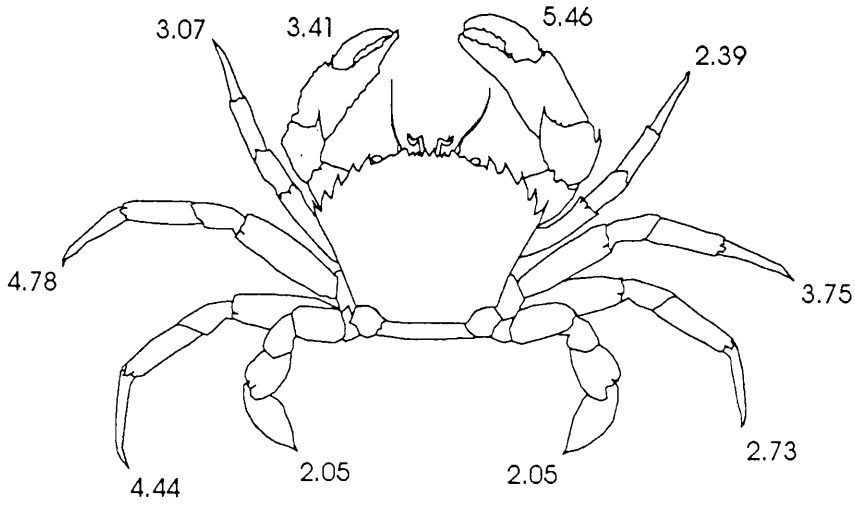
Table 6.8 The proportions of Liocarcinus puber of different injury status engaged in various activities.

	Number of missing limbs		
Activity	0	1	>1
Nothing	89.43	97.67	97.06
Feeding	3.22	2.33	2.94
Mating	1.38	-	-
Paired	5.98	-	-
Totals	435	86	34

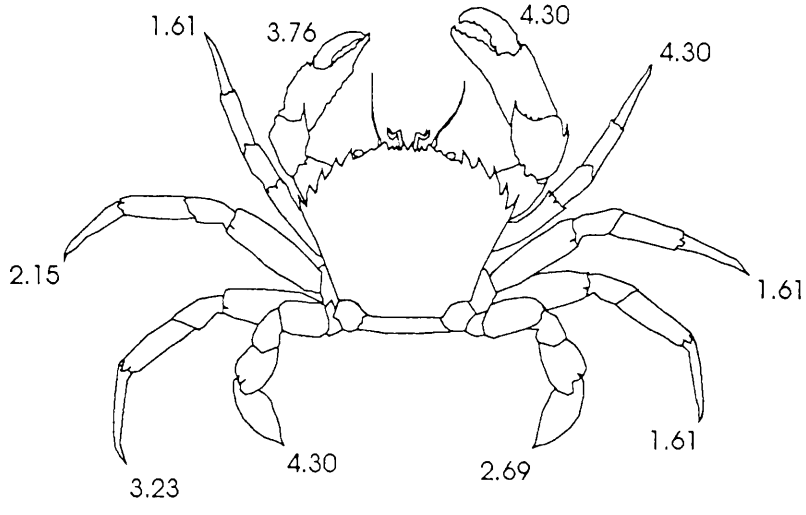
1. Table contents are percentages of the numbers of crabs of each injury status.

Figure 6.7 The incidence of missing limbs in males, females and juveniles. Figures are percentages of the crabs in each category missing the indicated limb.

(a) Males n=293



(b) Females n=186



(c) Juveniles n=76

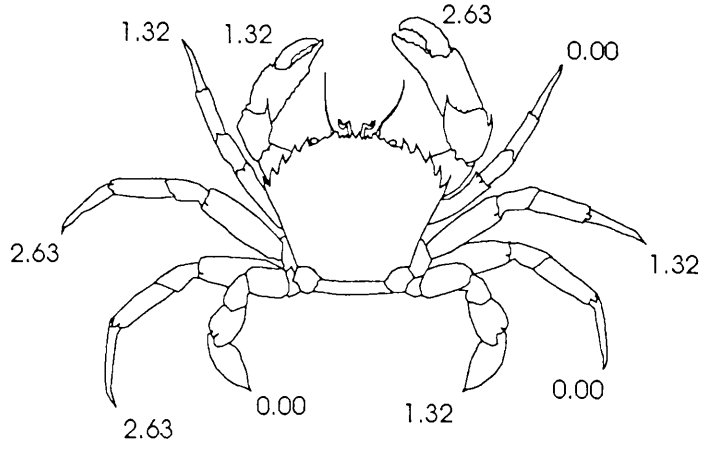


Figure 6.8 The mean carapace widths of males, females and juveniles. Error bars are 95% confidence intervals.

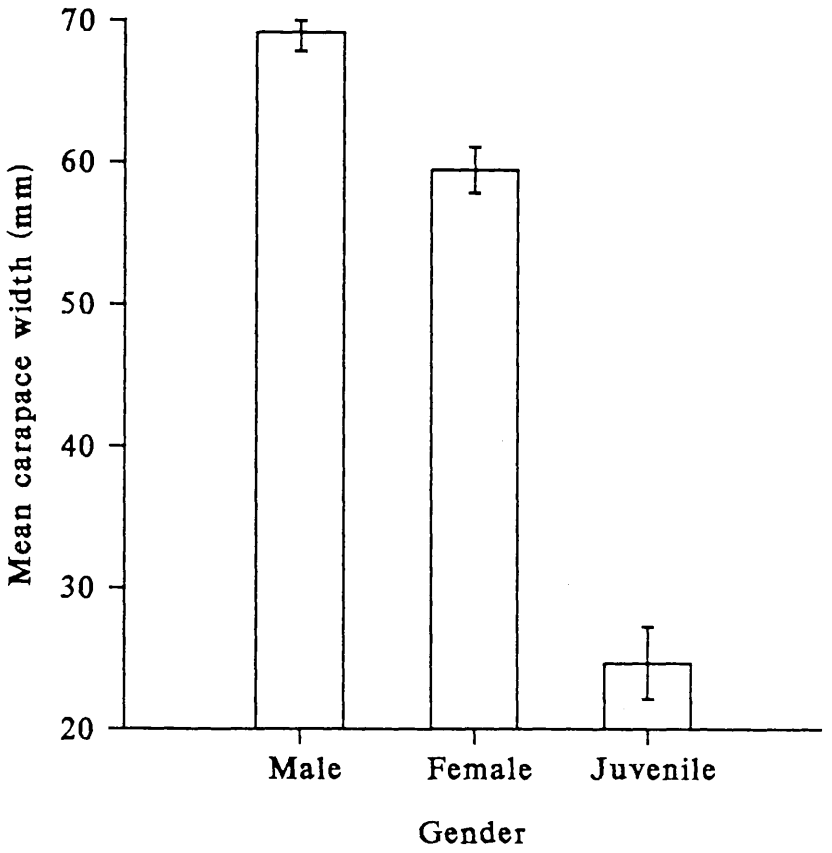


Table 6.9 The mean carapace widths of adult *Liocarcinus puber* recorded in the diving surveys.

Survey number[1]	Mean ± 95% c.l. (mm)	n
1	61.5 ± 4.67	94
2	59.4 ± 5.38	71
3	60.1 ± 4.55	99
4	56.5 ± 4.58	98
5	57.9 ± 6.41	50
6	61.3 ± 4.60	97
7	62.8 ± 6.68	46

1. The dates on which surveys were carried out are given in Table 6.1.

and copulating pairs). Data have only been included in this analysis from surveys in which reproductive activity was recorded (surveys 1-3, Table 6.1). The mean carapace width of males paired with females (70 ± 4.6 mm) was not significantly different from that of single males (68 ± 1.5 mm) ($F_{(1,149)}$ = 1.24, P>0.25). However, the mean carapace width of females paired with males (54 ± 3.7 mm) was significantly less than that of single females (59 ± 1.6 mm) ($F_{(1,90)}$ = 8.45, P<0.01). Males were always larger than the females they were paired with (mean difference between male and female carapace widths = 16 ± 4.8 mm, paired t-test; t = 7.19, df = 15, P<0.001), but there was no significant correlation between the carapace widths of males and that of the females they were paired with (r = 0.046, df = 14, P>0.50).

6.3.2 Additional diving observations

6.3.2.1 Agonistic behaviour

The greatest number of agonistic interactions observed while diving was when large numbers of *L. puber*, *Carcinus maenas* and *Cancer pagurus* were found in the inter-tidal zone at Routenburn during nocturnal high tides in late June and early July 1988. Crabs were feeding on barnacles and young mussels and there were frequent, brief interactions. The majority of these interactions took the form of a brief cheliped display by one crab and subsequent withdrawal of another. Crabs also used a single cheliped to fend off encroaching individuals. Similar interactions have been observed during the day, when several crabs were feeding on a single food item, such as a fish carcass. The movement of large numbers of *L. puber* onto the shore was not observed at other times in that year or at any time in the following year. Large numbers of *C. maenas* were regularly seen on the shore during nocturnal high tides in the summers of 1988 and 1989.

The most intense interaction observed while diving was at 14:30 GMT on the 28th August 1989. Two evenly sized males were apparently contesting a prominent position on top of a rock. When first seen the crabs were engaged in cheliped extend displays. After c.5 s one crab displayed with its swimming legs raised. The other crab immediately approached and struck it, whereupon the latter retreated by swimming. The loser remained close to the rock and its opponent for at least one minute after this. Another bilateral display interaction between two similarly sized crabs was observed on the 17th August 1989, but the reason for this interaction was not established.

On two occasions (15th October 1987 and 28th August 1989) one male was observed to approach a paired male and female in a cheliped extend display. On both occasions, the paired male retreated carrying the female underneath him.

6.3.2.2 Recently moulted crabs

Recently moulted males were seen from early July to mid-August. Recently moulted females were seen from mid-August to late November, although most were seen in late August and September.

6.3.2.3 Reproductive activity

Most pre- and post-copulatory pairs were found in August and September, although one pair was seen in late March and another in early December. Copulating pairs were most common in late August and September, although several copulating pairs were seen on one dive in early November.

6.3.2.4 Ovigerous females

Ovigerous females were recorded from mid-January to early July. No dives in areas of *L. puber* abundance were performed in late autumn or early winter, so the time of first occurrence of ovigerous females was not determined.

6.3.2.5 Feeding

Observations of *L. puber* feeding (Table 6.10) indicate that barnacles, mussels, hydroids and algae figure prominently in their diet. However, the occurrence of food items in these unsystematic records is influenced by the location of dives. For instance, where *L. puber* and ophiuroids co-occurred in abundance, *L. puber* could usually be found feeding on ophiuroids. Had a greater number of dives been carried out in such areas, ophiuroids would have figured more prominently in these records.

