LOBSTERS: BIOLOGY, MANAGEMENT, AQUACULTURE AND FISHERIES

Edited by

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Preface

The stimulus for this book was the publication of the *Biology of Freshwater Crayfish*, edited by David M. Holdich (2002, Blackwell Science Ltd). Several other books on marine lobsters have also been published over the last 25 years, however, the Holdich book is different. Although it deals with topics such as growth, nutrition, reproduction and behaviour, the full material for the commercial species is presented under each separate genera, rather than under fisheries, countries or topics such as management, aquaculture or conservation. We have followed the same approach except for a few minor instances where it was appropriate to make comparisons for clarity.

The amount of material which has been published on marine lobsters is vast by comparison to the freshwater species. For this reason I have encouraged the authors to concentrate on publications which have appeared over approximately the last 10 years, particularly if the material has been reviewed.

Not all genera of marine lobsters are covered in this volume. In selecting the material, I have chosen those genera with the most commercially important populations. Readers will no doubt find gaps in the topics examined. Space limitations precluded the inclusion of additional material.

Readers will find some overlap between chapters in this book. This is not a bad thing and essentially impossible to prevent. For example, Chapter 3 (Behaviour), Chapter 1 (Growth) and Chapter 5 (Pathogens, parasites and commensals), all include aspects discussed in a number of other chapters, but their comments are different, usually dealing with aspects of impact on fisheries, fishing, populations, or their detection or measurement.

Many people contributed to the development and production of this book. We cannot acknowledge them individually because there isn't space, but all the authors wish to thank the many colleagues who assisted them with their contributions.

Bruce F. Phillips

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Chapter 1

Growth and Development: Understanding and Modelling Growth Variability in Lobsters

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1.1 Introduction

Lobsters are among the largest-bodied and longest-lived modern marine arthropods (Wolff, 1978; Sheehy, 2001). They are ecologically important as consumers in a variety of temperate and tropical marine ecosystems (Robles *et al*., 1990; Mayfield *et al*., 2000). In many parts of the world, lobsters also support commercially valuable fisheries, in some regions the most economically important one (FAO, 2004). Because demographic processes such as survival, reproduction and movements are body-size dependent, understanding growth processes is central to any understanding of population dynamics, ecological function and sustainable management.

This chapter builds upon several previous edited volumes with specific chapters on growth and development in the Crustacea (Wenner, 1985a, b; Lee & Wickins, 1992), and lobsters in particular (Cobb & Phillips, 1980a, b; Phillips *et al*., 1994a; Factor, 1995; Phillips & Kittaka, 2000). These reviews cover aspects of growth, such as the physiology and endocrine control of moulting (Aiken, 1980; Hartnoll, 1982, 1985; Waddy *et al*., 1995; Chang *et al*., 2001; Hartnoll, 2001), intrinsic and external factors affecting growth (Waddy *et al*., 1995; Booth & Kittaka, 2000; Hartnoll, 2001), and practical approaches to culturing lobsters (Lee & Wickins, 1992; Aiken & Waddy, 1995; Booth & Kittaka, 2000; Kittaka, 2000). Although these publications provide a wealth of information on growth, spanning a range of lobster taxa, we did not find a synthesis or critical evaluation of the modelling approaches employed in the study of lobster population dynamics. An especially challenging aspect of the study of crustacean populations is the determination of age. The absence of conspicuous age markers in crustaceans makes it all the more necessary to have a clear understanding of the age-to-body size relationship and the factors that contribute to its variability.

Lobster growth can be highly variable, reflecting the effect of quantum changes associated with moulting and in the probability distributions of moult increments (Fig. 1.1). Here we focus on recent developments in our understanding of the factors influencing growth and how to incorporate variability in population dynamics modelling to improve our ability to assess and forecast population trends. We primarily draw upon peer-reviewed literature and technical reports on the relatively well-studied genera of clawed (*Homarus, Nephrops*) and spiny (*Panulirus, Palinurus, Jasus*) lobsters. This chapter aims to provide an update of literature since 1980; however we frequently cite earlier literature where it is particularly relevant. First, we give a brief comparison of the different taxon-specific patterns of development, growth and the onset of maturity, as well as an overview of the stages of the moult cycle. The second section reviews the tools employed to measure growth or determine age in lobsters. Third, we survey the range of environmental influences on growth and sexual maturity, and in the final section we describe different modelling approaches that have been used

