۲

Chapter 8 Juvenile and Adult Ecology

Mark J. Butler¹, Robert S. Steneck² and William F. Herrnkind³ ¹Department of Biological Science, Old Dominion University, USA

²School of Marine Sciences, Darling Marine Center, University of Maine, USA ³Department of Biological Science, Florida State University, USA

8.1 Introduction

The ecological dynamics that shape the benthic life of all lobsters are largely circumscribed by the settlement of postlarvae, the structure and availability of nursery habitats, prey availability and growth, predation risk, disease, patterns of movement, social and reproductive behaviours, and their interaction with humans and a changing environment. During the first synthetic effort to assess clawed and spiny lobster ecology, nearly three decades ago (Phillips & Cobb, 1977; Cobb & Phillips, 1980), these issues were identified as important directions for research. The great advances since then have come about for numerous reasons but foremost, the integration of basic life-history, ecology studies with applied fishery research, the application of field experimental and quantitative methods in a hypothesis testing framework, and the emergence of sophisticated computer-assisted modelling. In addition, more species have come under scrutiny by comparable methods, thus supplying the breadth necessary for recognition of general principles and of special cases. A sufficient knowledge of lobster ecology now exists so that in a single chapter we can proffer a synopsis of an array of ecologically relevant issues pertaining to lobsters, although much remains to be done.

In this chapter, we focus on the ecological processes that drive recruitment, the acquisition of shelter and food, predator–prey relationships, movement and migration, and in the case of spiny lobsters, sociality. Growth, reproduction, behaviour, and disease all play important roles in the ecology of spiny and clawed lobsters, but all are covered in depth in other chapters in this volume (Chapters 1, 2, 3 and 5 respectively) so our treatment of these subjects is minimal. Many species of lobster are also of commercial importance, and those species and the fisheries for them are highlighted in Chapters 9–14. We discuss the ecology of spiny and clawed lobsters separately, so as to emphasise the processes most important, or best known, for each. We also stress recent findings and attempt to avoid repeating detailed topical information provided in recent comprehensive reviews (see Factor, 1995; Phillips & Kittaka, 2000). We apologise for undoubtedly overlooking some of the pertinent literature, particularly that appearing in publications that are not peer-reviewed and therefore not widely distributed, and those written in languages other than English. Still, the information readily available on the ecology of juvenile and adult lobsters is voluminous and relevant whether one is interested in natural history, ecology, or fishery management.

8.2 Spiny lobsters

There are more than 45 species of spiny lobsters (Palinuridae), which are widespread and inhabit temperate and tropical seas worldwide, from the intertidal zone to depths approaching 1000m (Holthuis, 1995). The different genera do not generally co-occur; their distributions are defined in broad terms by latitude and water depth (George & Main, 1967; Cobb & Wang, 1985; Fig. 8.1). Often, only one or a few species of spiny lobster co-occur in a particular region (e.g. *Palinurus elephas* in the

263

4/11/2006 11:06:42 AM



Fig. 8.1 Approximate geographic distribution of spiny lobster genera as a function of water depth, latitude, and water temperature (adapted from George & Main, 1967).

Mediterranean; Panulirus argus and P. guttatus in the northern Caribbean), but where multiple species of spiny lobster co-occur they are generally segregated by habitat (e.g. the seven genera that co-occur in southern Africa; Berry, 1971). The morphologies of spiny lobster are quite similar and provide little insight into the varied ecological dynamics among the many species. Morphological features that reflect ecological differences are often minor or are obvious functional specialisations, including: sub-chelate or enlarged anterior pereiopods for prying and manipulating prey, elongate and gracile legs on migratory forms, and robust antennae on species often exposed to piscine predators. Otherwise, few morphological cues signify the particular combination of depth, hydrographic conditions, habitat, sociality, predators, or prey that define the ecology of each species. Yet, those ecologies can be remarkably different, spanning lifestyles that include shallow, semi-social, residential dwellers on coral reefs to gregarious, migratory species that live on open, particulate substrates at >300 m depth. Indeed, the versatile palinurid body design has successfully accommodated a broad range of benthic circumstances.

The benthic existence of spiny lobsters is preceded by an extraordinarily long (up to 24 months), oceanic larval phase followed by a brief (few weeks) stint as a fast-swimming, non-feeding postlarval phase, which links the offshore life cycle to its inshore, benthic component (see Chapter 7). The postlarvae of some species settle in crevices, others in architecturally complex vegetation. All have evolved chemical and tactile mechanisms that allow them to locate locally available microhabitats that provide both refuge and prey for the succeeding life stage: the early benthic phase juvenile. Early benthic phase juveniles are the benthic phase most vulnerable to predation and they suffer high mortality from an array of fishes and motile invertebrates (e.g. crabs and octopus), despite mitigating adaptations including use of physical refuges, overdispersed distributions, camouflage, cryptic behaviour, and nocturnality. As they grow, benthic juveniles increasingly attain a 'size refuge' from predation and many species of spiny lobster undergo ontogenetic changes in their use of shelters and habitats. All large juvenile and adult spiny lobsters are nocturnally active predators of the benthos, and all aggregate to some degree in appropriately sized crevices for daytime shelter. The large juveniles and adults of many species are nomadic, or participate in seasonal or ontogenetic migrations among habitats, but other primarily reef-dwelling species are philopatric and dwell within the intricately structured confines of coral or rocky reefs throughout their benthic existence. Unlike the solitary clawed lobsters, benthic spiny lobsters also exhibit

BMA08.indd 264

an ontogeny in sociality; abruptly changing from the asocial early benthic phase juvenile to the gregarious, social large juveniles and adults. Beyond these generalities, species differ strikingly in the details of their ecology that reflect unique evolutionary solutions to conditions in dissimilar ecological circumstances.

