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# Decapod crustacean chelipeds: an overview

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The structure, growth, differentiation and function of crustacean chelipeds are reviewed. In many decapod crustaceans growth of chelae is isometric with allometry level reaching unity till the puberty moult. Afterwards the same trend continues in females, while in males there is a marked spurt in the level of allometry accompanied by a sudden increase in the relative size of chelae. Subsequently they are differentiated morphologically into crusher and cutter making them heterochelous and sexually dimorphic. Of the two, the major chela is used during agonistic encounters while the minor is used for prey capture and grooming. Various biotic and abiotic factors exert a negative effect on cheliped growth. The dimorphic growth pattern of chelae can be adversely affected by factors such as parasitic infection and substrate conditions. Display patterns of chelipeds have an important role in agonistic and aggressive interactions. Of the five pairs of pereiopods, the chelae are versatile organs of offence and defence which also make them the most vulnerable for autotomy. Regeneration of the autotomized chelipeds imposes an additional energy demand called "*regeneration load*" on the incumbent, altering energy allocation for somatic and/or reproductive processes. Partial withdrawal of chelae leading to incomplete exuviation is reported for the first time in the laboratory and field in *Macrobrachium* species.

## 1. General morphology

Chelipeds of decapod crustaceans have attracted human curiosity and fired human imagination since Aristotle (Hopkins 1993) probably because they figure so prominently both in structure and function in the life of these animals. Crustaceans are mostly aquatic arthropods which breathe through gills, have two pairs of antennae, and numerous paired appendages on thorax and abdomen (Stebbing 1893; Schmitt 1965) that are grouped into cephalic, thoracic and abdominal appendages in relation to the body tagmata. The cephalic and thoracic regions are usually fused to form a cephalothorax and the appendages are known as cephalo-thoracic appendages. Decapod appendages are the best example of serial homology with a serial modification in basic structure from the first to the last walking leg (Wood and Wood 1932). With the exception of the antennules, which are uniramous, other appendages are basically biramous and possess a basal segmented protopod with a coxa and basis and may have lateral (exites) or medial (endites) protrusions (Manton 1977; McLaughlin 1982). From the protopod arise the exopod and endopod. Of the two, the latter has undergone a variety of specialisations resulting in its transformation for various functions like sensory reception, feeding, walking, burrowing and swimming while the exopod is drastically reduced or may even be lost. This has further been facilitated by mineralisation of the exoskeleton endowing rigidity and support to the appendages which are made flexible by the arthrodial membrane.

All decapods usually have five pairs of well developed walking legs with exceptions in the sergistid family of the Dendrobranchiata, many of the Anomura, and a few Brachyura. In these animals the fifth or fourth and fifth pair of pereiopods are reduced in size for special functions. Occasionally both pairs may be vestigial or absent (McLaughlin 1982). Structural modifications of decapod appendages due to diversified functions and life style have been described in different groups (Tiegs and Manton 1958; Kaestner 1970; Schram 1978). The major modifications

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of the appendages have evolved essentially from the feeding habits of the groups (either for filtering or for predation). However, the functional and structural modifications of crustacean chelipeds are not only due to feeding and locomotion (Dahl 1956; Bock and von Wahlert 1965; Manton 1977) but also change with environmental conditions (Smith and Palmer 1994) and species specific needs supplemented by *hox* genes (Averof and Patel 1997). Among decapods the chelate legs are unique with the first (Brachyura) or the second pair (among Macrura with first two chelate pereiopods) being the sole organ of offence and defence.

The typical cheliped or ambulatory pereiopod comprises of an exopod and endopod of which the latter is highly reduced or lost. The exopod comprises seven podomeres: (i) coxa, a short, stout cylinder, moving anterio-posteriorly in articulation with the sternum and epimeron, (ii) basis, a short cylinder with lesser average diameter than the coxa and articulated by hinge joints with the coxa, moving dorso-ventrally, (iii) ischium, larger and wider than the basis, fused immovably and curved upward, (iv) merus, (v) carpus, (vi) propodus, and (vii) dactyl. The basis and ischium when fused together form the basi-ischium (Lochhead 1961).