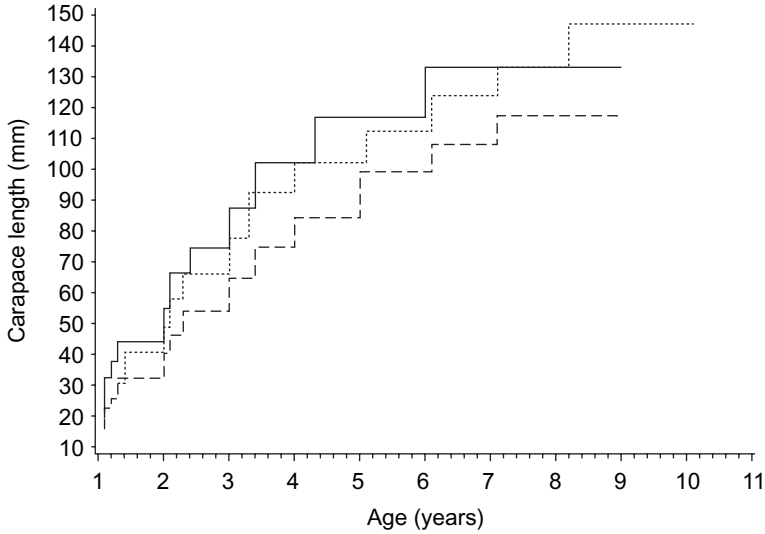

Fig. 1.1 Individual growth trajectories of American lobsters, *Homarus americanus*, reared in a culture facility illustrating variability in growth patterns (B. Estrella, personal communication).

to capture the influence of variability in size with age in population dynamics. This variability holds important implications for the development of demographic models for lobster populations.

1.2 Development, growth patterns and the moult

1.2.1 Larvae and postlarvae

All lobsters have a complex life cycle with a long-lived adult phase, relatively late onset of maturity, fertilisation by stored sperm when the eggs are extruded by the female; external brooding of embryos for several months; larvae hatch and are planktonic for weeks to months and metamorphose to a postlarva that eventually settles, moults to a juvenile and takes up a benthic existence. In lobsters, the nauplius larva develops entirely within the embryonic membrane (Gore, 1985; Helluy & Beltz, 1991) and hatches as the developmental equivalent of the first zoea of brachyuran crabs. In clawed lobsters (nephropids) this is referred to as the stage I larva, and in spiny and slipper lobsters (palinurids and scyllarids) as the stage I phyllosoma. The larval forms of clawed and spiny lobsters are widely divergent in morphology, behaviour and duration. The size of larvae and postlarvae split quite clearly along taxonomic lines. The larvae and settling postlarvae of clawed lobsters tend to be substantially smaller than those of spiny and slipper lobsters. It is important to be aware of the distinction between stages and instars – the former relates to morphological changes, the latter to the number of moults (Kittaka, 1994). In clawed lobsters, there are just three morphologically distinct larval instars, stages I–III. In spiny lobsters, there are many more larval instars (Table 1.1) and the morphological stages of the phyllosoma can less dependably be linked to a particular instar. As a result, *Jasus edwardsii*, for example, will complete all phyllosoma stages in 13 to 17 instars (Kittaka, 1994). The larvae of both spiny and clawed lobsters are planktivorous and preferentially feed on zooplankton (McConaugha, 1985; Kittaka, 1994; Ennis, 1995; Kittaka, 2000). After the final larval instar, lobsters undergo metamorphosis to a postlarva which is developmentally equivalent to the megalopa in brachyuran crabs. In spiny lobsters this stage is called the puerulus. The postlarval stage more nearly resembles the adult and is the stage that starts its benthic existence. Unlike the postlarva of clawed lobsters, which continues to feed, the spiny lobster puerulus does not feed (Kittaka, 1994, 2000).