8.2.1 Limits to recruitment

Postlarval availability and settlement

Phyllosoma abundance, coastal advective processes, and puerulus behaviour, condition and mortality all influence the supply of pueruli to coastal nurseries. The processes are reviewed elsewhere (see reviews by Butler & Herrnkind, 2001 and Chapter 7), so here we focus on the importance of postlarval supply as a factor that potentially limits the recruitment of juvenile spiny lobsters. Settlement of many palinurid species is estimated by sampling of pueruli and recently-molted earlybenthic juveniles on collecting devices ranging from artificial seaweed (Witham et al., 1968, Phillips, 1972) to artificial crevices (Booth 1979; Booth et al., 1991). Phillips and Booth (1994) provide a thorough review of the design, use, and effectiveness of these devices. Some have attempted to measure settlement in natural crevices or vegetated habitats (Marx & Herrnkind, 1985a; Booth & Bowring, 1988: Yoshimura & Yamakawa, 1988, Fitzpatrick et al., 1989; Jernakoff, 1990; Herrnkind & Butler, 1994; Butler & Herrnkind, 1997; Butler et al., 1997; Diaz et al., 2001 among others), but the high crypticity and low density of newly-settled palinurids has prevented common use of such techniques. Few studies have demonstrated that the catch of postlarvae on artificial collectors indeed reflects postlarval planktonic abundance and local settlement density (Herrnkind & Butler, 1994, Phillips *et al.*, 2003).

Most research employing postlarval collectors is primarily intended to establish predictive statistical relationships between relative postlarval abundance (i.e. catch of postlarvae on collectors) and catch in the commercial fishery (or pre-recruits to the fishery), which are of obvious importance for fishery management (Booth & Bowring, 1988; Breen & Booth, 1989; Cruz et al., 1995a; Gardner, 2001). To date, the most successful of these programmes is that for P. cygnus in Western Australia. There, puerulus settlement is strongly correlated with juvenile abundance on nearby reefs (Jernakoff et al., 1994) and with the commercial fishery catch four years later (Phillips, 1986; Caputi et al., 1995, 2003). Despite widespread attempts to duplicate the Western Australian model, only a few have shown promise (P. argus in Cuba, Cruz et al., 1995b; Jasus edwardsii in Tasmania, Gardner et al., 2001), partly because time-series are too short or spatial coverage insufficient. In other cases, the lack of a strong, consistent correlation between postlarval supply and recruitment to later juvenile or adult stages is probably real, reflecting the additional importance of post-settlement processes in regulating recruitment.

Several investigations have sought to correlate the local supply of postlarvae, as measured on collectors, with the subsequent recruitment of juvenile or adult spiny lobsters at specific locations with mixed results. Puerulus settlement in Western Australia is strongly correlated with juvenile abundance on nearby reefs (Jernakoff et al., 1994), just as it is with fishery catch, a proxy for adult abundance (Caputi et al., 1995). In New Zealand, interannual patterns in postlarval supply and the abundance of juveniles two to three years later are positively correlated at some sites but not at others (Breen & Booth, 1989; Booth et al., 2001). In Cuba, the relationship between the catch of postlarval P. argus caught on collectors and the abundance of juvenile lobsters dwelling in artificial structures several months later is inconsistent from year to year (Cruz et al., 2001). Varying postsettlement mortality due to hurricanes and variation in the amount of available settlement habitat (seagrass and macroalgae) are the explanations offered by the authors. Variability among sites in the strength of the relationship between P. argus postlarval supply and juvenile or adult abundance is a recurring theme in the Bahamas (Lipcius et al., 1997; Eggleston et al., 1998) and in Florida (Butler & Herrnkind, 1992a, b, 1997; Field & Butler, 1994; Forcucci et al., 1994), because of complex interactions between the local availabilities of settlers and of nursery habitat. Sites with abundant settlement

habitat (e.g. red macroalgae) and shelters for juveniles (e.g. sponges) generally attain the highest levels of settlement, but settlement is locally unpredictable even at the most 'optimal' sites, presumably because of small-scale variability in the arrival of pueruli.

Nursery habitats and demographic bottlenecks

In the past two decades, we have become increasingly familiar with the natural settlement habitat of many species of spiny lobster (see Herrnkind et al., 1994; Butler & Herrnkind, 2001). Still, the sparseness, small size, and crypticity of pueruli and earlybenthic phase as well as the complex topography of the microhabitat in which they reside, make the early life stages of nearly all spiny lobsters challenging to study. In general, the natural habitats that newly settled pueruli and early-benthic phase juveniles seek are either dense vegetation (e.g. red or brown macroalgae, seagrass) (P. argus: Marx & Herrnkind, 1985a; Herrnkind & Butler, 1986; P. interruptus: Serfling & Ford, 1975; Engle, 1979; Castaneda-Fernandez et al., 2005) or small holes in rocks or reefs scaled to their body size (P. cygnus: Jernakoff, 1990; P. echinatus: Vianna, 1986; Palinurus elephas: Diaz et al., 2001; P. homarus: Kuthalingam et al., 1980; P. japonicus: Yoshimura & Yamakawa, 1988: Norman et al., 1994; Norman & Morikawa, 1996; P. ornatus: Berry, 1971; Dennis et al., 1997; P. versicolor: George, 1968; Jasus lalandii: Pollock, 1973; P. guttatus: Sharp et al., 1997; Jasus edwardsii: Kensler, 1967; Lewis, 1977; Booth & Bowring, 1988; Edmunds, 1995; Butler et al., 1997; Booth, 2001). Lobsters are not unique in this respect. A recent meta-analysis of >200 papers describing the relative roles of seagrass and other habitats as nursery grounds concludes that structure per se, rather than the type of structure, was the most important determinant of the value of a habitat as a nursery (Heck et al., 2003).

After settlement, and a variable period of time spent dwelling within vegetation or in small holes, juveniles attain a transitional size (typically >15–20 mm CL) at which they begin to seek nearby crevice shelters (e.g. rock crevices, holes and

ledges; undercut coral heads and sponges) more appropriately scaled to their body size (P. argus: Cruz et al., 1986; Eggleston et al., 1990, 1997; Forcucci et al., 1994; Butler & Herrnkind, 1997; Childress & Herrnkind, 1997; Arango et al., 2001; J. edwardsii: Edmunds, 1995; Butler et al., 1997; P. ornatus: Dennis et al., 1997; Skewes et al., 1997; P. cygnus: Jernakoff, 1990; among others). Many studies focusing on P. argus, some using natural shelters and others artificial shelters, have shown that appropriately-scaled shelters and aggregations of lobsters increase survival of crevice-dwelling juvenile and subadult P. argus that occupy them (Eggleston et al., 1990, 1997; Smith & Herrnkind, 1992; Lozano-Álvarez et al., 1994; Mintz et al., 1994; Arce et al., 1997; Sosa-Cordero et al., 1998; Butler & Herrnkind, 1992a, 1997; Herrnkind et al., 1997, 1999; Losada-Torteson & Posada, 2001; and others). The same can be said for other species wherever the phenomenon has been tested (see Butler & Herrnkind, 2001).