Typically Caridean shrimps have chelate or subchelate first and second pairs of pereiopods; however, among the Processidae often only one pereiopod of the first pair is chelate, while the opposing member is simple. A very unique and exaggerated development of one chela of the first pair of pereiopod is characteristic of snapping shrimp of the family Alpheidae. After being cocked in the open position and building up tension, this large snapper claw (of up to half the animal's size) closes rapidly forming a thin water jet; its high velocity (25 m/s) results in the formation of a small cavitation bubble (3·5 mm in diameter), that collapses with an extremely loud and short sound (up to 248 dB re 1 μPa at 1 cm distance for 240 ns) (Schmitz 2000). This signal is used for intraspecific, hydrodynamic communication (Herberholz and Schmitz 1998) as well as for territorial defence and to stun or even kill small prey (small shrimp, crabs or fish) (MacGinitie and MacGinitie 1949; Hazlett and Winn 1962; Schultz *et al* 1998). Marked asymmetry of the first pair of chelate pereiopods is also common in a number of other decapods like lobsters and fiddler crabs.

## 2. Growth

Crustacean growth is discontinuous since the highly mineralised old exoskeleton is shed through a process known as ecdysis (= moulting) whenever a certain growth increment is achieved, whereas growth in vertebrates is continuous. In decapods three types of allometry exist: (i) positive allometry or progressive geometric growth, in which the dependent variable grows fast with respect to body size, (ii) isometric or arithmetic growth, and (iii) negative allometry or retrogressive geometric growth, in which the dependent variable grows slower than body size. Chelipeds are the best example of crustacean allometric growth. In males of the crab *Arenaeus cribrarius* (Pinheiro and Fransozo 1993), crayfish *Orconectes virilis*, and blue clawed (BC) males of *Macrobrachium rosenbergii* (Kuris *et al* 1987), chela growth shows positive allometry (Aiken and Waddy 1992), while it is isometric in juveniles and females (Pinheiro and Fransozo 1993). A detailed account of the types of allometric growth of cheliped in various decapod crustaceans is given in table 1.

In heterochelous decapods chelipeds are further differentiated into major (crusher) and minor (cutter) based on morphologically and functionally different dentition patterns (Levinton *et al* 1995). The large and robust chela with molariform teeth, known as the crusher, can yield more force than the minor, which has many cutting teeth and spiniform setae (figure 1) (Mariappan and Balasundaram 1997). Major and minor chelae possess differential operating forces measured as ideal mechanical advantage (IMA) (figure 2) (Warner and Jones 1976; Brown *et al*

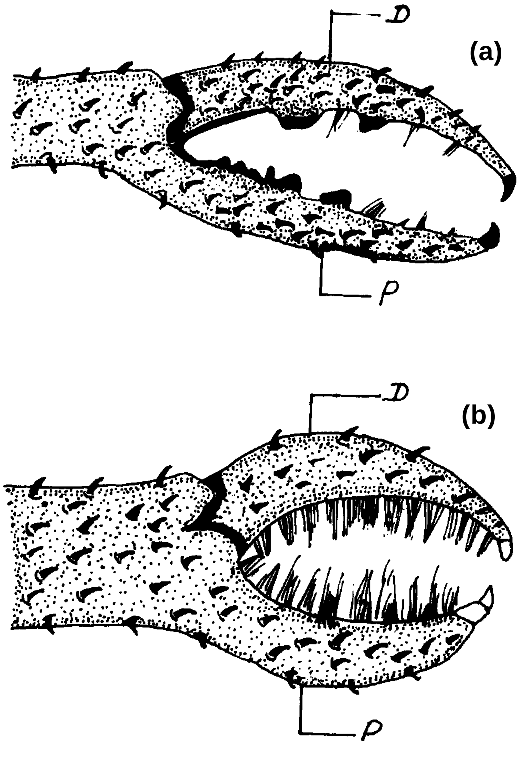

**Figure 1.** Morphological variations in the propodus of (**a**) major and (**b**) minor chela in *Macrobrachium nobilii*. D, Dactyls; P, propodus (from Mariappan and Balasundaram 1997).

**Table 1.** Allometric growth of crustacean chelipeds.

| Species | Sex | Allometric status | Source |
|---|---|---|---|
| *Arenaeus cribrarius* | M | + | Pinheiro and Fransozo 1993 |
| | F | – | |
| *Austropotamobius pallipes* | M | + | Grandjean *et al* 1997 |
| | F | – | |
| *Cleistostoma kuwaitense* | M | + | Clayton 1990 |
| | F | – | |
| *Liocarcinus depurator* | M | + | Muino *et al* 1999 |
| | F | + | |
| *Macrophthalmus birtipes* | F | + | Barnes 1968 |
| *Macrophthalmus setosus* | F | 0 | |
| *Macrobrachium nobilii* | M | + | P Mariappan and C Balasundaram, unpublished |
| | F | 0 | |
| *Macrobrachium rosenbergii* | M | + | Nagamine and Knight 1980 |
| *Orconectes propinquus* | M | + | |
| *Orconectes rusticus* | M | + | Garvey and Stein 1993 |
| *Orconectes virilis* | M | + | |
| *Trapezia ferruginea* | M | + | Finney and Abele 1981 |
| | F | 0 | |
| | B | + | |

M, Male; F, female; B, berried; +, positive allometry; –, negative allometry; 0, isometry.