6.3.3 Underwater television studies of discrete food items

6.3.3.1 Temporal distribution of crabs and intraspecific agonistic interactions

Bait attracted *L. puber* as well as other crustaceans and other taxa. *L. puber* was the most abundant crustacean in the field of view of the camera, with a maximum of 8 in view during the first 24 h period and 5 in the second. The mean number of crabs

Table 6.10 Numbers of *Liocarcinus puber* observed feeding on different items. These observations were made on dives at different sites and at different times of day and season.

Food item	Number of crabs
Barnacles/mussels[1]	>20
Hydroids	>10
Algae	10
Ophiuroids	5
Scyphozoans	5
Galatheids	4
Piscine carrion	4
Topshells	4
Amphitrite johnstoni	2
Lineus longissimus	1
Polynoid	1
Nudibranch	1
Cancer pagurus (juvenile)	1
Echinus esculentus	1

1. Crabs were observed feeding in the intertidal zone, in an area of abundance of small barnacles (*Semibalanus balanoides*) and mussels (*Mytilus edulis*). Crabs appeared to be feeding on both species.

in view during 30 minute periods has been calculated as:

$$\text{Mean no. in view} = \text{crab time} \bullet 30^{-1}$$

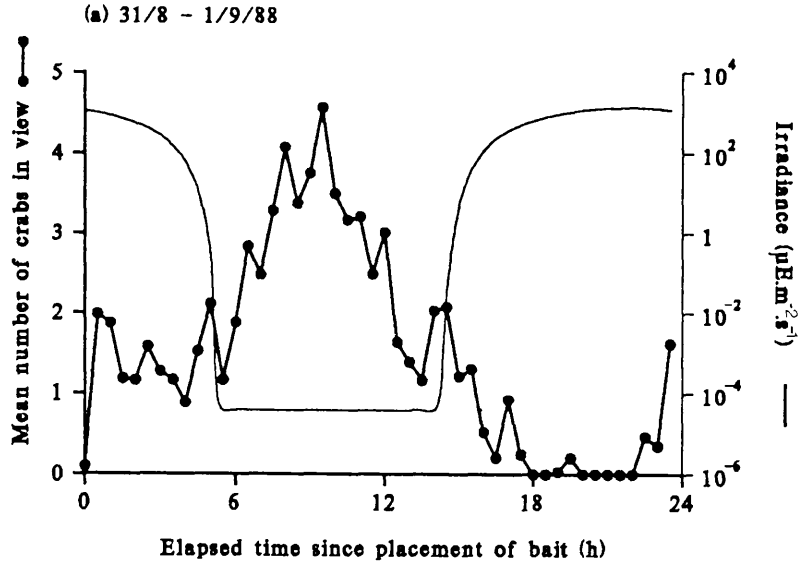
where crab time is the sum of the durations spent by individual crabs in the field of view (crab.minutes). Bait was positioned at 14:40 GMT at the start of the first session and 15:50 GMT at the start of the second session. The pattern of crab activity was similar in the two 24 h recording sessions, although numbers were fewer in the second session. Numbers increased following positioning of the bait and reached a maximum after approximately 10 h, before declining to a minimum after approximately 20 h (Figure 6.9). Light quantity is shown in Figure 6.9 for illustrative purposes. Illuminance was predicted from the formulae of Yallop (1978,1986), with corrections for reflectance at the water surface and absorption in the water column (Sverdup *et al.*, 1941), but without correction for cloud cover. Illuminance (lux) was converted to quantum irradiance ($\mu E.m^{-2}.s^{-1}$) by the factor 1.84×10^{-2} (Lüning, 1981).

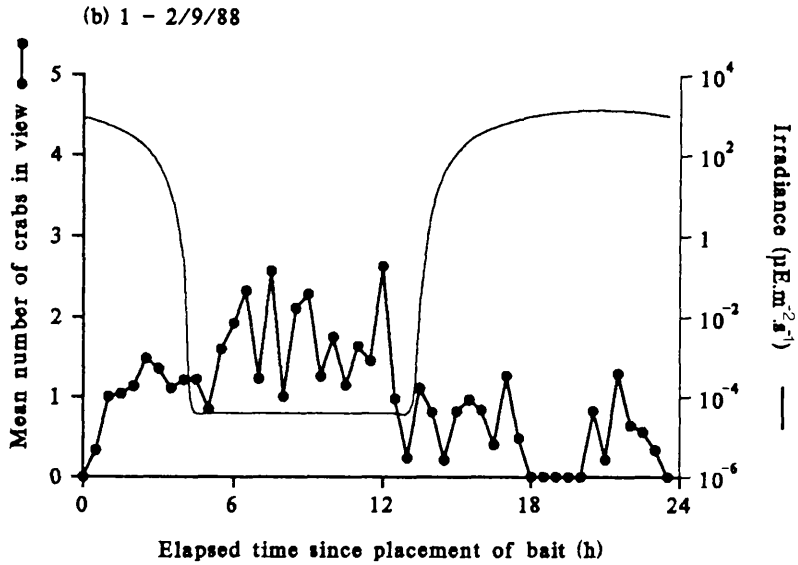
227 intraspecific agonisitic interactions were observed during the first observation session and 83 during the second. The temporal distribution of these was similar to that of the number of crabs in view (Figure 6.10). The incidence of agonisitic interactions was consequently positively related to the number of crabs in view ($F_{(1,94)} = 58.97$, $P<0.001$).

6.3.3.2 Interspecific interactions

Most agonistic interactions were intraspecific, but *L. puber* did interact with *C. maenas*, *C. pagurus* and *H. gammarus*. Individual lobsters (*H. gammarus*) entered the field of view on four occasions during the first 24 h period. None was observed during the second period. *L. puber* avoided lobsters and were consequently displaced from the bait. One rapid approach to the bait by a lobster resulted in the five *L. puber* present scattering, with one orienting a cheliped extend display towards the lobster. Lobsters appeared not to respond to *L. puber*. *Cancer pagurus*, which were usually larger than *L. puber*, displaced them also. However, *L. puber* often displayed in response to *C. pagurus* and *L. puber* were observed striking *C. pagurus*. The occasional, brief movements of the chelipeds by *C. pagurus* towards *L. puber* usually resulted in the retreat of the latter. Interactions between *L. puber* and the similarly sized species *C. maenas* appeared similar to intraspecific interactions.

Figure 6.9 The mean numbers of crabs in the vicinity of bait in relation to elapsed time and predicted irradiance.


(a) 31/8 - 1/9/88
Mean number of crabs in view
Irradiance (μE.m⁻².s⁻¹)
Elapsed time since placement of bait (h)


(b) 1 - 2/9/88
Mean number of crabs in view
Irradiance (μE.m⁻².s⁻¹)
Elapsed time since placement of bait (h)

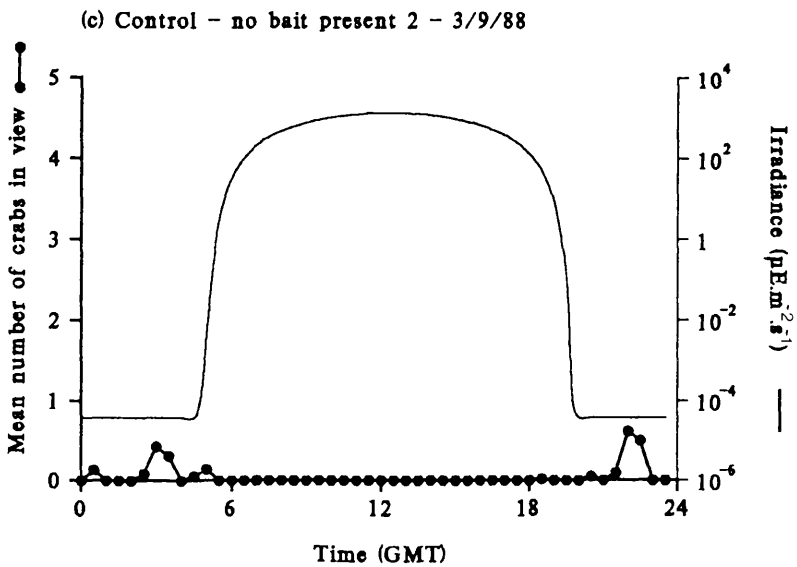
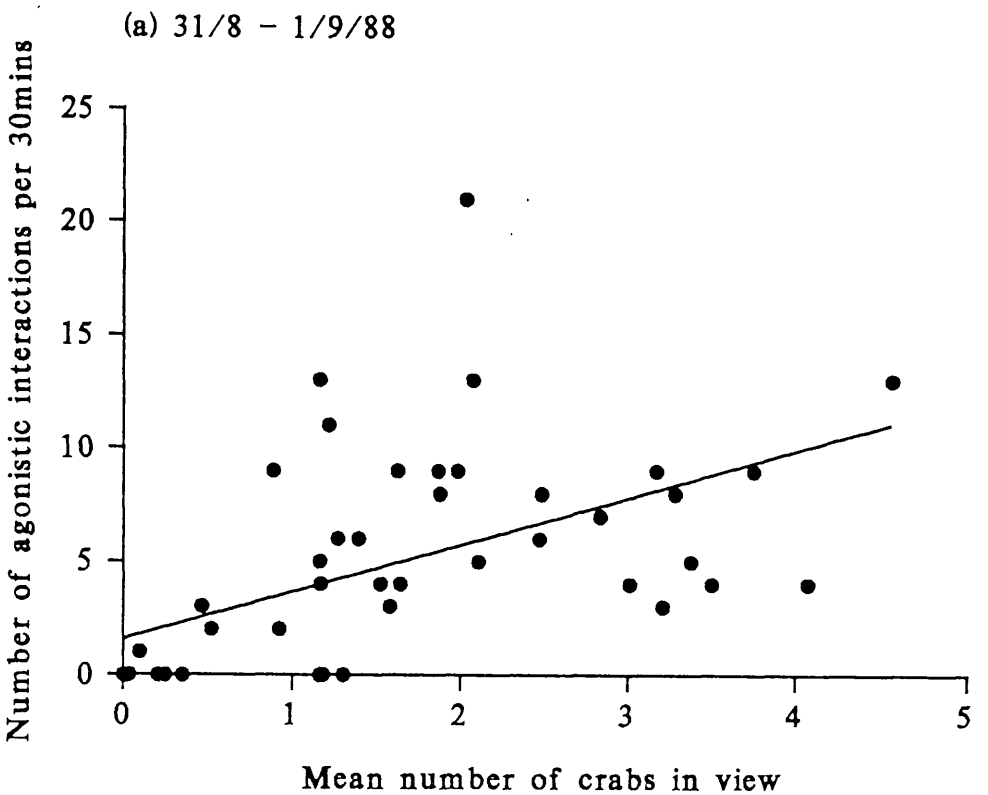
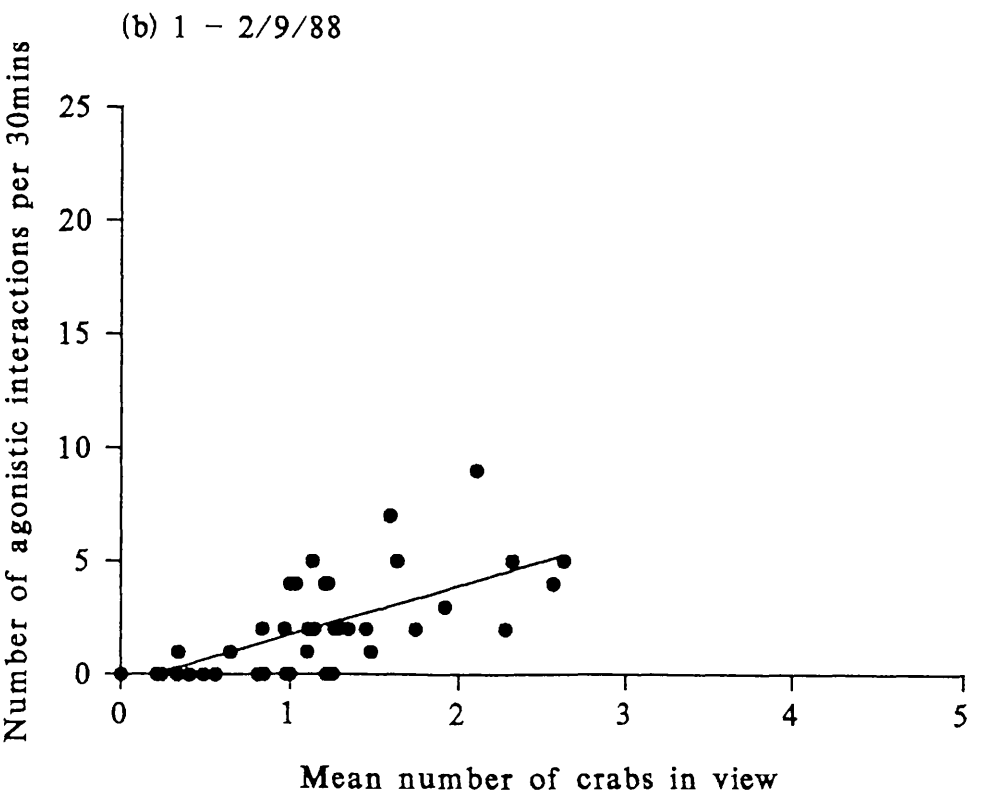