The daily energetic investment in growth during the larval stages is greater than during the first

Table 1.1 Comparison of selected lobster taxa by size and timing of larval, juvenile, and adult life history characteristics. CL = carapace length (mm). Numbers of larval instars for spiny lobsters were based on laboratory rearing studies and can vary; numbers in parentheses are presumed on the basis of observations of *J. verreauxi* (Kittaka, 2000).

	Number of larval instars	Larval duration (weeks)	Size at postlarval[a] settlement stage (CL)	Size at female maturity (CL)[b]	Age at female maturity (years)	Postlarval to adult growth factor[c]	Sources
Nephrops norvegicus	3	4–8	3.3–4.0	21–34	4.0–4.5	11.1	Morizur (1983), Pollock (1991),Tuck *et al.* (1997, 2000), Ulmestrand & Eggert (2001)
Homarus americanus	3	4–8	4.5	55–120	5–8	19.4	Aiken (1980), Pollock (1991), Estrella & MacKiernan (1989), Comeau & Savoie (2001)
Homarus gammarus	3	4–8	4.5	92–96	7–9[d]	20.9	Sheehy *et al.* (1999), Tully *et al.* (2000), Sheehy & Bannister (2002)
Jasus lalandii	(17)	44	10	56–74	7+	6.5	Annala (1991), Pollock (1991, 1997), Kittaka (1994, 2000)
Sagmariasus verreauxi	17	44	10.5	155–184	6–7	16.1	Annala (1991), Pollock (1991), Montgomery (1991) in Brown & Phillips (1994), Kittaka (1994, 2000)
Jasus edwardsii	(17)	43	11.4–12.3	<65–114	8	7.8	McKoy (1985), Annala & Bycroft (1988), MacDiarmid (1989a, b),Annala (1991), Pollock (1991), Brown & Phillips (1994), Kittaka (1994, 2000), Hobday & Ryan (1997), Phillips & Kittaka (2000)
Palinurus elephas	7–9	9–19	10	82–95	5–6	8.9	Kittaka (2000), Ceccaldi & Latrouite (2000)
Panulirus cygnus	9	39–47	7–8	90–100	6–7	11.3	Brown & Phillips (1994), Booth & Kittaka (2000), Phillips & Kittaka (2000)

Table 1.1 *continued*

	Number of larval instars	Larval duration (weeks)	Size at postlarval[a] settlement stage (CL)	Size at female maturity (CL)[b]	Age at female maturity (years)	Postlarval to adult growth factor[c]	Sources
Panulirus argus	11	26–34	6	75–91	2–3	13.8	Lewis (1951), Hunt & Lyons (1986), Baisre & Cruz (1994), Baisre (2000)
Panulirus guttatus	10	?	10	32	2–3	3.6	Pollock (1991), Sharp *et al*. (1997), Briones-Fourzán & McWilliam (1997), Robertson & Butler (2003)
Panulirus japonicus	27	49	6–8	38–42	1.5–2.0	5.7	Kittaka (1994), Nakamura (1994), Nonaka *et al.* (2000)

a. Postlarva = stage IV for *Nephrops* and *Homarus*; puerulus for *Jasus*, *Panulirus*, and *Palinurus.*
b. Size at 50% egg bearing.
c. Ratio of postlarval and adult carapace length using midpoints of size ranges where given.
d. Based on age pigment analysis.

benthic stages. For example, in the American lobster, growth rates were found to be almost twice as fast for planktonic postlarvae (0.46 mg per day) as they were for initial benthic stages (0.26 mg per day) (Juinio & Cobb, 1994; James-Pirri & Cobb, 1997). While clawed, spiny and slipper lobsters differ little with respect to the average growth factor between moults during larval development (Nephropidae: 127%, Palinuridae: 133%, Scyllaridae: 132%), the greater number of larval instars in spiny and slipper lobsters results in a dramatically greater overall length increase from first to last larval stage (Nephropidae: 185%, Palinuridae: 1258%, Scyllaridae: 926%; Gore, 1985). In contrast to the dramatic proportional size increase during larval development, intermoult growth factors during the juvenile and adult stages rarely amount to more than 15% in length, regardless of taxon (Table 1.1). There has been little speculation and virtually no research on the functional significance of the dramatic growth spiny and slipper lobsters undergo during their larval stages. For more detail on specific patterns of larval development, growth and allometry, readers are referred to Wenner (1985a).