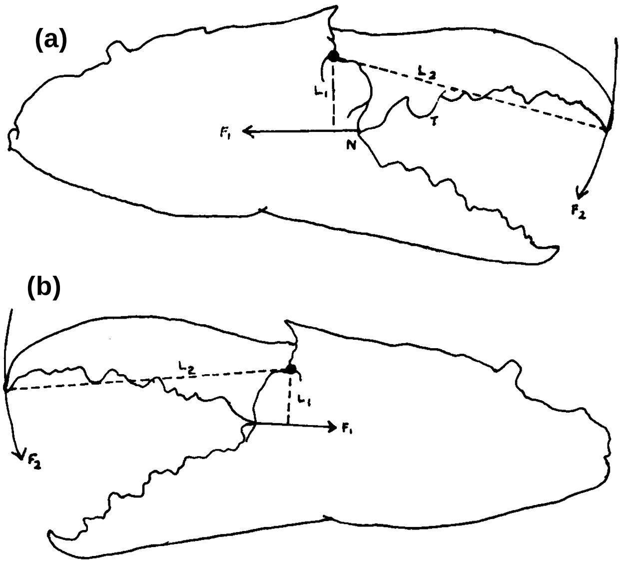

**Figure 2.** Ideal mechanical advantage (IMA) measurements of *Macropipus depurator* chelae (**a**) strong and (**b**) fast chela. The arrows show the direction through which forces F1 and F2 act. T, Tooth, N, notch (from Warner and Jones 1976).

1979). In male *Uca* and *Alpheus*, the major chela is used for aggressive and courtship displays, while the other is used for capture and manipulation of prey and grooming (Hazlett 1962; Nolan and Salmon 1970; Crane 1975). Many crustaceans have spatulate chelae which are used to scrap algae from rocks (McLaughlin 1982). The atyid shrimps use brush and spiny setae on chelipeds to scrape up debris (Fryer 1960). In *Macrobrachium australe* the minor chela endowed with abundant bristles serves as a sort of net to catch prey while the major chela is used to pick up prey. Such a differential function among chelipeds is also observed in *Homarus* spp. (Davis 1987). Chela size is also related to feeding habits. For instance, detritivorous crabs have small slender claws (Seed and Hughes 1995) while carnivorous counterparts like *Ocypode* spp. possess enlarged chelae to facilitate predation. In *Macrobrachium nobilii,* the robust second pair is used for prey capture and the slender first pair functions to deliver the food to the mouth (P Mariappan and C Balasundaram, unpublished data).

The crustacean chelipeds, thus differentiated in size in otherwise bilaterally symmetrical organisms, provide a prominent example of asymmetry, which is referred to as cheliped laterality or handedness (Govind 1989). The presence of a crusher chela on the right or left side in many decapod crustaceans and deviation from a 1 : 1 ratio has been widely reported (table 2). In predatory Brachyura the presence of the major chela on the right side facilitates handling of asymmetric hard shelled molluscan prey, providing a possibility for coevolution of a predator–prey complex (Abbay-Kalio and Warner 1989; Seed and Hughes 1995). This concept however becomes untenable when the handedness changes (Ahmed 1978; Govind *et al* 1988). Reversal of handedness from crusher to cutter and vice-versa or from pincer claw to snapper claw, when a chela is lost, has been well documented in some heterochelous crabs, lobsters, and snapping shrimp (Wilson 1903; Yamaguchi 1977; Mellon 1981; Govind 1989; Young *et al* 1994). In other species with plasticity in chela development into major or minor forms, the establishment of laterality (handedness) is determined by ecological factors (Davis 1987; Smith and Palmer 1994; Goldstein and Noetzli 1997), and the reversal of handedness depends on the age of the animal (Cheung 1976). However, in species where there is no reversal, genetic factors determine laterality (Bush 1930; Yamaguchi 1977). Apart from functional differences, structural variations between crusher and cutter also have been elucidated (Ogonowski and Lang 1979; Ogonowski *et al* 1980). After autotomy, the resultant changes in the composition of chela muscles at the time of chela development, reversal, and regeneration are well documented in lobsters (*Homarus americanus*), and snapping shrimp *Alpheus heterochaelis* (Stephens and Mellon 1979; Mellon and Stephens 1980; Govind and Lang 1981; Quigley and Mellon 1984; Govind *et al* 1987, 1988; Govind and Pearce 1988a, b, 1994; Govind 1989). In *Gecarcinus lateralis*, there is an attendant breakdown in claw muscle protein that occurs at moulting which allows the reduced claw to be drawn through the comparatively small foramen at the proximal end of the propus (Skinner 1966; Mykels and Skinner 1981).