(c) Control - no bait present 2 - 3/9/88
Mean number of crabs in view
Irradiance (μE.m⁻².s⁻¹)
Time (GMT)

Figure 6.10 The incidence of agonistic interactions in the vicinity of bait in relation to the number of crabs present.





6.3.3.3 Types of intraspecific interaction

All of the agonistic acts observed in this study have been observed in the laboratory. It was therefore possible to classify the intensity of these interactions according to the ordinal scale described in section 2.3.4 (Figure 6.11). The commonest type of interaction involved one crab displacing another with non-contact display while the other crab retreated without displaying (type 2). These interactions usually took the form of one crab "chasing" another away from the bait. Non-contact bilateral display interactions (display by both crabs without strikes or grasps - type 4) were next most frequent.

The proportions of different interaction types did not vary significantly between recording sessions (G_{adj} = 8.158, df = 4, P>0.05), so further analysis is based on data from both sessions. Analyses of interaction type have been performed with types 5-7 (bilateral contact interactions) pooled due to infrequent occurrence of types 6 and 7.

To investigate whether interaction types varied with time of day, they have been grouped into those occurring at 12:00-20:00 GMT, 20:00-04:00 GMT or 04:00-12:00 GMT. There were insufficient data to use smaller increments with this classification of interaction type. The proportions of the interaction types varied significantly between these time periods (G_{adj} = 27.864, df = 8, P<0.001, Figure 6.12). Repetition of this analysis without the 04:00-12:00 group indicated that much of the heterogeneity was due to this group (G_{adj} = 5.840, df = 4, P>0.05). Including this time period, but omitting interaction type 1, indicated that the increased proportion of unilateral non-contact interactions (and reduced frequencies of types 3 and 4) between 04:00 and 12:00 accounted for most of the heterogeneity (G_{adj} = 12.219, df = 6, P>0.05).

Categorizing interactions according to the presence or absence of strikes allowed analysis with respect to time periods of 21:00-03:00, 03:00-09:00, 09:00-15:00 and 15:00-21:00. The proportions of interactions involving strikes or grasps in these time periods were 20.0% (n=125), 17.2% (n=87), 62.5% (n=8) and 18.9% (n=90) respectively. The differences between these proportions are not significant (G_{adj} = 7.035, df = 3, P>0.05).

6.3.3.4 Initiation and resolution of interactions

In some cases it was not possible to determine the relative size of the initiator or winner of interactions due to the close sizes of interactants or because initiation

Figure 6.11 The proportions of agonisitic interactions of different types in the vicinity of bait. Definitions of interaction types are given in section 2.3.4.

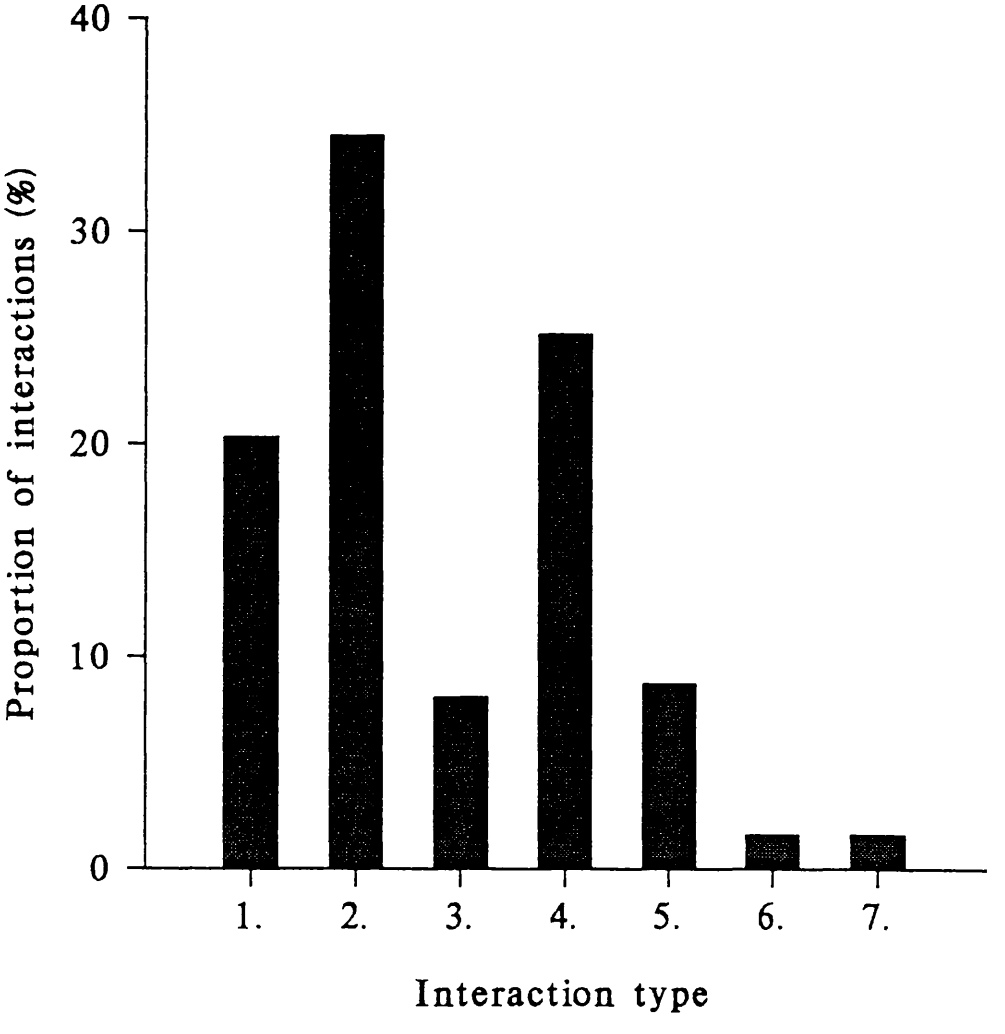
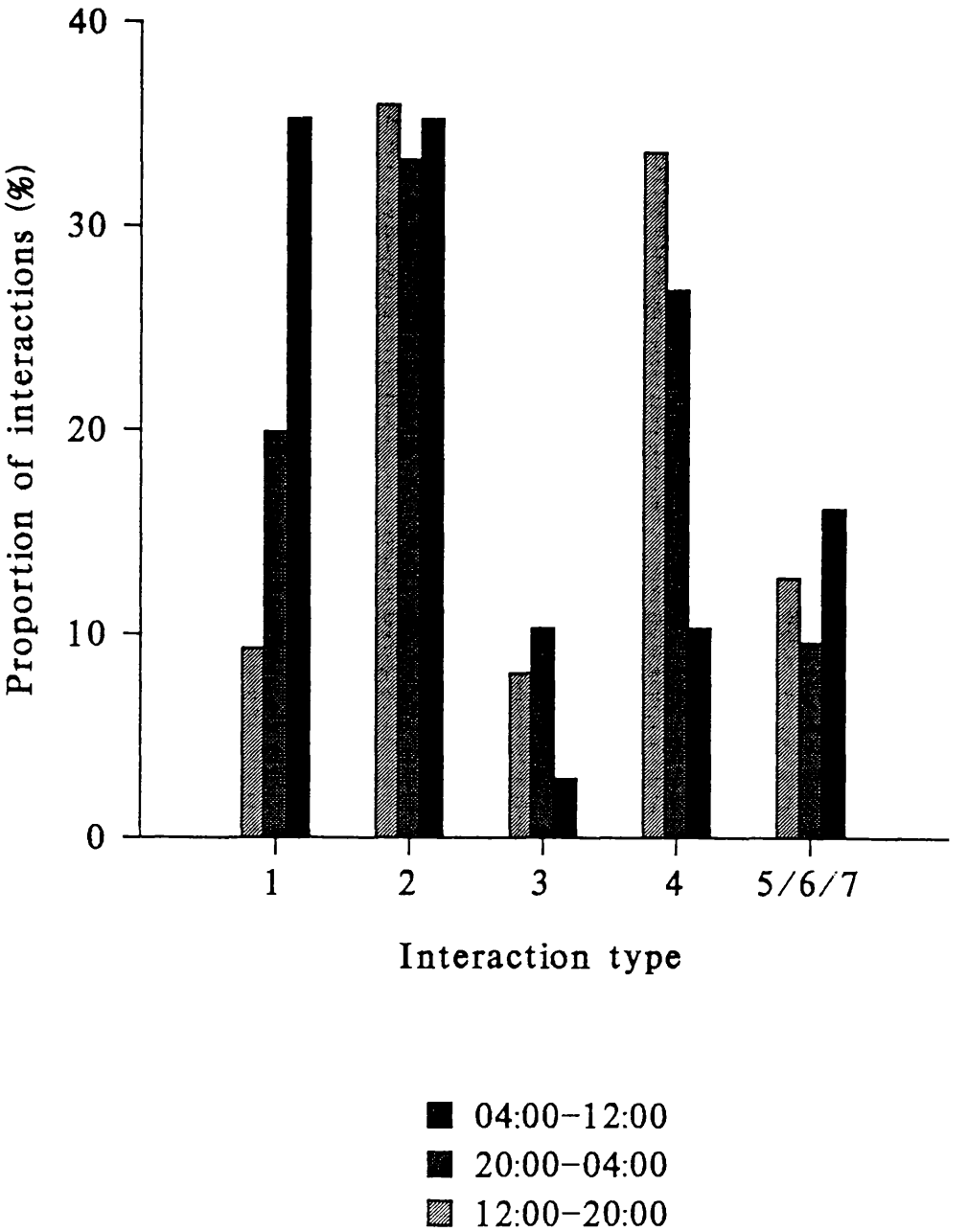