1.2.2 Juveniles and adults

Hartnoll (1982, 2001) refers to a range of growth patterns exhibited by the Crustacea, spanning taxa with indeterminate growth and reproduction at every instar after maturity to those with a terminal, or maturation moult that reproduce only once. Lobsters fall at one end of the continuum by uniformly exhibiting indeterminate growth and being capable of reproducing at every instar after the onset of maturity. The intermoult period increases with size from a few days in the larval and early juvenile stages to a few years in large, older adults. On the other hand, the percent increment of growth per moult typically diminishes with body size (e.g. Aiken, 1980). Although the intermoult growth factor during the benthic stages is small by comparison to the planktonic larvae, overall growth during benthic life is far greater, the difference between the settling postlarva and sexually mature

adult often being many times in carapace length and several orders of magnitude in body mass (Table 1.1).

The early benthic phase of lobsters is typically cryptic, sedentary and solitary, rarely leaving shelter, the nursery habitat being a complex substratum – rocks, coral rubble, macroalgae or sea grass – providing protection to the young lobster (e.g. Pollock, 1997). Most lobsters are omnivorous, consuming molluscs, other crustaceans and algae, although different levels of trophic specialisation are documented (*J. lalandii* – Mayfield *et al.*, 2000). Suspension feeding has been documented in juvenile *N. norvegicus* and *H. gammarus* (Loo *et al.*, 1993). Juveniles undergo an ontogenetic shift in behaviour in which they either become wider ranging in their movements or change habitats altogether. While clawed lobsters remain largely solitary in their shelter use, spiny lobsters become more social and gregarious, and are often found sharing shelters or migrating in groups (Chapter 8).

The growth rate and onset of maturity varies widely among spiny and clawed lobsters, and in general the taxa from warmer environments grow faster and mature sooner than those in cooler regions (Table 1.1). Males of all taxa mature physiologically at a smaller size than females, however, it is likely that males need to be as large as or larger than females to successfully mate. There is more than one mature instar and all female instars after maturity are capable of being ovigerous. The age and size at maturity varies from species to species (Table 1.1). Maturation, in turn, has a retarding effect on growth and the effect is usually greater on females than males because of the greater energetic allocation to reproduction. Taxonomically or ecologically similar groups can vary widely in size at maturity (Table 1.1). Growth rates and the onset of maturity within taxa are strongly under the influence of the environment, and the nature of the proximate, environmentally induced variability is discussed in Section 1.4. The ultimate cause of this variability among taxa has been difficult to identify, although Hartnoll (1985) proposed the idea that early survivorship will be an important determinant of lifetime egg production, and therefore a significant force in the evolution of the size and age of maturity in Crustacea.

Maturation also brings on sex-specific allometric growth patterns. The onset of maturity is typically earlier and at a smaller size in male than in female lobsters and the instars over which it occurs depends on the environment. When females begin to mature, their intermoult period begins to increase relative to males in the same instar. Sexual differences in allometry can be a useful indicator of the size at onset of sexual maturity (Aiken & Waddy, 1989; Megumi & Satoru, 1997; Robertson & Butler, 2003). For example, in *H. americanus* claws become relatively larger in males while the abdomen becomes relatively larger in females (Aiken & Waddy, 1989; Conan *et al.*, 2001; MacCormack & DeMont, 2003). In spiny lobsters, the first and second pereiopods become relatively longer, but the surface area of pleopods becomes relatively smaller in males than in females (*P. argus* – Aiken, 1980; Hartnoll, 1985; Mykles & Skinner, 1985; Skinner *et al.*, 1985; Waddy *et al.*, 1995; *Panulirus japonicus* – Megumi & Satoru, 1997; Chang *et al.*, 2001; Robertson & Butler, 2003).