It is therefore not surprising that the local abundance of juvenile lobsters can be limited by the availability of crevice shelters. For example, changes in the availability of natural shelters for juvenile P. argus in Florida brought about by a mass die-off of sponges resulted in dramatic declines in juvenile abundance and patterns of shelter use (Butler et al., 1995; Herrnkind et al., 1997, 1999). Similarly, experimental manipulations of artificial shelters designed to mimic small, widely-distributed natural shelters (i.e. sponges and small coral heads) showed that the availability of crevice shelters for juveniles can limit the local recruitment of juveniles (Butler & Herrnkind, 1997; Herrnkind et al., 1997; Briones-Fourzán & Lozano-Álvarez, 2001). Field surveys in the northwest Hawaiian Islands and the Bahamas suggest that the abundances of juvenile P. marginatus and P. argus are linked to the availability of high relief habitat (Parrish & Polovina, 1994; Lipcius et al., 1997). Although habitat bottlenecks to juvenile recruitment can be shown to exist at some sites and at small spatial scales for these two species (P. argus and P. marginatus), regional recruitment patterns in Florida, the Bahamas, and Hawaii are tied to both the levels of puerulus supply and habitat

4/11/2006 11:06:43 AM

structure (Forcucci *et al.*, 1994; Polovina *et al.*, 1995; Polovina & Mitchum, 1994; Butler & Herrnkind, 1997; Lipcius *et al.*, 1997). To generalise, many regions can be viewed as ecological mosaics where the processes that drive local recruitment vary locally depending on spatial and temporal patterns of habitat structure and postlarval supply (Fig 8.2).

In some situations, however, where nursery habitat is less dynamic and perhaps more uniform, there is little evidence for density-dependent regulation of juvenile abundance through habitat bottlenecks. Chittleborough and Phillips (1975) initially proposed that density-dependent processes limited the numbers of early-benthic phase juveniles on nursery reefs. This hypothesis has been revised because puerulus settlement was later found to highly correlate with juvenile abundance on nearby reefs (Jernakoff et al., 1994) and was also highly correlated with commercial catches four years later (Phillips, 1990). A similar situation may exist for J. edwardsii along parts of the rocky coasts of Tasmania (Edmunds, 1995) and New Zealand (e.g. Stewart Island; Breen & Booth, 1989) where the settlement of pueruli is correlated with local juvenile abundance a few years later. The situation for all other species is unknown.

Simulation modelling has recently been used to explore the sources of recruitment variability in spiny lobster, and to integrate our understanding of the recruitment process with the growing body of data on benthic habitat structure. Two different types of models have been developed for spiny lobsters: those that are oceanographic in context and those that focus on benthic processes. Several spatially-explicit, biophysical oceanographic models are now available that depict larval release, the oceanic transport of passive or behaviourally active spiny lobster larvae and, in some cases, the arrival of postlarvae to the coast. Models include those constructed for P. marginatus in Hawaii (Polovina et al., 1999), P. argus in Exuma Sound in the Bahamas (Stockhausen et al., 2000; Stockhausen & Lipcius, 2001), P. cygnus in Western Australia (Griffin et al., 2001) and J. edwardsii in New Zealand (Chiswell & Booth, 1999). Attempts at validating these models against empirical patterns of postlarval supply have not been altogether successful, but each has yielded insights into the importance of oceanographic features and larval behaviour in influencing larval dispersal and postlarval arrival in coastal nurseries (see Chapter 7).

We are aware of only one simulation model that encompasses the post-settlement ecology of a palinurid lobster, that being a spatially-explicit, individual-based model of P. argus recruitment in the Florida Keys (Butler et al., 2001, 2005; Butler 2003). That model uses geographical information system (GIS)-based habitat information and field surveys of habitat structure to depict the benthic landscape, whose biogenic features (e.g. sponges, corals, seagrass) are dynamic and can change in response to environmental factors such as harmful algal blooms and salinity. The effects of spatial and temporal variation in postlarval supply on recruitment are incorporated into the model from either empirical data or theoretical depictions. Model predictions of juvenile recruitment (i.e. abundance of 50mmCL lobsters) in response to a large-scale environmental disturbance (sponge die-off) were in good accord with predicted changes in recruitment suggested by data from field surveys and fishery catch (Butler et al., 2005). Other simulations support the idea that local variation in habitat availability and postlarval settlement can affect recruitment success (Butler et al., 2001). In particular, those simulations suggested that spatiotemporally variable postlarval supply result in the highest recruitment of juveniles, because the potential for density-dependent regulation in patchily distributed nursery habitat, is diminished by varying levels of postlarval arrival. Model predictions were less sensitive to changes in the spatial depiction of habitat structure than those in postlarval supply, but the most spatially explicit (i.e. finegrained) and realistic portrayal of habitat structure produced marginally significant differences in recruitment in contrast to more generalised spatial scenarios. These findings parallel a growing body of empirical evidence that in general, postlarval abundance driven by spawning stock and the vagaries of oceanographic survival and transport determine the regional potential for recruitment

BMA08.indd 267

4/11/2006 11:06:43 AM



۲



۲

۲

۲

No.

in spiny lobster, modified by local variation in postlarval delivery and the condition of the nursery habitat.

8.2.2 Post-recruitment patterns and processes

The ecological role of sociality

Sociality, common among palinurids, is an important, widespread ecological adaptation (Childress & Herrnkind, 1996; Herrnkind *et al.*, 2001), mediated by sophisticated sensory processes, especially olfaction and behaviour (Zimmer-Faust *et al.*, 1985; Ratchford & Eggleston, 1998). Initially, small juveniles are ineffective at cooperatively defending against predators but they eventually attain sufficient size and defensive ability to reduce predation mortality by co-occupying dens (Butler *et al.*, 1999). Several species (e.g. *P. argus, P. ornatus*) form queues or defensive rosettes while away from crevices, gaining increased vigilance and facilitating active defence against predators, as well as reducing drag during migration.