Figure 6.12 The distribution of interaction types in relation to time of day. Definitions of interaction types are given in section 2.3.4.



or resolution occurred outside the field of view of the camera. The initiator was not determined in 68 cases and the winner in 71 cases.

Of the 242 interactions with a determinate initiator, the larger crab initiated 172, significantly greater than 50% (G_{adj} = 44.122, df = 1, P<0.001). The larger crab won 212 of the 239 interactions with a determinate winner, also significantly greater than 50% (G_{adj} = 161.840, df = 1, P<<0.001). Overall, initiators were more likely to win interactions than responders (G_{adj} = 27.080, df = 1, P<0.001). When unilateral and bilateral display interactions were considered separately, this last association was found only in unilateral contests (unilateral n = 155, Fisher exact test, P<<0.01 ; bilateral n = 87, P=0.344). In other words, where one crab retreated without display, the initiator was the winner by definition. However, where the non-initiator responded offensively to its opponent, the probability of success seemed equivalent for either crab.

6.3.3.5 Duration of interactions

The durations of interactions were approximately log-normally distributed. They have therefore been transformed to their common logarithms for analysis. A 3-way ANOVA, with recording session as a fixed effect factor and interaction type and initiator as random effects factors (Sokal and Rohlf, 1981), indicated that there was no significant difference in the mean duration of interactions in the two recording sessions (session 1: mean duration ± 95% confidence limits calculated from log-transformed data = 5 +0.7, -0.6 s; session 2: 4 +1.0, -0.8 s; $F_{(1,287)}$ = 2.654, P>0.05) or between interactions initiated by the smaller crab, the larger crab or an indeterminate initiator (Table 6.11; $F_{(2,8)}$ = 0.016, P>0.25). Much of the variation in interaction duration was accounted for by the classification of interaction type (Figure 6.13; $F_{(4,8)}$ = 58.644, P<0.001). The mean durations of these interaction types increased in the same order as the ordinal intensity scale. The shortest interactions were non-display unilateral interactions and the longest were bilateral display interactions involving strikes.

6.3.4 Underwater television studies of creels

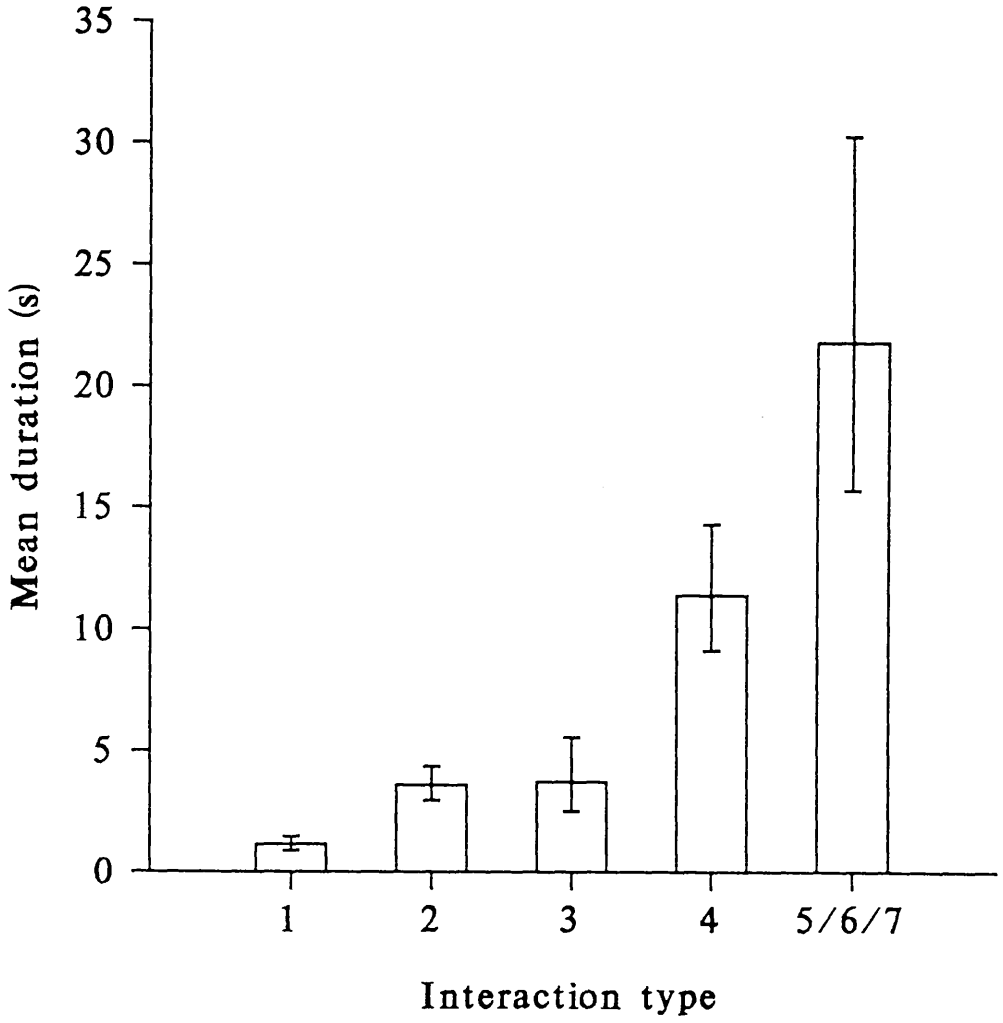
The constraints on the camera height and angle imposed by its supporting frame prevented the elimination of a large blind spot behind the creel. A view of one end of the creel was initially thought desirable as crabs could be observed approaching

Table 6.11 Mean durations of intraspecific agonistic interactions of Liocarcinus puber recorded in the vicinity of bait, classified with respect to the type of interaction and the initiator. Means and 95% confidence intervals (in parentheses) were calculated from log-transformed data and are presented in their original unit of measurement (seconds).

Interaction type[1]	Initiator		
	Smaller	Larger	Indeterminate
1	1.0 (0.51 - 1.95) n = 9	1.1 (0.76 - 1.46) n = 38	1.4 (0.85 - 2.31) n = 16
2	3.9 (1.60 - 9.51) n = 5	3.5 (2.82 - 4.39) n = 81	3.8 (2.43 - 5.82) n = 21
3	2.6 (1.08 - 6.43) n = 5	4.9 (3.01 - 7.92) n = 17	1.4 (0.46 - 4.57) n = 3
4	11.6 (8.26 - 16.39) n = 34	13.4 (8.70 - 20.78) n = 21	9.5 (6.23 - 14.59) n = 22
5/6/7	22.4 (13.8 - 36.27) n = 17	19.0 (11.32 - 31.75) n = 15	30.8 (12.62 - 75.28) n = 5

1. See section 2.3.4 for definitions of interaction types.

Figure 6.13 The mean durations of different types of agonistic interaction in the vicinity of bait. Means and 95% confidence intervals were calculated from log transformed data.



both openings to the creel. However, with this orientation the openings themselves could not be seen and activity near them was obscured by the mesh of the creel covering. This problem was accentuated at night when glare was caused by light reflected from the white mesh. A side view was the best compromise. Crabs could be detected entering either entrance and some of the area behind the creel could be seen through the covering mesh. Only one 24 h period was recorded with the creel in this orientation and reliable records of numbers of crabs approaching and entering the creel are available only for this period.

The changes in the number of crabs in the creel with time since deployment are illustrated in Figure 6.14. The number in the creel increased to a maximum of 8 at 9 h 44 min after deployment. One small *L. puber* escaped from the creel after 12 h 32 min. This was the only crab observed to escape in any of the four 24 h records of creels.

The maximum number of crabs in view at one time outside the creel was 7 after an elapsed time of 1 h 55 min. The mean number of crabs in view during successive 30 minute periods peaked after a elapsed time of 2 h 30 min (Figure 6.15). After 6 h, when there were 7 crabs inside the creel, very few crabs were observed outside. As crabs could not be identified individually, it is not possible to say how many individuals were attracted to the creel. There was a total of 35 entries into the field of view of the camera and 28 exits, compared with 8 entries into the creel and 1 exit. All crabs that entered the field of view approached the creel. 18 of the exits from the field of view occurred when there was more than one crab in the field of view and 2 of these appeared to be the direct result of agonis tic interactions. The remaining 16 exits when other crabs were present did not obviously involve interference by another crab.

The numbers of agonistic interactions observed in the four recording sessions were 6, 6, 2 and 29 respectively. In all four recording sessions there was nearly constant activity inside the creel, but this could not be observed clearly due to the covering mesh. The temporal distribution of interactions outside the creel corresponds with that of the number of crabs outside the creel in the session where this could be accurately recorded (session 4, Figure 6.16).

Of the 43 interactions observed over the four 24 h periods, fifteen were type 1, nineteen were type 2, two were type 3 and seven were type 4. Most interactions therefore involved the retreat of one crab without it displaying. There was

Figure 6.14 The time course of capture of *L. puber* by a creel.