Sexual dimorphism in cheliped size has also been established in crabs (Crothers 1967), lobsters and crayfish (Snedden 1990), mantis shrimp (Schuster and Caldwell 1989), snapping shrimp (Read and Govind 1997), and freshwater prawns (Mariappan and Balasundaram 1997). Generally such a dimorphism between a cheliped pair (Darby 1934) is mainly based on size rather than form (Lee 1995) and when adjusted for size variations their functions are similar as in *Ozius verreauzii* (Hughes 1989). However in *Alpheus heterochaelis* the male pincer claw really differs in form from that of the female structurally (Read and Govind 1997). The development of a dimorphic pattern begins at the time of puberty moult (Hartnoll 1974; Pinheiro and Fransozo 1993, 1998), which is a prerequisite for functional sexual maturity (see e.g. *Hyas lyratus*, Stevens *et al* 1993). In some decapods the attainment of puberty moult is identified by the level of change in propodus length (e.g. *Nephrops norvegicus*, Farmer 1974). Differences in chela allometry are used to

**Table 2.** Handedness in decapod crustaceans.

| Species | Handedness | Source |
|---|---|---|
| *Calappa philargius* | R | Ng and Tan 1985 |
| *Callinectes sapidus* | R | Hamilton *et al* 1976 |
| *Carcinus maenas* | R | Abby-Kalio and Warner 1989 |
| *Glabropilumnus laevimanus* | R | Tweedie 1950 |
| *Globopilumnus globosus* | R | Tweedie 1950 |
| *Heteropanope glabra* | R | Tweedie 1950 |
| *Heterozius rotundifrons* | R | Jones 1978 |
| *Macrobrachium nobilii* | R | Mariappan and Balasundaram 1997 |
| *Menippe mercenaria* | R | Cheung 1976 |
| *Necora puber* | R | Norman and Jones 1991 |
| *Neopanope texana* | R | Swartz 1972 |
| *Pilumnus hirtellus* | R | Tweedie 1950 |
| *Uca lactea* | R | Yamaguchi 1973, 1977 |
| *Uca vocans* | R | Barnwell 1982 |
| *Uca tetragonon* | R | Barnwell 1982 |
| *Uca formosensis* | R | Barnwell 1982 |
| *Ocypode gaudichaudii* | L | Trott 1987 |
| *Synalpheus brevicarpus* | L | Herrick 1911 |
| *Alpheus dentipes* | – | Dawes 1934 |
| *Alpheus heterochaelis* | – | Young *et al* 1994 |
| *Chlorodopsis melanochira* | – | Tweedie 1950 |
| *Homarus americanus* | – | Herrick 1911 |
| *Macrobrachium australe* | – | Davis 1987 |
| *Nephrops norvegicus* | – | Farmer 1974 |
| *Ocypode quadrata* | – | Haley 1969 |
| *Thalassina anomala* | – | Pillai 1990 |
| *Uca formosensis* | – | Shih *et al* 1999 |
| *Xantho exartus* | – | Tweedie 1950 |

R, Right handed; L, left handed; –, equal distribution of right and left handed animals.

differentiate immature from mature phases in *Pagurus prideauxi* (Paulian 1936). Factors like feeding, mate-guarding, and fighting influence the development of such dimorphic patterns of chelipeds (Vermeij 1977; Hughes 1989). Parasites exert a remarkable negative effect on the growth of chelipeds in various crustaceans. Bopyrids, entoniscids and sacculinids are the common parasites known to affect the normal growth of chelipeds. Infection of a bopyrid *Gyge branchialis* on *Upogebia littoralis* and *Probopyrus pandalicola* on *Palaemonetes*, *Ione thoracica* on *Callianassa laticauda*, an entoniscid *Entonella monoensis* and a sacculinid *Sacculina polygenea* on *Hemigrapsus sanguinesus* showed a significant reduction of chela size when compared to uninfected forms (Tucker 1930; Reverberi 1943; Morris 1948; Hartnoll 1960; Yamaguchi and Aratake 1997).