The general assertion that palinurids widely exhibit sociality belies the range and complexity of social processes represented with the taxon and the large changes in sociality during ontogeny in certain species. Research during the past decade has concentrated on a few species, particularly P. argus and J. edwardsii. That work includes careful field and captive observations, as well as experiments that reveal both the consequences of sociality in the natural ecological setting (Childress & Herrnkind, 1997; Butler et al., 1999) and the mechanisms of the processes involved (Ratchford & Eggleston, 1998; Childress & Herrnkind, 1994; 2001a, b) (Fig. 8.3). Further inference is available from observations on numerous species including: P. cygnus, P. guttatus, P. interruptus, P. marginatus, P. japonicus, P. ornatus, Palinurus elephas, and J. lalandii (Lindberg, 1955; Berrill, 1976; MacDonald et al., 1984; Holthuis, 1991; Yoshimura & Yamakawa, 1988; Childress & Herrnkind, 1996; Dennis et al., 1997; Butler et al., 1999; Butler & Herrnkind, 2001; Herrnkind et al., 2001; Lozano-Álvarez & Briones-Fourzán, 2001). Because P. argus and J. edwardsii differ ecologically and bio-



Fig. 8.3 A number of palinurid lobsters are initially solitary and cryptic. Sociality and the tendency to congregate in dens occurs during an ontogenetic shift later in the juvenile period. *Jasus edwardsii* in New Zealand (top two panels) and *Panulirus cygnus* in Western Australia (bottom panel) den in large groups after about 20 mm CL (adapted from Butler *et al.*, 1999 and Jernakoff, 1990, respectively).

logically, they represent disparate points along the palinurid spectrum.

Palinurid postlarvae typically settle in a dispersed pattern within complex habitats and the early benthic phase juveniles are asocial, display outline-disruptive colouration, and remain in refuge or forage in darkness within centimetres of shelter (see Butler & Herrnkind, 2001). Asocial behaviour, which maintains large inter-individual distances, reduces mortality by forcing the predators of these vulnerable stages to hunt for each solitary individual over a large area in highly cryptic habitat (Butler *et al.*, 1997). For example, early juvenile *P*.

argus placed together in contiguous vegetation, move apart within a day while those in small patches surrounded by open substrate remain residential but probably suffer higher predation (Herrnkind & Butler, 1986).

The onset of sociality, the point at which individuals begin to seek out conspecifics, occurs abruptly at about 20 mm CL in P. argus and J. edwardsii, and general observations suggest that the same is true in most palinurids (Marx & Herrnkind, 1985a; Butler et al., 1999). This change in social behaviour coincides, in P. argus, with an ontogenetic habitat switch from initially remaining in vegetation at all times to diurnal dwelling in sponge, coral, or rock crevices (Andree, 1981; Childress & Herrnkind, 1996). In the case of J. edwardsii, P. japonicus, P. elephas, P. guttatus and other species with hole-dwelling early benthic phase juveniles, the shift in habitat is less dramatic as they simply vacate small holes to occupy larger rocky crevices nearby (Yoshimura et al., 1994; Sharp et al., 1997; Butler et al., 1999, Diaz et al., 2001). Emergence of the adult markings and gradual loss of the post-settlement pattern as well as strong social facilitation of behaviour, including queuing, begin in *P. argus* at this size (Childress & Herrnkind, 1999). Limited information from other species suggests similar shifts (Butler et al., 1999).

With this shift in habitat use and sociality, cohabitation of dens becomes prevalent, altering juvenile spatial distribution according to the distribution of larger crevices (Butler et al., 1999). At the same time, social juveniles begin to produce a waterborne odour that attracts other juveniles during the pre-dawn hours (Zimmer-Faust et al., 1985; Childress & Herrnkind, 1996; Ratchford & Eggleston, 1998; Butler et al., 1999; Nevitt et al., 2000). This odour 'guides' shelter-seeking individuals from several metres away to a crevice, which the resident is usually willing to share (Childress & Herrnkind, 2001a). Orienting to a den already occupied by a conspecific is theoretically beneficial in two ways. First, it reduces exposure time, thus decreasing the probability of a predator encounter in the open. Second, it makes group defence against predators possible (Butler et al., 1999). At the initial social shift size, juveniles are

probably too small to benefit from cooperatively defending against predators (Childress & Herrnkind, 1997) but, hypothetically, may gain if their den mates are larger and capable of repulsing a predator (Butler et al., 1999). In P. argus, juveniles choose either solitary dens or tightly-packed dens depending on the nature of the predator, shelter availability, and shelter dimensions (Eggleston & Lipcius, 1992). This presumably applies generally to spiny lobsters and may explain why patterns of aggregation among juvenile spiny lobsters vary despite the fact that all are social. For example, rocky crevices of appropriate dimensions to house large aggregations of juvenile lobster are common along the New Zealand coast where the majority of juvenile J. edwardsii are found clustered together in dens (Butler et al., 1999). In Florida, dens for juveniles are widely scattered and most are only small crevices, thus only about half of the juvenile *P. argus* are found sheltering by day in groups (Behringer, 2003; Fig. 8.4).

Another factor that alters patterns of den cooccupancy for *P. argus* in Florida is the presence of a newly-discovered viral disease (Shields & Behringer, 2004). Field observations and labora-



Fig. 8.4 Sociality in spiny lobsters can be altered by pathogens, as shown in this figure depicting patterns of den cohabitation by healthy and PaV1 virus infected juvenile (20–55mmCL) *P. argus* in the Florida Keys during three census periods. Note the solitary nature of infected lobsters, which occurs because healthy lobsters avoid cohabitation with diseased conspecifics (adapted from Behringer, 2003).

tory experiments confirm that healthy lobsters can somehow detect when others are infected and will not cohabit with them, resulting in an increase in the frequency of solitary inhabitants (Fig. 8.4) – the only confirmed instance of disease avoidance by any animal in nature. Whether other species of spiny lobster respond similarly to conspecifics that are diseased or in poor health is unknown. However, such behaviour, along with characteristics of available shelter and predator risk, may also explain why normally social species are often found alone.