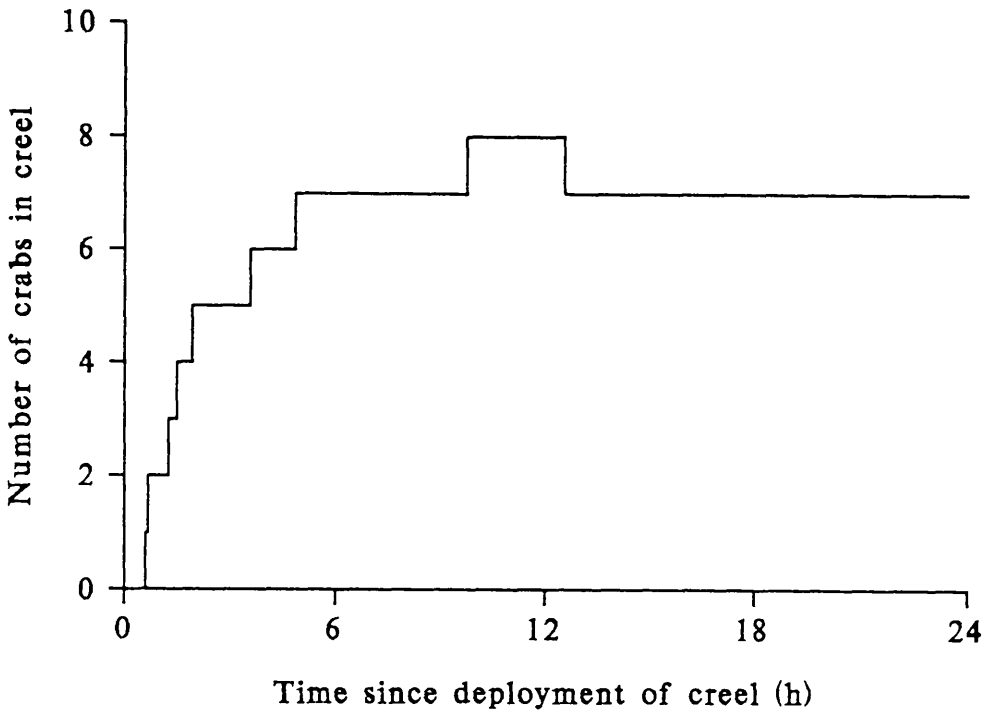


Figure 6.15 The mean number of *L. puber* in the vicinity of a creel in relation to time since creel deployment.

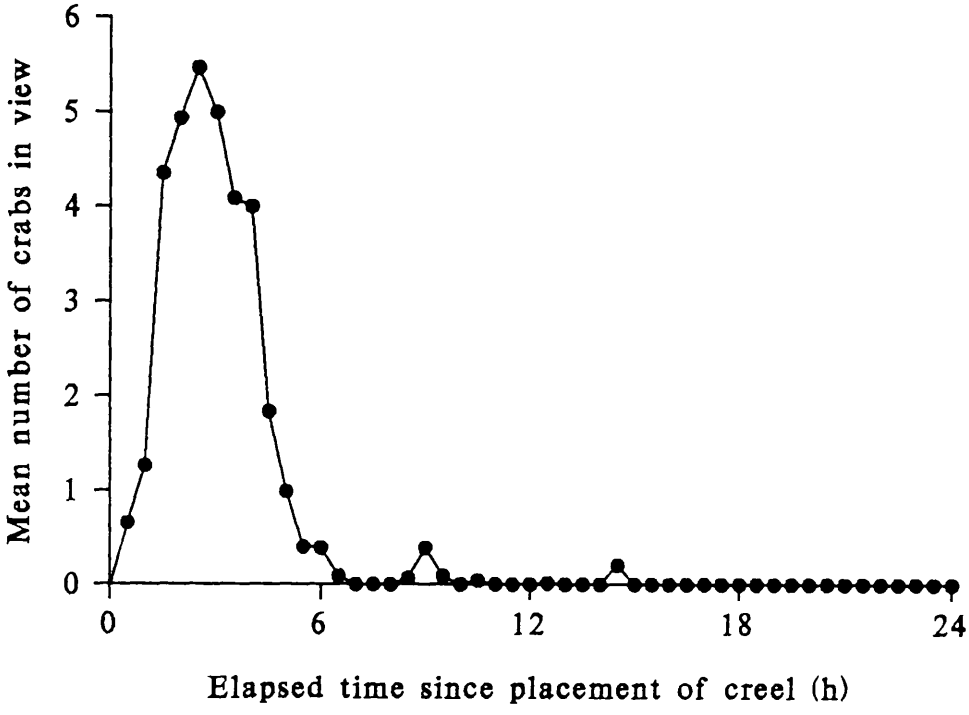
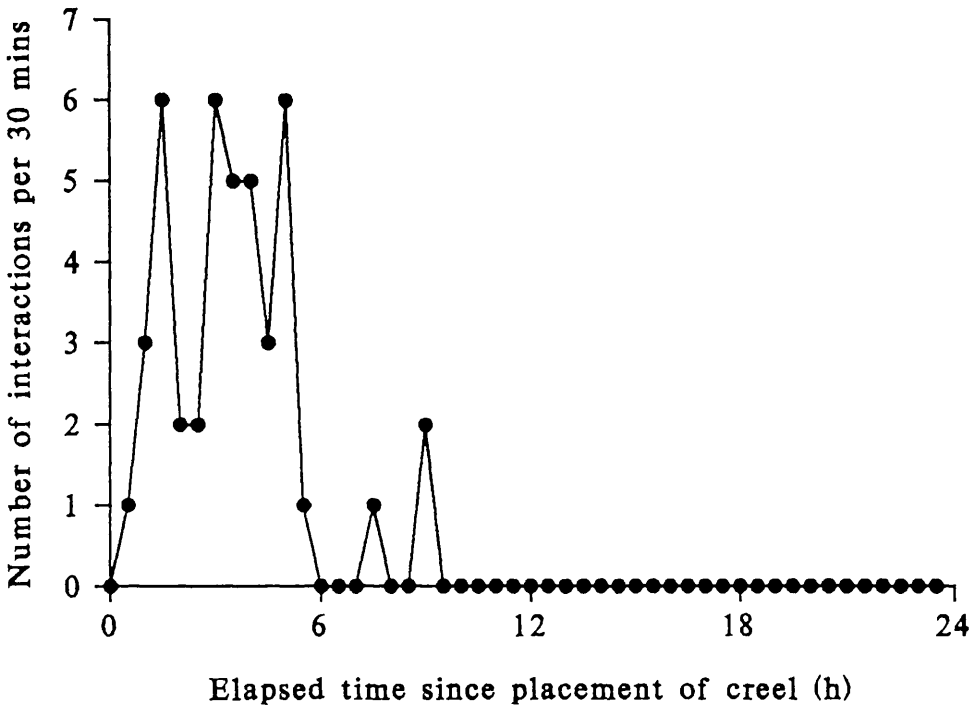


Figure 6.16 The incidence of agonistic interactions between crabs in the vicinity of a creel in relation to time since creel deployment.

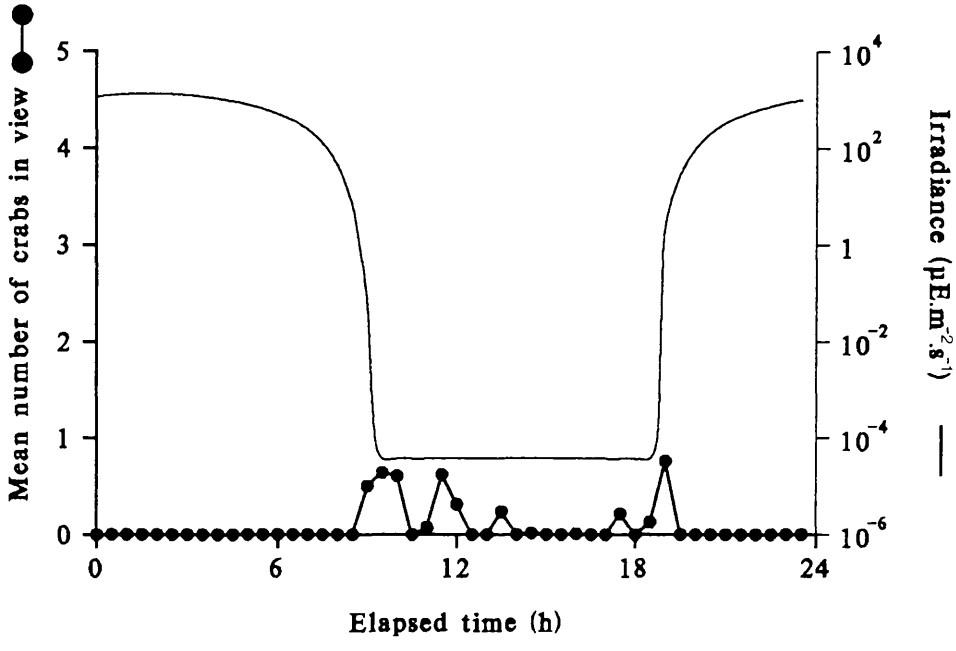


consequently a strong association between initiating and winning (Fisher's exact test, P = 0.0001) and interactions were short (mean interaction duration ± 95% confidence limits calculated from log transformed data = 2.6 +1.30, -0.86 s).

6.3.5 Underwater television studies of receptive females

In one of the recording sessions, the female escaped from the monofilament tether and in another, the female died of an unknown cause. There was only one recording session where the female remained in view for 24 hours. The number of other crabs in view was small compared with that attracted to bait (Figure 6.17). On four occasions more than one crab was present in addition to the female. Two of these were due to the entry into the field of view of a pre- or post-copulatory pair. The other two occasions both resulted in agonistic interactions. The first at 20:53 involved one crab avoiding the non-display approach of a larger individual. In the other at 20:55, one crab approached an individual larger than itself in display. The latter moved away. One other interaction was observed between the tethered female and another *L. puber* at 20:05. A brief cheliped extend display by the female resulted in a similar sized crab moving away from the group of rocks to which the female was tethered.

Figure 6.17 The mean number of *L. puber* in the vicinity of a tethered female in relation to time since placement of the female.