1.2.3 Moult stages and endocrine control

The mechanism and physiology of moulting has been reviewed in some detail by Aiken (1980), Hartnoll (1985), Skinner *et al.* (1985), and Waddy *et al.* (1995). The key events of the moult cycle are summarised here. The moulting process undergoes a sequence of stages in which the old skeleton separates from the underlying epidermal cells and a new cuticle is formed, which, after the old skeleton is shed, thickens and hardens to form the new one. As the old exoskeleton is decalcified from underneath, calcium carbonate is temporarily conserved in crystalline form as a pair of gastroliths on the lateral walls of the foregut. Given the opportunity, as another means of conserving calcium, lobsters will consume their cast-off exoskeleton after their mouthparts have hardened.

The externally-conspicuous characteristics of the five stages (A–E) of the moult cycle are outlined here, modified somewhat from an earlier scheme developed by Drach (1939). The stages have been particularly well illustrated for *H. americanus* by Waddy *et al.* (1995). Starting immedi-

ately after ecdysis, stage A occupies the brief time – usually 24–48 hours – it takes for the soft and wrinkled newly-exposed integument to stretch out to its now larger form and deposit the first of several inner layers of the new exoskeleton, the endocuticle. The endocuticle lies below the exocuticle and epicuticle already laid down just prior to the moult. Stage B is completed when the final layers of the endocuticle have been deposited. During stage C, the exoskeleton achieves maximum rigidity by virtue of chemical changes that harden the already deposited endocuticle; and at this point intermoult has been reached, the protracted period lasting until the onset of physiological changes that prepare the integument for another moult. Stage D, premoult or proecdysis, involves the separation of the endocuticle of the old skeleton from the underlying epidermis, followed by the deposition of what will be the outer layers of the new exoskeleton, first the epicuticle and then the exocuticle. Through demineralisation, a conspicuous softening in parts of the old skeleton and the ecdysial sutures occurs during this stage, that facilitates ecdysis. During ecdysis, stage E, water is ingested and absorbed with the effect of increasing hydrostatic pressure within the body which causes the ecdysial sutures, such as the one along the dorsal midline of the carapace, to break. In 10–20 minutes of immobility, the animal rolls on its side, the exoskeletal membrane between the thorax and abdomen ruptures, and the animal withdraws, thereby completing the cycle.

Most growth and regeneration occurs during intermoult and early premoult periods. Muscle tissue, for example, grows in size by elongation; the number and arrangement of muscle fibres (cells) remain constant while the number of thick and thin myofibrils (myosin and actin) increases (Skinner *et al*., 1985). The control of form and morphogenesis was reviewed by Mittenthal (1985). During proecdysis, just prior to the moult, the muscles atrophy temporarily by an enzyme-mediated degradation of actin myofibrils (Mykles & Skinner, 1985) presumably aiding the animal in withdrawing from the old exoskeleton, although it is likely to be accompanied by partial and temporary loss of mobility.

While the hormonal regulation of moulting is often presented as a simple system of two antagonistic hormones, as so aptly put by Waddy *et al*. (1995), crustacean moulting physiology 'is a profoundly complex process about which much is known, but little is understood'. Hormonal biochemistry and physiology has been intensively studied in *H. americanus* (Waddy *et al*., 1995; Chang *et al*., 2001). Three families of hormones come into play: (1) moulting hormones (ecdysteroids), (2) moult inhibiting hormone (MIH) and related crustacean hyperglycemic hormone (CHH) neuropeptides, and (3) terpenoid methyl farnesoate (MF). Each of these hormone groups serves a diversity of functions, in some cases changing at different stages of development. Their role in lobster growth is briefly summarised below. Greater detail may be found in useful reviews by Waddy *et al*. (1995) and Chang *et al*. (2001).

Moulting hormones (ecdysteroids) induce the physiological changes that lead to the moult. This family of hormones is produced by the Y organ, a pair of hypodermal glands to either side of the thorax. Haemolymph titres of ecdysteroids peak at premoult sub-stage D_1 and D_2 when pre-exuvial cuticle is being formed. At substage D_3, levels drop dramatically when the old exoskeleton is being resorbed and remain low after ecdysis from stage A to D_0 when premoult begins.