For at least one species, P. guttatus, social aggregations appear to be of lesser importance. Panulirus guttatus is an obligate inhabitant of coral reefs in the Caribbean, where it rests by day in small groups in deep, inaccessible crevices, emerging only well after dusk to forage solitarily on the reef close to shelter (Briones-Fourzán, 1995; Sharp et al., 1997; Robertson, 2001; Acosta & Robertson, 2002). Although P. guttatus will co-occupy dens with conspecifics, as well as with P. argus, it is more aggressive toward conspecifics and relies less on communal defence from predators than does P. argus (Lozano-Álvarez & Briones-Fourzán, 2001). Panulirus guttatus attains sexual maturity by 40 mm CL (Sharp et al., 1997; Robertson & Butler, 2003), about the same size at which juveniles of P. argus and J. edwardsii first benefit from active social defence. That is, cryptic behaviour in a sheltered habitat, rather than large size and sociality, serves as a deterrent to predation for P. guttatus and presumably other species that are obligate dwellers of coral reefs.

Large juveniles and non-reproductive adults of most palinurids commonly co-occupy dens, exhibiting higher proportions of multiple than of solitary occupancy (Atema & Cobb, 1980; MacDiarmid, 1994; Eggleston & Lipcius, 1992). The actual number and frequency of solitary and co-occupant lobsters may vary with locality and with season. In adult *P. argus*, for example, the frequency of multiple den occupants ranges from ~45% to 98% (Herrnkind *et al.*, 2001). Local occupants at any time are a mixture of long-term residents of one to three dens (used interchangeably) in the vicinity and transients, either immigrants or past residents that have been elsewhere and returned (Herrnkind et al., 1975). Many of the occupants can re-orient themselves and return back to a den even after being displaced several hundred metres to a kilometre away (Herrnkind & McLean, 1971; Nevitt et al., 2000; Boles & Lohman, 2003). This ability suggests selective and repeated use of known shelters for months by old adults. In this case, cooccupancy of dens might be a by-product of the attractiveness of a large den, or social attraction by chemical signals from a den's residents, or some combination of the two. Displacement by aggression also influences the den occupancy pattern, presumably when den space is rare or the residents enforce a dominance hierarchy (Berrill, 1975, 1976). Both tolerant and antagonistic social interactions interact with den features and predation to produce the observed local distributions and residential patterns.

Intensive field experiments using scaled artificial shelters, which provide space for multiple occupants, reveal a complex relationship among physical dimensions of a shelter, lobster density (local numbers), lobster size distribution, type and number of predators, and whether the predators are actively feeding (Eggleston et al., 1990; Eggleston & Lipcius, 1992). That is, the number and size of den co-occupants change when one or more of the above conditions is substantially altered. When the choice is among smaller crevices, juveniles co-den until a nurse shark is introduced and attacks, causing a switch to solitary den use (Childress, 1995). Lobster social rearrangement in dens in the presence of predators hypothetically reduces predation risk, but the degree of benefit from having more or fewer co-residents has not been determined (Childress & Herrnkind, 1997).

Direct evidence from the field and from observations in large tanks, as well as indirect inferences from information provided by fishers, indicates that several palinurids congregate to travel over open terrain (Herrnkind 1980). Head-to-tail queues of up to 60 lobsters, which form a radial, outward facing group when attacked, were first described in *P. argus* (Herrnkind & Cummings, 1964) but are now documented or strongly inferred for *P. ornatus*, *P. marginatus*, *P. cygnus*, *Palinurus delagoae*, and *J. edwardsii* (Herrnkind *et al.*, 2001). Although benefits remain to be fully tested in any species, these behaviours yield theoretical anti-predatory advantages of dilution, vigilance, and cooperative defence, in addition to drag-reduction (i.e. locomotory efficiency) during queuing (Herrnkind et al., 2001). In New Zealand, large J. edwardsii regularly gather in radial pods well away from shelter, leave to forage nightly, and then regroup afterward (Kelly et al., 1999). The pods seem to have few predators although at spawning, gravid females release larvae while using their antennae to parry fish attacking the egg mass or spawn. Without shelter or enhanced defence, even large spiny lobsters in some habitats are subject to debilitating injury and death from triggerfish, octopus, and large sharks (Kanciruk, 1980). That is, they cannot out-swim the predator, yet the armoured spiny carapace alone is insufficient to resist either octopus or carapace-crushing predators.

Movement and migration

Migration is common among shallow-water palinurids, although some non-migrating species exist (Fig. 8.5). For example, the spotted lobster, P. guttatus, settles on crevice-rich reefs and remains there through adulthood, isolated by open substrate from neighbouring reefs (Briones-Fourzán, 1995; Sharp et al., 1997; Robertson, 2001). Most widelydistributed, large-growing species collectively exhibit a wide range of ontogenetic, seasonal, reproductive, or episodic population movements. Palinurid migrations reflect changing ecological conditions of the benthic life stage during ontogeny and eventual movement to oceanic sites for larval transport. That is, pueruli settle into shallow nursery microhabitats distant from spawning reefs. Newly-hatched larvae must access oceanic currents that then transport the phyllosoma stages offshore to return them later near the coastal nursery. In several palinurid species, whose larvae settle far down current from the spawning site, the benthic stages make long migrations to counter the larval transport (Herrnkind, 1980, 1983; Booth, 1986; Pitcher et al., 1992, Groeneveld, 2000; Groeneveld & Branch, 2002)(Fig. 8.5).