6.4 DISCUSSION

6.4.1 Distribution and movements of *Liocarcinus puber*

During the diving surveys, short term, localized changes in the density of *L. puber* were recorded. Such fluctuations in density can be interpreted as movement of individuals when the number of individuals missed due to sampling bias at one location can be assumed not to change appreciably from one time period to another. Several previous studies have made such inferences (e.g. Naylor, 1962; Wilber and Herrnkind, 1986; Smith and Jamieson, 1989). In the present case, this assumption was probably valid for the search area on the mid-shore. The nature of the substratum was such that all crabs present could be recorded and crabs were only present there during nocturnal high tides. The numbers of crabs recorded moving onto the shore during diving surveys were small compared with those seen during preliminary dives at this site. At that time, large numbers of *Carcinus maenas* and *L. puber* were seen feeding on barnacles and small mussels. This phenomenon was observed in one year only, in early summer, prior to the onset of reproductive activity among *L. puber*. Crabs may have been feeding intensely in response to rising temperatures and the impending breeding season, when feeding opportunities may be limited. It is somewhat mysterious that this phenomenon was not observed the following year. *Carcinus maenas* continued to feed in large numbers in the intertidal zone during nocturnal high tides. There was intense fishing activity for *L. puber* in that part of the Firth of Clyde prior to and during these surveys which probably reduced the local density of crabs. *L. puber* is known to be vulnerable to localized over-exploitation (MacMullen, 1983). The number of crabs on the shore may have reflected the abundance of active crabs in the area. Nocturnal high tide feeding in the intertidal zone has been observed previously of *L. puber* in Lough Hyne (=Ine), Northern Ireland (Ebling *et al.*, 1964) and has been inferred from gut content analysis of this species from the Gower Peninsula, South Wales (Choy, 1986). Such activity has also been reported for other sublittoral crustaceans (*Panulirus interruptus*: Robles, 1987; *Cancer productus*: Robles *et al.*, 1989).

Fluctuations in the density of *L. puber* at the search area 80 m ground distance from the level of mean high water of spring tides are more difficult to interpret, due to the probability of greater variation in sampling error at this location. The sampling technique was biased against crabs under cover, in inaccessible crevices or under

large rocks. The substratum at this sampling location consisted of boulders with many interstitial crevices and there was dense kelp cover. As crabs apparently became more cryptic during daylight, lower densities recorded during the day compared to night at this location may have been the result of the divers' inability to locate all hiding crabs. There were no marked changes in crab abundance in adjacent areas to indicate movement on- or offshore from this location during the day.

A detailed study of the movements of individuals requires crabs to be repeatedly located. Norman (1989) carried out a mark and relocate study on a predominantly intertidal population of *L. puber*. He found that in the short term, there was much emigration from his study site, although some individuals remained in the area over long periods. His sampling regime was not designed to allow short term movements to be monitored.

The sex ratio of *L. puber* at Routenburn was slightly male biased overall, but females were relatively more abundant nearer the shore. In general, sex ratios of crustaceans can be very variable, both within and between species. The sex ratio of individual species may vary with both location (e.g. *Carcinus maenas*: Edwards, 1958: *Callinectes sapidus*: Wenner and Wenner, 1983; *Menippe mercenaria*: Wilber, 1986,1989) and time (e.g. *Clibanarius vittatus*: Lowery and Nelson, 1988; *M. mercenaria*: Wilber, 1986,1989). Unbiased sex ratios have been reported previously for *L. puber*, but with an increased proportion of females before spawning (González Gurriarán, 1978; Borja, 1988). Male biased sex ratios have been reported for *L. puber* by Choy (1988) and Norman (1989).

6.4.2 Activity

Both diving and underwater television studies indicated that *L. puber* are active predominantly at night, as are many species of crab (Warner, 1977), although no activity was observed exclusively at night. These studies were carried out in shallow water, where there are large variations in light intensity. Crabs in deeper water may not have such a marked nocturnal peak of activity. Glass (1985) found that *Liocarcinus depurator* collected from shallow water exhibited marked circadian activity rhythms in the laboratory, but those from deeper water showed less variation in activity. Activity of the latter group may have been related to tidal patterns of water movement. Male *L. puber* appeared to be more active than females or juveniles, but the large proportion of crabs recorded at all times doing nothing, under

cover suggests that the average crab is inactive for a large proportion of the time. The sampling technique in the diving surveys probably underestimated crab activity, as disturbance by a diver was more likely to result in an active crab becoming inactive than *vice versa*. As the television camera was positioned in an area remote from potential shelter, only crabs active in the open were observed with this technique. Determination of a detailed time budget for *L. puber* would require individuals to be monitored for long periods, as has been done for the tropical crab, *Cataleptodius floridanus* (Engstrom and Lucenti, 1983). That study indicated that crabs spent most of the time in burrows and less than 1% in foraging bouts and social interactions.

L. puber were observed feeding on a wide variety of materials, in keeping with the predatory and scavenging habits common among crabs in general (Warner, 1977) and reported for *L. puber* in particular. Direct observations and gut content analyses have shown *L. puber* to feed on algae, principally laminarians (Choy, 1986; Norman, 1989), polychaetes (Choy, 1986), gastropods (Ebling *et al.*, 1964; Muntz *et al.*, 1965; Choy, 1986), bivalves (Kitching *et al.*, 1958; Ebling *et al.*, 1964; Muntz *et al.*, 1965; Romero *et al.*, 1982; Choy, 1986), barnacles (Choy, 1986), small crabs (Romero *et al.*, 1982), including juvenile *L. puber* (Choy, 1986), sea urchins (Muntz *et al.*, 1965) and piscine carrion (Choy, 1986). In the present study, direct observations have been made of *L. puber* feeding on all of the above as well hydroids, a nemertean, ophiuroids and dead scyphozoans.

The pattern of breeding activity of *L. puber* in the Firth of Clyde was similar to that reported elsewhere. As recorded in a more detailed study by Norman (1989), the peak of moulting of adult males was approximately 1 month before that of adult females. This asynchrony results in males being in the inter-moult stage at the time that females moult and become sexually receptive. In the present study, most reproductive activity was observed in August and September, when the incidence of female moulting was highest. In some crab species, as in other arthropods (Crespi, 1989), males which successfully pair and mate are larger than their mate and larger, on average, than single males (Hazlett *et al.*, 1977; Hazlett, 1979; Berrill, 1982; Asakura, 1987; Christy, 1987; Diesel, 1988; Sekkelsten, 1988). The fecundity of female crustaceans is generally related to their size, and this is true of *L. puber* (González Gurriarán, 1985; Choy, 1988; Norman, 1989). The potential reproductive output per mating for a male is therefore related to the size of female with which he mates. In some species, females in pre-copula, copula or post-copula

(paired females) are larger than solitary females, or the size of males and females in pre- or post-copula are correlated (Huber, 1985; Sekkelsten, 1988). Norman (1989) found that male *L. puber* paired with females, were usually larger than their mates and were larger, on average, than single males in the population. Males in the present study were, on average, larger than females and males were always larger than females with which they were paired. Males paired with females were not larger, on average, than solitary males and there was no correlation between the sizes of males and the females with which they were paired. However, paired females were smaller than average. This may be because large females at this site were anecdysic, because males were physically unable to pair and mate with large females, because small females moult more often and therefore comprised a large proportion of currently receptive females, or because males selected small females. Constraint on the locomotor abilities of males during pre-copulatory pairing has been cited as one of the factors governing size assortative mating in crustaceans (Greenwood and Adams, 1984; Adams *et al.*, 1985; Naylor and Adams, 1987; Adams *et al.*, 1989). In *L. puber*, pre-copulatory pairing can last from 1 to 9 days, copulation from 4 to 20 hours and post-copulatory pairing from 0 to 3 days (González Gurriarán, 1985). Although most reproductive pairs were seen to be inactive and under cover, some were active. The female does not contribute to the locomotor activity of a pre- or post-copulatory pair, so that the feeding opportunities of a male in pre- or post-copula are likely to be negatively related to the size of female he is carrying. Two instances of males retreating with their mates from approaching, solitary males suggest that mobility may be important in allowing paired males to avoid potentially costly agonisitic interactions. If male *L. puber* compromise between maximal reproductive output and minimal hinderance to locomotion, it would be interesting to know what activity most demands mobility in pre- or post-copulatory pairs.

Crabs without a full complement of limbs appeared to be less active than uninjured individuals. Overall, 22% of the population sampled at Routenburn were missing one or more limbs and 7% were missing one cheliped. The number of missing limbs was correlated with crab size. Norman (1989) also found a size dependent incidence of injury in *L. puber*. In the population he studied, the proportion of crabs missing at least one limb ranged from 10% of the smallest crabs to 40% of the largest. Large and therefore older crabs moult less often and may therefore accumulate injuries. Crabs readily autotomize damaged limbs. Undamaged

limbs are also readily autotomized if the animal is disturbed shortly after moulting. The causes of the injuries recorded in this study are not known. They may have resulted from predation, agonisitic interactions, crushing by rock movement during storms or minor injury and subsequent infection. Similar findings have been reported for other crustaceans. Sekkelsten (1988) found that 10% of male *Carcinus maenas* were missing one or both chelipeds, although the incidence of injury was again related to the size of crab. More than 40% of large male *C. maenas* were missing one or both chelipeds. Karnofsky *et al.* (1989b) noted that 27% of the lobsters (*Homarus americanus*) in a shallow cove were missing chelipeds and 41% of large males were injured in this way. Spivak and Politis (1989) reported a size and sex specific incidence of limb autotomy in the intertidal grapsid, *Cyrtograpsus angulatus*. 92% of intermediate sized females and 80% of intermediate sized males were missing at least one limb. Small crabs of both sexes had the lowest incidence of limb autotomy - approximately 30% of these crabs were missing at least one limb.

Although data are available for only a small number of reproductive pairs, no crabs that were missing limbs were found in pre-copula, copula or post-copula. Injured crabs may be less active overall, or the capacity to engage in sexual activity may be diminished in some way by injury. Intermediate sized *C. maenas* that were missing one or both chelipeds were found in pre-copula proportionately less often than uninjured crabs (Sekkelsten, 1988). In addition, large handicapped male *C. maenas* were found in copula proportionately less often than uninjured large males. As male crabs can be displaced from their mates by larger individuals (Edwards, 1966; Berrill and Arsenault, 1982), Sekkelsten (1988) ascribed these differences to the inferior competitive ability of handicapped males. More data are required on *L. puber* pairs before further comment can be made on this species.

6.4.3 Agonistic behaviour

In captivity and in natural conditions, *L. puber* usually interact agonistically when they encounter conspecifics. The incidence of agonistic interactions in natural conditions should therefore be a function of the density and movements of crabs. In the habitat surveyed in this study, *L. puber* occurred in low density for much of the time and this seems to be typical for this species (Muntz *et al.*, 1965; Norman, 1989; personal observations). The frequency with which crabs encounter each other may therefore depend largely on how far, at what speed and with what degree of

directionality crabs move when active. No data on these variables are available from the present study. This information can only be obtained by tracking individuals. High densities and rates of activity of crabs were only observed when they were attracted to a food source such as the mussel bed at Routenburn or the bait at Millport. Most crabs were observed in these locations at night and many agonistic interactions occurred then. Changes in the number of crabs present at a discrete food item, such as the bait, must result from the detection of attractive chemicals from the food source and the responsiveness of crabs to this stimulus. In the present study, the delay in the increase in crab numbers present at the bait and the nocturnal peak of these numbers may have been due to the time that food odour took to reach the crabs and for them to move to the bait. Alternatively, crabs may not have responded to the bait as soon as they detected it. Bjordal (1986) suggested that Norway lobsters, *Nephrops norvegicus*, responded to the bait in a creel when on a foraging excursion, but not when in their burrows. The interaction between the delay in crabs detecting attractive stimuli and their response to these stimuli could be investigated by positioning bait at different times of day. The involvement of activity rhythms could be investigated by maintaining fresh bait over a period of at least 24 h, to determine whether crab numbers fluctuate cyclically.