The moult inhibiting hormone (MIH) is considered the main regulator of moulting. It is structurally similar to crustacean hypoglycemic hormone, which may also play a role in moult regulation. The X organ–sinus gland complex, a specialised neural tissue located in the eyestalks, produces this family of neuropeptides. Heightened levels of MIH typically present during intermoult, suppress the synthesis of moulting hormones in the Y organs. As the location of the X organ suggests, environmental factors, particularly light levels, photoperiod and temperature can influence the synthesis of MIH, explaining the responsiveness of the moult cycle to changes in the environment. The peptide sequence of MIH is very similar to CHH, however one derivative, CHHa, has both a hypoglycemic and moult inhibiting effect, while the other, CHHb, has only a hypoglycemic effect (Chang *et al*., 2001). Levels of CHH appear to increase in the haemolymph in the latter part of the moult, apparently play-

ing a role in increasing water retention during exuviation.

Methyl farnesoate (MF), a sesquiterpene, is a precursor of juvenile hormone and can also play a role in the regulation of the moult cycle by retarding the moult in larvae (Borst *et al.*, 1987). MF is secreted by the mandibular organ. In adult lobsters it is also thought to play a role in reproduction; larger mandibular organs and higher haemolymph concentrations of MF in adult females suggest it has a sex-specific function and may be important in sexual differentiation (Chang *et al.*, 2001).

1.3 Measuring growth

Growth in crustaceans has been measured by both direct and indirect methods. Direct measures of growth per moult or per unit time have been provided by rearing studies of captive animals or tag–recapture studies in the wild. Indirect measures of growth and size at age are provided by the analysis of size frequency distributions of samples of wild lobster populations. The quantification of so-called 'age pigments,' metabolic by-products that accumulate with age, have been used with varying degrees of success in lobsters and crayfish as a proxy for age. Additional methods such as RNA : DNA ratios can provide further information on the nutritional status of the animal and therefore its growth potential.

A large number of laboratory and hatchery-based studies of lobster growth have accumulated over the decades. A comprehensive review of rearing techniques for larval and postlarval stages of lobsters is provided by Lee and Wickins (1992). Virtually all growth studies of larvae and a large number of post-settlement stage studies have been conducted in the laboratory. One of the great advantages of conducting laboratory growth studies is that it has provided a valuable setting in which to conduct factorial experiments to evaluate heritable and environmental effects (Van Olst *et al.*, 1976; Jong, 1993; Rahman *et al.*, 1997; Crear *et al.*, 2000, 2003) as well as for detailed descriptive studies of the moult cycle (Aiken, 1980; Dupre, 2000). Experiments have been conducted to evaluate the effect of temperature, photoperiod, space, substrate, feeding regimes, and stocking density among other factors. Many of these studies report valuable information on growth increment, intermoult duration and factors affecting growth, and have demonstrated the potential for widely divergent growth patterns of individual lobsters (Fig. 1.1).

Exact estimates of intermoult duration (or alternatively, the number of moults per unit time) are particularly difficult to obtain in the field. Laboratory observations have proven to be extremely valuable in this regard although caution is always necessary in extrapolating their results to wild populations. An illustration of the variability in the number of moults for different age classes of American lobster in a culture facility is provided in Fig. 1.2. The variation in the number of moults

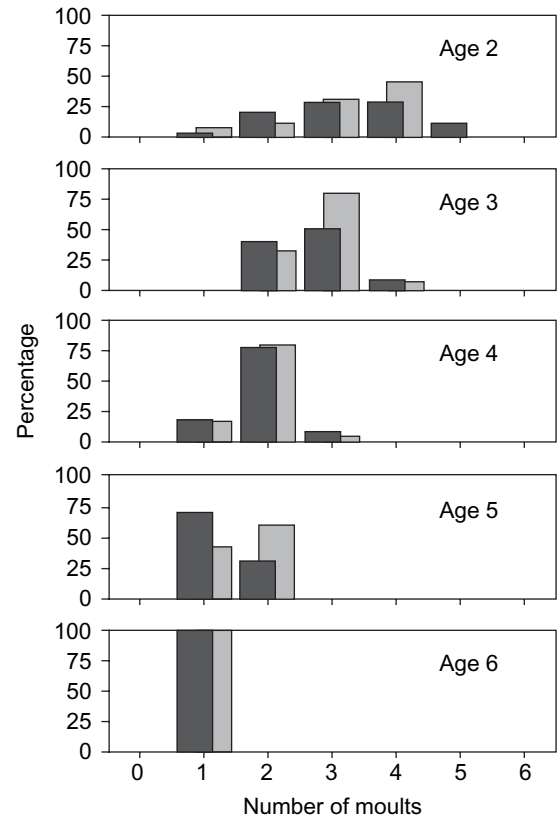

Fig. 1.2 Number of moults per age (age groups 2–6) of American lobsters, *Homarus americanus*, reared in a culture facility (B. Estrella, personal communication).