In *Macrobrachium rosenbergii* the development of polymorphic males is common in natural as well as communally cultured populations. These males are differentiated into (i) small males (SM), with delicate, clear or light pink claws and with a low ratio of claw to body length and much smaller than the other two morphotypes, (ii) orange-clawed males (OC) with non-spineous, often orange claws, having a higher claw to body length ratio, and (iii) blue-clawed males (BC) with blue, spineous claws and a high ratio of claw to body length. Small males can transform into blue-clawed males through orange-clawed forms in the absence of dominant BC males or when raised in isolation (Ra'anan and Cohen 1985; Kuris *et al* 1987). Among mature males of *Pisa* spp., *Jassa falcata* and *Inachus leptochirus*, even within the same age group there is a remarkable difference in the size and

**Table 3.** Variations in the percentage of limb loss in field populations of various decapod crustaceans.

| Species | Category | Per cent | Source |
|---|---|---|---|
| *Atergatis flloridus* | M | 41·30 | Norman 1995 |
| | F | 18·40 | |
| *Callinectes sapidus* | – | 24·80 | Smith 1990a, b |
| *Cancer magister* | – | 25·00 | Shirley and Shirley 1988 |
| *Cancer magister* | – | 45·00 | Durkin *et al* 1984 |
| *Cancer pagurus* | M | 13·20 | Bennett 1973 |
| | F | 9·90 | |
| *Carcinus maenas* | M | 12·50 | Abello *et al* 1994 |
| | F | 7·90 | |
| *Carcinus maenas* | M* | 1·70 | Sekkelsten 1988 |
| | M** | 17·90 | |
| *Carcinus maenas* | M | 53·30 | McVean 1976 |
| | F | 55·00 | |
| *Chionoecetes bairdi* | J | 34·60 | Edwards 1972 |
| | M | 43·00 | |
| | F | 23·00 | |
| *Cyrtograpsus angulatus* | – | 80·00 | Spivak and Politis 1989 |
| *Homarus americanus* | M | 44·40 | Moriyasu *et al* 1999 |
| | F | 61·30 | |
| *Homarus americanus* | – | 21·00 | Estrella and Armstrong 1994 |
| *Homarus americanus* | M | 40·00 | Briggs and Mushacke 1979 |
| | F | 30·20 | |
| *Macrobrachium nobilii* | J | 10·90 | Mariappan and Balasundaram 1999b |
| | M | 15·22 | |
| | F | 22·30 | |
| *Necora puber* | J | 23·00 | Norman and Jones 1991 |
| | M | 32·80 | |
| | F | 28·80 | |
| *Nephrops norvegicus* | M | 62·00 | Chapman and Rice 1971 |
| | F | 41·00 | |
| *Panulirus argus* | – | 40·30 | Davis 1981 |
| *Paralithodes camtschatica* | J | 29·40 | Edwards 1972 |
| | – | 14·80 | |
| *Paralithodes camtschatica* | M | 15·30 | Niwa and Kurata 1964 |
| | F | 19·50 | |

J, Juveniles; M, males; F, females; –, not categorised.
Carapace width: *20–34·9, **65–79·9 mm.

shape of the chela (Sexton and Reid 1951; Hartnoll 1963). Season-induced cyclic changes in chela polymorphism has been reported in males of *Orconectes propinquus* (Stein 1976).