Maturing adults of most well-studied palinurid species exhibit either an incremental ontogenetic migration culminating in mating and spawning in distinct adult habitats, or seasonal inshore-offshore movements for mating or foraging. The track may be relatively short, a few kilometres as in P. interruptus and J. edwardsii that live on narrow coastal shelves, or scores of kilometres, as is the case for P. argus, P. ornatus, and P. cygnus that recruit nearshore but must cross wide coastal shelves to reach oceanic currents. During gradual ontogenetic migration, juvenile P. argus use corridors of foodrich habitat, particularly shallow seagrass meadows, within which individuals move about nomadically in a spatial pattern dictated by the location of prey and shelter (Cox et al., 2001; Briones-Fourzán et al., 2003). That is, lobsters cluster where cover is located adjacent to feeding habitat although these sites may be hundreds of metres apart (Herrnkind et al., 1975). That is particularly so for juvenile and subadult lobsters. In Belize, for example, P. argus are significantly more abundant around mangrove and coral islands surrounded by seagrass than those surrounded by sand or rubble (Acosta & Butler, 1997; Acosta, 1999). Furthermore, immigration and emigration rates of lobster were nearly four times greater for islands surrounded by seagrass than rubble, demonstrating the importance of vegetated habitats as corridors for movement by juvenile lobsters (Herrnkind & Butler, 1986; Acosta 1999).

Although movement by pre-adults onto reefs for reproduction peaks in Florida and the Bahamas during the late winter just prior to reproduction in spring, gradual offshore movement by nomadic juveniles also takes place throughout the year (Herrnkind, 1980; Gregory & Labisky, 1996). Movement is largely nocturnal and solitary, rather than in groups. One of the most detailed studies of movement in adult palinurids comes from a recently-completed eight year mark-recapture study of >1300 J. edwardsii in northern New Zealand (Kelly & MacDiarmid, 2003). That study confirms that large adults show greater site fidelity than smaller individuals, and that movement varies markedly with season. In Western Australia, P. cygnus undergoes a marked physiological transition to the migratory phase signified by the moult from the typical red carapace to the white phase (Melville-Smith et al., 2003). In contrast to P. argus, migratory white P. cygnus move continu-



۲

Fig. 8.5 Examples of migratory movements from nursery areas to reproductive or spawning areas, at different scales, based on tag return data. (Top) *Panulirus argus* in Florida settle and grow in expansive shallow vegetated habitats then move ~20–30 km to reef sites, especially bordering the Atlantic Ocean (adapted from unpublished data, Florida Department of Natural Resources, 1980). (Centre) *Panulirus cygnus* grow nearshore then have to move 40–50 km offshore to the shelf edge to spawn (adapted from Phillips, 1983). (Bottom) Maturing *Panulirus ornatus* move several hundred kilometres across the Gulf of Papua to release larvae that drift back westward to settle along the northeast Australian coast (adapted from Prescott *et al.*, 1986).

۲

()

ously over long distances, across deeper, less preyrich habitats (Phillips, 1983).

Some of the longest migrations, in both duration and distance, take place in species (or populations of particular species) whose nursery habitats and spawning sites lie far apart along the streamline of the larval transport current (Herrnkind, 1980, 1983; Booth, 1986, Pitcher et al., 1992). That is, the benthic life phase must travel back to the spawning point to assure that the cycle is completed. Among such long distance migrants, P. ornatus settle and grow up in coastal reef areas on the west side of the Gulf of Papua then, as maturing pre-adults, they initiate a mass migration hundreds of kilometres eastward (Bell et al., 1987). They mate during this time then spawn on the other side of the Gulf in concert with the seasonal shift in winds and ocean currents that deliver the larvae back to the nursery region (Pitcher et al., 1992). Evidence is mounting that deep water South African Palinurus delagoae and P. gilchristi make a long ontogenetic upcurrent migration over months and years, theorised to counter phyllosomal drift after spawning (Groeneveld, 2000; Groeneveld & Branch, 2002).

The localised, brief but spectacular nonreproductive mass 'migrations' by P. argus are probably rapid evasive movements from areas of disturbance (subject to rapid cooling and high turbulence) to more stable sites (Herrnkind, 1985). In the northern Caribbean and Bahamas, P. argus abruptly begin to march in single-file queues both day and night across open substrata, resting for several hours in the open in radial rosettes or filling and overflowing crevices along the route (Herrnkind et al., 2001). The movements are triggered by autumnal storms, sometimes by hurricanes, well after the preceding spawning season and several months before peak spring spawning; egg-bearing females or even those with developing ovaries are rare among these migrants (Herrnkind, 1980; Kanciruk, 1980). In Bahaman populations, about half of the migrants are immature size but off north-eastern Yucatan, nearly all are mature (Herrnkind, 1985). Although tag-recapture evidence shows that some individuals return within the following year to the shallow feeding habitats near the tagging site, no instances of a mass return movement *per se* have been documented. Lobster mortality during episodic severe cooling in juvenile habitats suggests the selective advantage of leaving shallow areas of rapid cooling and high turbulence (Herrnkind, 1980, 1985). These highly-oriented movements may also promote the redistribution of individuals into new habitat. Boles and Lohman (2003) provide compelling evidence that lobsters can accurately navigate during such movements. *Panulirus argus* possesses both a magnetic directional compass and a geographic position sense. The latter capability, equivalent to vertebrate navigation (e.g. birds, sea turtles), hypothetically serves long-distance migration and homing in palinurids.

Competition

With the exception of intraspecific competition for mates (see Chapter 2), competition among spiny lobsters for shelter or food in the wild is not well documented and is presumably rare. Certainly, in some instances palinurids aggressively compete over food (Kanciruk, 1980), over a den following foraging (Berrill, 1975), and among adult males as they establish harems (MacDiarmid, 1989), but these agonistic displays of interference competition are typically for localised resources and are of short duration, in keeping with the social nature of palinurids. Although experimental enhancement of shelter availability in the wild often results in greater numbers of lobsters in an area (see Section 8.2.1 on limits to recruitment), no evidence indicates that a density-dependent depression of growth results (Ford et al., 1988; Behringer & Butler, in press). In Western Australia, Ford et al. (1988) found that lobster survival was higher on rocky reefs where densities were experimentally reduced, but they did not account for the potentially confounding effects of immigration and emigration. Results from a recent study of juvenile P. argus in Florida also failed to find evidence of intraspecific competition (Behringer & Butler, in press). In that study, lobsters were marked and recaptured over several seasons and years on sites that naturally varied in shelter and lobster density, and on sites where shelter (and thus lobster density) was experimentally manipulated. High densities had no

effect on lobster nutritional condition, mortality, or disease incidence, even though residency of lobsters on a site increased with density.