at younger age classes sets the stage for wide variation in length at age throughout the lifespan.

It is important to state at the outset that while carapace length is used almost universally as the measure of lobster body size, it cannot be assumed to vary isometrically with body mass. It is therefore important to determine the carapace-length-to-body-mass relationship by sex for each species, and preferably by region within a species. Because body mass varies approximately as the cube of body length, some workers have used the cube root of body mass, the so called 'nominal length,' as a linear proxy for body mass, providing a way to study allometric deviations of actual linear dimensions of the body from an isometric slope of 1.0. For example, in a study of regional differences in allometry of the American lobster, MacCormack and DeMont (2003) found that relative to nominal length, carapace length became proportionally larger in males and smaller in females by scaling factors of 1.05 and 0.86, respectively. To our knowledge, a similar analysis of carapace length against nominal length has not been done for other lobster taxa. In practice, carapace length remains the conventional index of body size, and it is understood that the carapace-length-to-body-mass relationship is one of the first morphometrics to assess in any study of growth, so that size-dependent processes, whether physiological or ecological, may easily be expressed as a function of body mass.

1.3.1 First moult in captivity

A common approach to obtaining measures of growth increment that are likely to be free of laboratory artefacts and representative of growth in the wild is to hold newly-captured premoult lobsters in captivity only long enough for them to moult and allow their new skeletons to harden (e.g. *J. lalandii* – Hazell *et al*., 1998; *N. norvegicus* – Castro *et al*., 2003). This provides a valuable measure of moult increment as a function of size before the moult (see the Hiatt model, Section 1.5.1). The assumption is that the effects of laboratory artefacts on the growth increment are minimal because the factors affecting growth up to that moult would already have acted.

1.3.2 Tagging

Tag–recapture methods have been widely employed to assess growth of lobsters in the wild. This is probably the most widely used method of obtaining growth data that is in most cases unbiased by artefacts associated with handling or captivity (but see Brown & Caputi, 1985; Phillips *et al*., 1992). In the 1960s, the development of internal spherion tags that are anchored in the musculature and not lost during the moult was a methodological breakthrough for the study of growth in wild populations of crustaceans (e.g. Wilder, 1963). Since then a number of innovative tags have been invented for different applications ranging from internally anchored, but externally visible t-bar and streamer tags (e.g. Campbell, 1983a; Comeau & Savoie, 2001) to entirely internal microwire tags that are detected magnetically (Walker, 1986; Bannister *et al*., 1994; Incze *et al*., 1997; Cowan, 1999) and internal coloured latex tags (Robertson & Butler, 2003).

Internal tagging is not without risks, however. Of most concern is the mortality associated with tagging, either from the trauma of the tagging process itself or secondary infection. Also of concern is the loss of tags either from natural wear and tear, contact with other lobsters especially in traps, or during the moulting process itself. This is why it is highly recommended that any tagging study includes an assessment of tag-loss rates and lethal and sublethal effects (e.g. Brown & Caputi, 1985). Double tagging is one way to assess tag losses in the field.

A particularly innovative tagging approach developed by Shelton and Belchier (1995) has been to embed a small section of cuticle and underlying dermal tissue within a large muscle. The embedded tissue continues to go through the normal moult cycle, but since the cast-off cuticles are trapped within the musculature, they accumulate in layers, thereby giving a record of the number of moults occurring over the time elapsed. However, this living tag method has yet to be used widely.

Aside from trauma-related effects of tagging or handling, it is important to be aware of more subtle biases that may occur in mark–recapture sampling. In developing size-transition probabilities from