## 3. Autotomy

Autotomy refers to a reflex severance of one or more limbs in response to injury or its threat, which occurs always in a predetermined breakage plane (Wood and Wood 1932; Robinson *et al* 1970; McVean 1982). A number of factors contribute to the prevalence of autotomy, which has been extensively studied and reviewed from time to time (Wood and Wood 1932; Bliss 1960; McVean 1982; Juanes and Smith 1995). Crustaceans widely practice self amputation of one or more limbs during inter- and intraspecific competition for limited resources like food, shelter, mate and also as a strategy to avoid predation and wound limitation (Wood and Wood 1932; Bliss 1960; McVean 1982). Apart from such biological reasons, commercial factors like intentional harvesting of chelipeds in species like *Menippe mercenaria* (Savage and Sullivan 1978), incidental damage by fishing gear (Kirkwood and Brown 1998), and culling of undesirable individuals (Kennelly *et al* 1990) are also responsible for the loss of chelipeds. In the polymorphic male population of *M. rosenbergii*, cheliped loss is a periodic event among the dominant blue-clawed males (bulls) on attaining a critical value of 1 : 2·8 ± 0·18 body length/chela length as a growth strategy (Schmalbach *et al* 1984). Males of *M. nobilii* (28%) (carapace length: 1·6–2·5 cm) resort to chela autotomy during exuviation even when reared individually under ideal laboratory conditions (Mariappan and Balasundaram 1999a); even multiple limb autotomy occurs in *M. malcolmsonii* in the field (P Mariappan and C Balasundaram, unpublished data). The limb loss varies from species to species (1·7% in *Carcinus maenas*, Sekkelsten 1988; 80% in *Cyrtograpsus angulatus*, Spivak and Politis 1989), within a species (*C. maenas*, 1·7%, Sekkelsten 1988; 55%, McVean 1976) and as a function of size within a species (*Necora puber*, 12% in juveniles and 38% in adults, Norman and Jones 1991) (table 3). To a certain extent temporal and geographic variations also contribute to autotomy in a given population (Shirley and Shirley 1988; Smith 1990a). Though the autotomised animals get immediate advantage in terms of survival, in the long term the need to divert body resources for regeneration has an adverse effect on the regular energy budget. Further the injured animal becomes less dominant and remains more vulnerable to further attacks in a community; autotomy also limits its access to shelter, food gathering potential, and its ability to find a mate (Kuris and Mager 1975; Sekkelsten 1988; Davenport *et al* 1992; Abello *et al* 1994; Smith 1995).

## 4. Regeneration

Crustaceans have the ability to replace lost limbs by means of regeneration, which is linked with moulting (Prizbram 1901; Bliss 1960; Skinner 1985). However, at any given time, in a wild population of *Cancer magister* the proportion of animals with regenerating limbs (5%) is comparatively lower than that of animals with lost limbs (18%) (Shirley and Shirley 1988), suggesting an increased vulnerability of autotomised animals to predation (McVean and Findlay 1979). In some species the process of limb regeneration affects the moult increment and moult interval but in others no such effect has been reported (Smith 1990b; Spivak 1990; Cheng and Chang 1993). Regeneration of a lost limb to its original size depends upon age and time of loss in a given moult cycle. Normally the lost limb regenerates within 2–3 moults, faster in juveniles than in adults (Skinner 1985; Smith 1990b).

## 5. Abnormalities in chelipeds

Abnormalities or malformation of chelipeds have been reported widely in various decapod crustaceans like lobster (*Homarus americanus*, Faxon 1881; *H. gammarus* and *Nephrops norvegicus*, cf. Shelton *et al* 1981), crayfish (*Procambarus clarkii*, Chokki and Ishihara 1994; Nakatani *et al* 1997), crab (*Geryon affinis granulatus*, Okamoto 1991; *Macrophthalmus japonicus*, Suzuki 1963), and the Japanese edible crab (*Chionectes japonicus*, Motoh 1971). Most of these claw abnormalities are mainly due to a lateral outgrowth in the propodus, which results especially from abnormal wound healing following the damage of the propodus (Okamoto 1991; Nakatani *et al* 1992); this phenomenon could also be induced in the laboratory (Murayama *et al* 1994; Nakatani and Kitahara 1999).

## 6. Cheliped display

Communication in crustaceans often involves the display of antennae and chelipeds. The roles of the chelipeds in agonistic and aggressive interactions during inter- and intraspecific competition for a limited resource is well documented in the literature (Hazlett 1972; Salmon and Hyatt 1983). The possession of chelipeds plays a major role in acquisition and retention of shelters in *Homarus americanus* (O'Neill and Cobb 1979) and *Macrobrachium nobilii* (Balasundaram and Mariappan 1998). Different kinds of acts or movements for cheliped presentation have been reported in various crustaceans (*Liocarcinus depurator* and *Necora puber*, Huntingford *et al* 1995; *H. americanus*, Atema and Cobb 1980; *Macrobrachium rosenbergii*, Barki *et al* 1991; *M. australiense*, Lee and Fielder 1983). A detailed account of the use of chelipeds in communication is provided by Salmon and Hyatt (1983). Cheliped extension, meral spread, strike, lifting of claw, scissoring, thrust, cheliped striking, embrace, nip and push are the major events mediated by chelipeds (table 4 and figure 3).