Evidence for interspecific competition between lobster species, or between lobster and other taxa is largely circumstantial and confounded by predatory interactions. Instances of non-overlapping use of habitats by different species of lobster in sympatry, implies the evolution of habitat segregation, but this 'ghost of competition past' (sensu Connell, 1983) has no experimental confirmation. Furthermore, some species actually share dens (e.g. P. argus and P. guttatus) and in such cases, intraspecific agonism is more common than interspecific aggression (Lozano-Álvarez & Briones-Fourzán, 2001). Spiny lobsters might conceivably compete with other taxa (e.g. predacious gastropods, crabs and fish) for prev or shelter when those resources are limiting, but we know of no published accounts of such competition. Where lobsters occur, there are octopuses. Beyond their role as predators of lobsters, octopuses also require the same crevice shelters and prey (e.g. molluscs and crustaceans) as spiny lobsters and thus could compete with lobsters for those resources (Berger & Butler, 2001), but experimental evidence indicates that predation indeed dominates the lobster-octopus interaction, mitigated to some degree by the presence of alternative prey and group defence by lobsters (Lear, 2004).

Predation

During benthic life, palinurids are subjected to a wide variety of predators, mainly piscine (but also octopus, as noted above), and they experience the highest relative mortality during their early life stages (Butler & Herrnkind, 2001; Phillips et al., 2003). For example, pueruli and early benthic phase juvenile P. argus are vulnerable to pelagic and benthic predators, especially in coral reefs (Acosta & Butler, 1999). A year after settling, juvenile P. argus in Florida will have suffered 96–99% mortality (Herrnkind and Butler, 1994: Sharp et al., 2000). A large fraction of that predation on juveniles happens at the transition from the initial fully alga-dwelling stage to the crevice-dwelling stage at ~15-25 mmCL (Fig. 8.6) (Butler & Herrnkind, 2001).

Rapid growth to a large size serves as an important mechanism for predator avoidance. Among crustaceans, palinurids include some of the largest and fastest-growing species. Growth rate, both generally and within a species, seems to be dictated by the local temperature regime and the nutritional quality and abundance of prey (Mayfield et al., 2000; Butler & Herrnkind, 2001; Chapter 1). Most spiny lobster species attain 1-10kg in weight and overall lengths of 30-50 cm (excluding antennae). Some, including P. ornatus and P. argus, reach a weight of one kilogram only 2-4 years after settlement (Olsen & Koblick, 1975; Trendall et al., 1988; Sharp et al., 2000). Maximum size is not correlated with thermal regime because several temperate species attain large size (45-60 cm total length (TL); J. edwardsii, Sagmariasus verreauxi, Palinurus elephas, P. interruptus), whereas numerous warm water species do not (25-30 cm TL; P. guttatus, P. laevicauda, P. regius, P. echinatus). Large spiny lobsters can be defensively formidable while fending off piscine predators by antennal whipping and thrusting, especially when bunched tightly together in a den or in radial rosettes in the open. Very large (5-15 kg), well-armoured adults probably have very few non-human predators, especially in recent decades because fishing has reduced the abundance of large fishes and sharks. In fact, large spiny lobsters will move about solitarily over open terrain or reefs during the day, especially large males during the breeding season.

The primary determining factor that mitigates predator success is abundant crevice shelter adjacent to good foraging, which reduces the exposure time of the vulnerable juveniles. Sparse, dispersed shelter or prey creates the population bottleneck effect theorised by Caddy (1986), in which growing individuals must move about to locate everdecreasing numbers of appropriately-sized shelters. Although sites differ in predator risk, tethering studies confirm an extremely high probability of predation on exposed juveniles in nursery habitats (Herrnkind & Butler, 1986; Eggleston et al., 1990; Smith & Herrnkind, 1992; Childress & Herrnkind, 1994; Mintz et al., 1994; Lipcius et al., 1998; Briones-Fourzán et al., 2003). Field studies suggest a similar process in P. cygnus (Howard, 1988) and J. edwardsii (Butler et al., 1999) juveniles.



۲

Fig. 8.6 Predation risk in spiny especially the early lobsters, benthic phases, depends greatly on size and shelter features. (Top) Exposed algal phase juvenile Panulirus argus (7–11 mm CL) suffer high predation compared to those in structure (S, sand; SG, seagrass; AC, algal clump; AB, algal bed) at all times of day (adapted from Herrnkind & Butler, 1986). (Centre) Relative survival of sheltered juvenile P. argus depends on the relationship between shelter size (artificial 'casitas') and lobster size (small lobsters 35-45 mm CL; medium lobsters, 46-55mmCL) (adapted from Eggleston et al., 1990). (Bottom) Shelter from predators is exceedingly important during the algal and early postalgal period in P. argus (<25 mm CL)(composite tethering data from Smith & Herrnkind, 1992; Eggleston et al., 1990).

Shallow-dwelling tropical species face the most diverse predator array (Howard, 1988; Smith & Herrnkind, 1992), although temperate species may suffer similarly high mortality from less diverse yet highly abundant predatory species (Wahle & Steneck, 1992; Butler *et al.*, 1999). The predators' tactics include active nocturnal and diurnal hunt

and chase, ambush, probe-and-grab, and others cued by visual, hydrodynamic, and chemical cues. All palinurids, in turn, exhibit a combination of evasion ('avoidance of predatory encounters') and escape ('survival of a predatory encounter') tactics that reduces predation mortality (Barshaw *et al.*, 2003). The most ubiquitous tactic is sheltering in

۲

۲

interstices, which either reduces the chance of being encountered or protects the inhabitant from attack once discovered. A second near-universal tactic is adoption of solitary nocturnal foraging, which reduces the risk from visual predators. Staying within shelter and emerging only in darkness is especially characteristic of juveniles. Palinurids also use chemical cues to detect and avoid encounters with certain predators, such as octopods (Berger & Butler, 2001), but are unable to detect others (e.g. red grouper, *Epinephalus morio*; Schratweiser, 1999) by the same means.