Although the highest densities of crabs and incidence of agonistic interactions were observed at night, interactions were not exclusively nocturnal. Indeed, the most intense interactions recorded by both diving and underwater television occurred in daylight. The low number of diurnal interactions prevented a powerful analysis of the relationship, if any, between time of day and the intensity or duration of interactions.

All of the agonistic acts observed in the field have been observed in the laboratory and *vice versa*. Qualitatively therefore, agonistic behaviour in the laboratory is representative of that in natural conditions. The relationship between interaction content and the relative size of interactants could not be investigated in detail in the field, as crabs could not be accurately sized. An underwater television camera directed vertically downwards would allow crabs to be observed and sized without disturbance. The majority of interactions were between crabs of markedly different sizes and were of the same form as such encounters in the laboratory. The larger crab initiated and won brief, low intensity interactions. The higher intensity interactions observed both by diving and by underwater television were all between more closely matched crabs. Some of these were initiated by the smaller crab, as

found in laboratory studies. For a given type of interaction, those in the field were of shorter duration than interactions in the laboratory. The confines of an observation tank may have artificially prolonged interactions. Nevertheless, in relative terms, the durations of different interaction types followed the same pattern in the field as they did in the laboratory.

The study of the capture efficiency of creels was hampered by poor visibility and low abundance of *L. puber*. As with bait, agonistic interactions were observed in the vicinity of creels, although due to the smaller number of crabs attracted, interactions between crabs outside the creel was not a major cause of crabs leaving the area. Agonistic behaviour has been found to be a significant cause of individuals leaving the vicinity of creels in both large observation tanks (*Cancer productus*: Miller, 1978; *Homarus americanus*: Karnofsky and Price, 1989) and in the field (*Nephrops norvegicus*: Bjordal, 1986).

Diminishing capture rate of *L. puber* was associated with declining numbers of crabs attracted to the creel. Further observations in an area with a greater abundance of *L. puber* are required. A vertical camera view, such as that used by Bjordal (1986) would allow the numbers of crabs entering and leaving the area to be monitored precisely. Such a system may also allow investigation of the relative importance in deterring entry of interactions between crabs outside the creel and interactions between crabs outside and those inside. Controlled experimentation is required to separate the potential effects on capture rate of bait deterioration and agonistic interactions between crabs inside and those outside the creel. The importance of bait deterioration in limiting the entry of crabs to the creel could be investigated by re-baiting the creel and leaving captured crabs inside. The possibility that crabs within the creel can deter the entry of other crabs, should be studied by leaving old bait in place and removing captured crabs.

7. DISCUSSION

In *Liocarcinus puber*, as in several species of Crustacea (Hyatt, 1983) and other taxonomic groups (Archer, 1987), the size difference between participants in agonistic interactions greatly influences the content, duration and outcome of these interactions. In both the field and laboratory, relative size was well correlated with agonistic ability, as interactions were usually won by the larger crab (chapters 2 and 6). The correlation was not perfect, however, as some interactions were won by the smaller crab, including some escalated interactions that involved strikes and grasps by both crabs. Smaller crabs were only successful when the size difference between opponents was relatively small. Interactions between disparate crabs were brief and involved little forceful contact, due to the rapid retreat of the smaller crab. Interactions between size-matched crabs were longer and often involved potentially injurious behaviour - strikes and grasps with the chelae. Although smaller crabs only won interactions when the size difference was small, some crabs initiated interactions or continued offensively against larger opponents that they apparently had little chance of defeating. This behaviour is not unique to *L. puber*. Glass and Huntingford (1988) found that smaller *L. depurator* were as likely to be the initiator of an agonistic interaction as the larger crab. Superficially at least, this behaviour is not in accord with predictions from game theory. Game theory analyses indicate that interactions should be resolved according to asymmetries that are correlated with the ability to inflict "costs" (Parker, 1974; Maynard Smith and Parker, 1976; Hammerstein and Parker, 1982). In addition, there may be circumstances where an ESS prescribes that contests should be settled by uncorrelated asymmetries (Maynard Smith and Price, 1973; Maynard Smith and Parker, 1976; Hammerstein and Parker, 1982). To compare the behaviour of an animal with this prediction one must know the relative costs of assessment and escalation and the accuracy with which individuals can assess asymmetries (Archer, 1987). In *L. puber*, escalated interactions can result in injury - particularly damage to limbs (chapter 4). Damaged limbs are usually autotomized, leading to potential loss of mobility and agonistic ability (Berzins and Caldwell, 1983), diminished growth rate (Norman, 1989) and a possible reduction in mating opportunities (Sekkelsten, 1988; chapter 6) during regeneration of the autotomized limb. Escalated interactions also involve greater expenditure of

time (chapter 2) and probably also energy (chapter 5). There appeared to be visual assessment of relative size when there was a large size difference, as the smaller crab usually retreated immediately when its opponent displayed. Crabs that displayed with the chelipeds contacting those of their opponent may have been able to compare their cheliped span tactually with that of their opponent. Pushing bouts may have allowed direct assessment of relative strength. Assessment of relative agonistic ability, using either visual or tactile cues, is probably less detrimental to fitness than escalated interactions involving strikes or grasps.

Some means of determining the visual acuity of *L. puber* in relation to size discrimination is desirable. At present, it is not known whether progression from extended cheliped displays at a distance to displays in close proximity and pushing bouts results from an inability to detect small size differences, or because the smaller crab has detected a small size difference and consequently an improved chance of success.

During an agonistic interaction, there was a tendency for the intensity of agonistic acts to increase. For example, strikes or grasps were usually preceded by non-contact displays. However, often there was not a sequential progression through acts of increasing intensity: crabs often reverted from high intensity (exaggerated extended cheliped displays with the swimming legs raised, strikes and grasps) to low intensity (extended cheliped displays with reduced pereiopod extension) acts during the course of an interaction. These complexities in the structure of interactions mean that the assumptions of the sequential assessment game (Enquist and Leimar, 1987) were not valid, although the predictions from that model and others (Parker, 1974; Maynard Smith and Parker, 1976; Hammerstein and Parker, 1982) of longer and more intense interactions between closely matched crabs were supported by the data. A more detailed analysis of the sequence of agonistic acts by the eventual winners and losers of interactions and the rôle of these acts in assessment of relative agonistic ability is required. Previous sequence analyses of crustacean agonistic acts have employed information theory (Steinberg, 1977) to determine the degree of "communication" between interactants (Hyatt, 1983). However, use of information theory to analyze escalation is hindered by the fact that what is sought - a change in act probabilities during an interaction - itself violates one assumption necessary for the computation of information theoretic measures, namely that the communication system is stationary, i.e. act probabilities do not change (Losey, 1978).

Since relative size greatly influences the character of agonistic interactions in *L. puber*, it is of interest to know the distribution of relative sizes of crabs interacting in the field. Although many interactions were recorded with the underwater television system (chapter 6), it was not possible to size the interactants accurately. If crabs encountered each other at random, the distribution of relative sizes would depend on the variation in the absolute size of crabs. The smaller the variance of sizes, the greater would be the proportion of evenly matched pairs of crabs. For example, a computer simulation of 2000 random encounters between individuals from a population of mean carapace width 59.9 mm and standard deviation of 17.07 mm (the values for the samples at Routenburn) indicated that the distribution of size ratios would be skewed towards evenly matched interactions with a mode of 0.94 and a median of 0.77. The parameters for males only ($\bar{x}$ = 69.2 mm, s = 9.02 mm) gave the same shape of distribution with a mode of 0.94 and a median of 0.88. However, crabs are unlikely to move randomly and there may be size and sex specific differences in short term movement patterns that would affect the relative sizes of interacting crabs. Information on the movement of individuals is desirable.

The movements of individuals are also likely to affect the frequency of agonistic interactions in the crabs' natural environment. In both the field and laboratory, an agonistic interaction was the probable outcome of an encounter between individual *L. puber*. The incidence of agonistic behaviour in the field therefore largely depends on the encounter rate of individuals, which will be influenced by their rate and directionality of movement. There is anecdotal (Bell, 1853) and indirect evidence (Norman, 1989) that *L. puber* are highly mobile, but little is known of their short term movements. In Lough Hyne (=Ine), Northern Ireland (Ebling *et al.*, 1964) and in the Firth of Clyde (chapter 6), there was onshore movement of *L. puber* to mussel beds during nocturnal high tides in summer. There were many encounters between crabs and brief agonistic interactions at these times. Tracking of individuals is desirable, by mark and relocate methods or by using acoustic transmitters, to determine their movement patterns at other times.

In the laboratory studies (chapters 2, 3, 4 and 5), the agonistic behaviour of males only was investigated, as previous studies have shown that in species where males are more active and have larger chelipeds than females, only males fight, or they fight more (Hyatt, 1983). In *L. puber*, there is sexual dimorphism in cheliped size and males are more active than females (chapter 6), particularly ovigerous

females (Choy, 1986). Field observations indicated that females do engage in agonistic interactions (chapter 6), although the frequency of these interactions compared with those involving males is not known. A comparison of female agonistic behaviour with that of males would be interesting in view of the difference in cheliped morphology between males and females. Jacoby (1983) found that large male *Cancer magister*, which had proportionately larger and more powerful chelipeds than females or juveniles, used fewer potentially injurious agonistic acts. Possession of less dangerous weapons reduces the potential cost of escalated interactions. Application of game theory to such circumstances gives rise to predictions that escalated interactions should occur more often and over less valuable resources (Maynard Smith, 1982) and the process of escalation should be shorter (Enquist and Leimar, 1987).

In their natural environment, *L. puber* used agonistic behaviour to compete for food and space, and observations of males paired with females retreating from single males suggest that there may be competition for mates also (chapter 6). Male *L. puber* certainly competed vigorously for receptive females in the laboratory (chapter 4). The nature of the agonistic behaviour of male *L. puber* depends in part on the resource being contested and in part on the physiological condition of the interactants. Interactions became more intense during 5 days of food deprivation, both with and without the odour of food (chapter 3). A reduction in interaction intensity after 12 days of food deprivation may have been due to a diminution of agonistic ability or to an energy conservation strategy in the absence of tangible food items. Exposing males to the odour of receptive females prolonged agonistic interactions and the few interactions observed in direct competition for a receptive female indicated a high risk of injury (chapter 4).