## 7. Courtship and mating

The role of chelipeds in courtship display and the presence of chelipeds as an aid in mate access have been extensively studied. In *Uca pugilator* there is a marked difference in display patterns between mature and immature males (Salmon *et al* 1978). Since chelae have a major role in displays during agonistic interactions, the degree of dominance is expressed by the type of chela morphometry. An animal with robust chelae has easy access to mates during inter-male competition and also through sexual selection by females. Autotomy also plays a crucial role in mating since such handicaps lead to a negative effect on mate access as observed in small and medium sized males of *Carcinus maenas* (Sekkelsten 1988). Variations in mating and reproductive patterns are observed among polymorphic males of *Macrobrachium rosenbergii*. The dominant blue-clawed males (bulls, BC males) effectively court and protect mates (Ra'anan and Sagi 1985), while intermediate males (OC males) show reduced reproductive activity in the presence of BC males (Ra'anan and Cohen 1985). Submissive small males are also sexually less competent, but mate successfully in the absence of BC and OC males (Sagi 1984).

## 8. Implications of chelae for decapod culture

In communal culture of crustaceans, the possession of large crusher chelae triggers aggression between individuals leading to physical damage of body parts (especially chelipeds) aggravating the rate of limb loss and mortality. Indeed chelipeds constitute 10–26% of the body weight in

**Table 4.** Cheliped mediated displays in decapod crustaceans.

| Act | Description |
|---|---|
| Cheliped extension[2,3,5,6] | Extension of chelae towards the opponent without contact |
| Cheliped presentation[2] | Ambulatory legs in walking position and both chelipeds in presentation position |
| Cheliped shaking[3,5] | Rapid oscillations of the dactyls while (without touching propodus) the claw is partly extended in the direction of another prawn |
| Complete lifting[3,5] | Lifting of the claws and anterior part of the body towards another individual |
| Incomplete lifting[3] | Similar to complete lifting, but the claws remain in the horizontal plane |
| Crouching[6] | Chelipeds are folded tightly against the body |
| Fending[6] | Outward swinging of one or both chelipeds |
| Grasping[1,6] | Seizing of another individual with thoracic appendages 3–5 |
| Meral spread[1,3] | Outward spreading of the enlarged meri of the appendages |
| Nip[3,4] | One animal closes down the tips of its chelae on a body part of another animal |
| Push[3,4,5] | One animal pushes one of its chelae against a body part of another animal |
| Shielding[6] | Holding the chelipeds like a shield |
| Strike[1,3] | A blow delivered by one individual to another with the dactyls of one or both raptorial appendages |
| Scissoring[3,5,6] | Bringing the two claws together from the complete lifting position in a scissoring motion |
| Thrust[3] | Rapid simultaneous opening of the two claws in the direction of another prawn |

Sources: 1) Dingle 1969, 2) Hazlett and Bossert 1965, 3) Barki *et al* 1991, 4) Peebles 1979, 5) Lee and Fielder 1983, 6) Jachowski 1974.

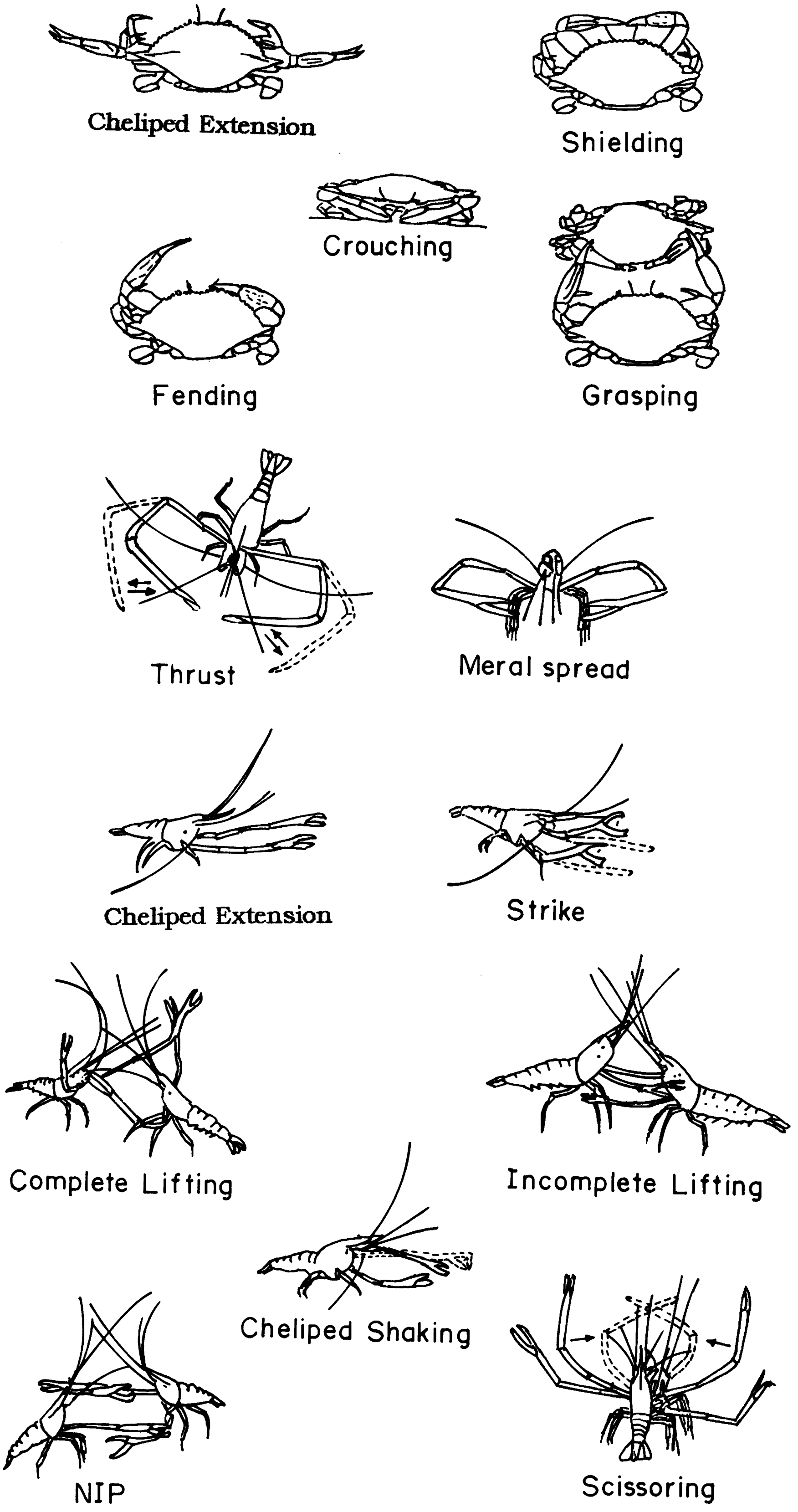

**Figure 3.** Agonistic acts in decapod crustaceans (Jachowski 1974; Barki *et al* 1991).

*Macrobrachium nobilii* (Mariappan and Balasundaram 1999a), 20% in *Carcinus maenas* and *Liocarcinus holsatus* (Lee and Seed 1992), and 50% in *Menippe mercenaria* (Simonson and Steele 1981). In *H. americanus*, the possession of the crusher claw is essential for acquisition of limited resources, as well as establishment and maintenance of dominance hierarchies (O'Neill and Cobb 1979). In such cases the autotomised animal becomes subjugated and more subordinated during further attacks. In *C. sapidus*, the loss of chelipeds was shown to have not only a negative effect on foraging ability and prey handling time (Juanes and Hartwick 1990; Smith and Hines 1991), but also the incumbent has to channelise more metabolic energy for the regeneration of chelipeds. Thus in species like *Callinectes sapidus* (Ary *et al* 1987; Smith 1990b), the loss of chelipeds leads to a reduction in moult increment due to energy diversion; such energy demand is called regeneration load (Skinner 1985), which may reduce reproductive output (Norman and Jones 1993; Luppi *et al* 1997). Chelotomy, dactylotomy and immobilisation of the dactyls have been shown to reduce the degree of cannibalism in *H. americanus* (Kendall *et al* 1982) and in *M. rosenbergii* (Karplus *et al* 1989; Diaz *et al* 1990). However the decreased survival rate due to forced severance of limbs and subsequent regeneration are major constraints that reduce the harvest size (Powell *et al* 1998).

## 9. Conclusion

Though autotomy, moulting and regeneration of chelipeds have been reviewed periodically, a collective perusal of literature attempted in this review reveals that the diverse functional and structural modifications of chelipeds are not only influenced by feeding and locomotion patterns, but also by environmental conditions and species-specific needs. A number of biotic and abiotic factors influence the development of chelae. The chelae are most vulnerable to autotomy and their regeneration imposes a regeneration load in the regular energy budget of the animal resulting in a telling effect on the other regular somatic and reproductive processes. In aquaculture experimental removal of chelae minimizes aggressive interactions but the problem is recurrent due to regeneration potential and hence is of limited applicability. Since it takes more than one moult for total regeneration of the chelae, their use as a taxonomic character is doubtful.

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