Food and mates are obviously valuable resources and contests for these resulted in more costly behaviour, either in terms of risk of injury (food and mates), or contest duration (mates), than in control groups. Qualitatively, these results are in accord with game theoretic predictions (Bishop *et al*, 1978; Hammerstein and Parker, 1982; Enquist and Leimar, 1987), although contest duration and the incidence of strikes and grasps are probably only crude correlates of the costs resulting from agonistic behaviour. The force with which strikes and grasps are delivered is probably variable. It is difficult to gauge the cost of contest duration *per se*, without a knowledge of the time spent in other activities and the constraints on time

expenditure. The large proportion of crabs that were recorded inactive in the field suggests that the average crab is inactive for a large proportion of the time, but focal individual observations (Martin and Bateson, 1986) are necessary to confirm this. It was also noteworthy that some crabs spent much time excluding others from a discrete food item and spent little time actually feeding (chapter 6).

The fecundity of female *L. puber*, and consequently the potential reproductive output per mating for a male, is strongly correlated with female size (González Gurriarán, 1985; Choy, 1988; Norman, 1989). However, males at Routenburn were paired with smaller than average females (chapter 6). There was no evidence that males in precopula, copula or postcopula were larger than single males, nor was there a correlation between the sizes of males and the females with which they were paired. These results are based on a rather small number of recorded pairs and this subject would bear further study. There are several possible reasons why males should pair with small females. Large females may mate less frequently because they moult less often or because they are able to store spermatozoa during moults (González Gurriarán, 1985; Choy, 1988; Norman, 1989). All but the largest males may be physically incapable of pairing with large females. Laboratory observations (chapter 4) indicated that females are not always cooperative when males hold them in a "precopulatory embrace" and a certain amount of subdual may be involved (Hartnoll, 1969). Males may select small females to retain mobility during precopulatory attendance, which may be required to permit feeding and avoidance of other males (Greenwood and Adams, 1984; Adams *et al.*, 1985; Naylor and Adams, 1987; Adams *et al.*, 1989).

Another resource important for crustaceans which is often contested by agonistic behaviour is shelter (Dingle, 1983). Most *L. puber* in the field were recorded under rocks or in crevices, but little is known of the pattern of shelter use by this species. In view of the heterogeneous nature of the habitat at Routenburn, it is unlikely that shelters are in limited supply and crabs may not return to the same shelter after an excursion. Nevertheless, this possibility should be investigated by tracking individuals and marking shelters that they use. Shelters may be in limited supply in other areas where *L. puber* are abundant, for example where the substratum is predominantly bedrock with few boulders. Norman (1989) noted agonistic interactions in such areas at dawn, when crabs may have been seeking shelter after nocturnal foraging. From a theoretical viewpoint, shelter is a resource amenable to experimental manipulation,

allowing quantitative control of resource value.

Shelter is presumably necessary for protection from predators. However, the species of predators and intensity of predation on *L. puber* is not known. In the sublittoral zone, potential predators of *L. puber* are cephalopods such as octopus, *Eledone cirrhosa*, large fish such as conger eels, *Conger*, birds such as eiders, *Somateria* spp. (Cramp *et al.*, 1977), or mammals such as otters, *Lutra* (Chanin, 1985). Glass (1985) speculated that seals (*Halichoerus grypus* or *Phoca vitulina*) preyed on *L. depurator* in Loch Sween, Argyll. Seals are often present in areas where *L. puber* are abundant, but there is no evidence that they are important predators. Octopus may be important in some localities. Although a number of fish species are certainly capable of preying on juvenile *L. puber*, adults are probably safe from all but the largest fish. Conger eels are common in the Firth of Clyde, but few are large. Potential avian predators are present in the Firth of Clyde and may be important. All of these putative predators are visual hunters. The agonisitic behaviour of *L. puber* is visually conspicuous, and it remains to be seen if agonistic displays render crabs vulnerable to predation. Increased predation risk resulting from certain types of behaviour are known for other crustaceans. Caprellid amphipods are more susceptible to fish predation when engaged in conspicuous feeding behaviour (Caine, 1989). Lawton (1989) found that subordinate juvenile American lobsters, *Homarus americanus*, were exposed to greater predation risk than dominant individuals, as they spent more time in the open, or in inadequate shelters.

Comparison of animal contest behaviour with game theoretic predictions demands a knowledge of the relative costs associated with alternative strategies. In addition to predation risk, the costs of agonistic behaviour are likely to be manifested as risk of injury and expenditure of time and energy (Archer, 1987). While injuries do occur in agonistic interactions between male *L. puber* and may have severe consequences for fitness, they do not appear to be a common result of agonistic behaviour in this species. Losers usually manage to escape before being injured. The main costs associated with the agonistic interactions of *L. puber* may therefore be time and energy expenditure. Investigation of the energetic expenditure of crabs during this behaviour is hampered by the difficulty of making physiological measurements without disrupting the animals' behaviour. The scaphognathite rate has been used as an indicator of the oxygen consumption of interacting crabs (chapter 5). Scaphognathite rate is one of the few respiratory variables that can be measured from

individual crabs, without severely restricting their behaviour. The scaphognathite rate was closely correlated with the rate of oxygen consumption of crabs recovering from exhausting exercise. Anaerobic metabolism did not seem to be an important route of energy production during agonistic behaviour, as there was not a significant increase in haemolymph L-lactate concentrations following interactions. The energetic expenditure of crabs during agonistic behaviour should therefore have been closely related to their rates of oxygen consumption and scaphognathite rates. During agonistic interactions, the pattern of scaphognathite beating was irregular, with periods of extreme hyperventilation and ventilatory pauses. The maximum scaphognathite rates during interactions were among the highest reported for a range of similar decapod crustaceans in response to a variety of stresses. During interactions, the respiratory activity of both the eventual winner and loser was related to the degree of escalation and the duration of the interaction. Certain activities, such as strikes and pushing bouts were associated with high rates of scaphognathite beating. These acts may be energetic in themselves, or the respiratory rates of crabs may be elevated in preparation for future acts. Anticipatory increases in metabolic rate are known for other arthropods. For example, the metabolic rate of moths increases during a pre-flight warm-up period (Bartholomew *et al.*, 1981). If crabs could be induced to display in a respirometer, it may be possible to measure the oxygen consumption associated with individual acts. It would be interesting to measure the extraction efficiency of oxygen from the water by the gills at such high ventilatory rates. Several authors have reported that crustaceans produce strong respiratory currents during agonistic behaviour (Erpenbeck and Altevogt, 1966; Rubenstein and Hazlett, 1974; Jachowski, 1974; Barron and Hazlett, 1989). It has been suggested that these currents may be used in assessment of relative agonistic ability or vigour (Jachowski, 1974; and Barron and Hazlett, 1989). This is a difficult suggestion to test as energetic behaviour would inevitably result in high rates of ventilation. Barron and Hazlett, (1989) found that the resolution of interactions between hermit crabs was often immediately preceded by a strong jet of water from the winner. In the present study, the flow rate of the scaphognathite-generated current was not detectable, but the maximum scaphognathite rates of winners and losers during interactions were not significantly different.

Scaphognathite rates generally remained high after the end of interactions. Recovery was prolonged in some cases, but on average was less than the time to

recover from exhausting exercise. The existence of significant post-exercise respiratory activity without a build up of L-lactate was presumably due to recharging of oxygen and phosphagen stores, but there is a need for identification of the components of excess post-exercise oxygen consumption in response to sub-maximal exercise in crustaceans. An estimate of the energetic cost of agonistic behaviour was based on respiratory activity during the interaction and subsequent recovery. This estimate was correlated with the interaction content and duration for losers but not winners, although there was no significant difference between losers and winners in this estimate. The differences in behaviour between interactants, which usually occurred towards the end of an interaction, do not seem to result in differences in energetic expenditure (as estimated from the excess scaphognathite activity). This study also indicated that, in the laboratory at least, there are behavioural differences between winners and losers after resolution of the interaction. Winners exhibited more spontaneous locomotor activity than losers, which tended to remain quiescent. It is of interest to know if this laboratory observation has some basis in reality in nature.

This study has shown that it is possible to make physiological measurements of crabs that are related to their energy expenditure, without severely disrupting their behaviour. Such measurements cannot be related to fitness in absolute terms, but comparisons with the respiratory consequences of other activities may indicate the relative energetic expenditure of crabs during agonistic behaviour. The present results indicate that the respiratory consequences of this behaviour last much longer than the duration of the interaction itself, but not as long as recovery from exhausting exercise. A wider range of interaction intensities, and interactions over different resources should now be examined.

Agonistic behaviour has important consequences for the commercial exploitation of some species of Crustacea. Agonistic behaviour in and around traps reduces the capture rate, as large individuals exclude others from the area (Miller, 1978; Bjordal, 1986; Karnofsky and Price, 1989). The animals may also damage each other during subsequent holding and transport if they are given the opportunity to interact with each other. Although injuries are not common when *L. puber* are able to escape from their opponents, when confined in artificial conditions, injuries are common (personal observations). *L. puber* are usually transported in crates or fish boxes and are packed in such a way that agonistic behaviour is not a problem. The supply of oxygenated

water is the main problem during transport (Johnson and Uglow, 1985).

Agonistic interactions occur when *L. puber* are attracted to discrete food items, such as the bait in a creel. However, in an area where *L. puber* abundance was low due to intense commercial fishing, agonistic behaviour was not important in reducing the catch rate of creels (chapter 6). Diminishing capture rate with time was associated with declining numbers of crabs attracted to the creel. Unfortunately, it was not possible to carry out this study in an unfished area. *L. puber* were more abundant during the earlier video study of the response to discrete food items. Many agonistic interactions occurred in that situation, and in some cases, individual crabs excluded others from the bait. Although a small number of crabs left the vicinity of the creel as a result of agonistic interactions outside the creel, there was no evidence that crabs were directly prevented from entering by individuals within. However, the presence and agonistic activity of individuals within the creel may have been partially responsible for the large proportion of crabs that approached the creel but did not enter.

Further studies of the capture of *L. puber* by creels should be carried out in an area without intense commercial exploitation, using a vertically oriented, downwards camera view of a creel with a covering mesh of low visibility (such as dark twine or monofilament nylon). This would allow assessment of the relative importance of interactions between crabs inside and outside the creel. The importance of bait deterioration and agonistic behaviour in limiting the capture rate should be investigated by analyzing the performance of creels in which fresh bait is maintained, but captured crabs are not removed and creels in which captured crabs are removed, but bait is not renewed.

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