The number and size of predators can predictably alter the abundance or size of local spiny lobsters. Field measures and experimental evidence show that octopuses cause juvenile P. argus to move from nearby dens or to select dens well away from an octopus lair (Berger & Butler, 2001). Red groupers and Nassau grouper, E. striatus, also cause reduced local abundances of small lobsters either by direct predation or by influence on den choice and residency by the lobster (Eggleston et al., 1997; Schratwieser, 1999). Eggleston et al. (1997) found greater juvenile lobster abundances on artificial patch reefs from which groupers had been removed. The community-level influence of increasing numbers and size of large lobster predators has become an important facet of marine reserve design.

Pathogens

Evans et al. (2000) recently reviewed the few known diseases of spiny lobsters, and this subject is covered for both spiny and clawed lobsters in Chapter 5. We therefore only touch on the matter of disease in spiny lobsters as it relates to their ecology in the wild - a brief discussion indeed, because almost nothing is known. Most reports of disease come from laboratory or aquaculture conditions, where handling stress and inappropriate water quality probably exacerbate the incidence and severity of infection. Remarkably few natural diseases appear to be fatal. Shell disease from chitinoclastic bacteria causes lesions around the tail and uropods of several species (Iversen & Beardsley, 1976; Sindermann & Rosenfield, 1976; Booth, 1988; Porter et al., 2001), and some helminths use spiny lobsters as intermediate hosts (Deblock et al., 1990). Infections by Vibrio spp., bacteria, protozoans, and fungi also occur in lobsters held in captivity (Bach & Beardsley, 1976; McAleer, 1983; Kittaka & Abrunhosa, 1997; Diggles et al., 2000). The recently-discovered pathogenic viral disease (PaV1) infecting P. argus in Florida (the first report of a viral disease in lobsters), is one of the few known to occur at high incidence in nature and it is nearly always lethal (Shields & Behringer, 2004). It affects the ecology of P. argus in other ways as well (Behringer, 2003). Susceptibility to PaV1 disease declines with ontogeny, with early benthic phase juveniles and small crevice-dwelling juveniles being the most susceptible. Furthermore, the spatial distribution of juvenile lobsters is altered where the disease is prevalent, because healthy individuals can identify diseased conspecifics and will not cohabit with them (Fig. 8.4). The occurrence of PaV1 in other areas of the Caribbean is not known, but pandemics of several shrimp viruses have spread widely across the tropical and subtropical regions of the world with catastrophic results to the aquaculture and fisheries for penaeid shrimps.

Human and environmental effects

'When one tugs at a single thing in nature, one finds it attached to the rest of the world.'
John Muir, American naturalist (1838–1914)

The ecology of spiny lobsters does not operate in isolation from the large-scale environmental changes that periodically affect marine communities, nor is it immune to the reverberations of human activity. Often, the two are intermingled; therefore ascribing the impact on lobsters to one or the other can be difficult. Because spiny lobsters are the targets of valuable fisheries worldwide, the influence of fishing on their ecology has received the most scrutiny. Wahle (1997) summarised and expounded on a discussion of the consequences of fishing on lobsters held at the Fifth International Conference and Workshop on Lobster Biology and Management in Queenstown, New Zealand in

1997. The points raised there are still relevant today and few are unique to lobsters. The most immediate and obvious impact of fishing is the culling of large individuals from the population, followed by reductions in population density under more severe levels of fishing. Commensurate with those changes in population structure, theoretically, come alterations in population dynamics, including: reductions in average size at maturity and per capita fecundity, increases in growth (due to intraspecific competitive release), mating system anomalies, and potential changes in genetic structure. The first of these changes has been realised in various populations around the world (DeMartini et al., 1993; Pollock, 1995; Chubb, 2000). As far as we know the others have not, except in limited circumstances or under laboratory conditions. For example, the disproportionate loss of large male spiny lobsters could limit fertilisation success through sperm limitation as demonstrated in experiments on J. edwardsii, P. argus, and P. guttatus (MacDiarmid & Butler, 1999; Robertson, 2001; Heisig 2003). Other potential effects of fishing on spiny lobsters include: reduced growth and increased susceptibility to disease due to handling stress and injury, loss of habitat caused by destructive fishing gear, enhanced food availability in the form of bait, competitive or predatory release as a result of fishing of other species, and incidental mortality of lobsters as by-catch in non-targeted fisheries, among others (Jennings & Kaiser, 1998).

Spiny lobster populations are also buffeted by environmental changes - some natural, and some not - that compound the effects of fishing. The National Research Council (1994) and the US Ocean Commission (2004) categorise the problems facing our seas similarly: (1) pollution and eutrophication, (2) habitat destruction (primarily coastal and benthic habitats), (3) over-exploitation of fishery resources, and (4) climate change. Although degraded water quality is a ubiquitous problem and laboratory studies show that juvenile spiny lobster are sensitive to it (Herrnkind et al., 1988; Field & Butler, 1994; Booth & Kittaka, 2000), few published reports address the impact of poor water quality on lobsters in nature. The most dramatic and well-documented events are the periodic mass

mortalities of J. lalandi observed along the southwest coast of South Africa (see Cockcroft, 2001). Episodes of hypoxia caused by blooms of dinoflagellates at times corresponding with severe El Niño events, are the culprits. In the 1990s, over 2000t of dead lobsters were stranded along the coast. Similar hypoxic events in the past are hypothesised to have resulted in the local extirpation of spiny lobster from certain isolated islands in South Africa, where lobster populations have never recovered. In response to the loss of a higher trophic level predator (i.e. lobsters), the communities on those islands are believed to have achieved an 'alternative stable state' (sensu Sutherland, 1974) where predatory gastropods dominate the benthos (Barkai & McOuaid 1988).

Phytoplankton blooms also wreaked havoc on lobsters in south Florida in the 1990s. The ultimate cause of the phytoplankton blooms that blanketed portions of south Florida in the early 1990s cannot be pinpointed with precision, yet compelling circumstantial evidence suggests that a series of hot, dry summers coupled with diversion of freshwater within the Everglades from Florida Bay sparked the problems to come (Fourgurean & Robblee, 1999). In short, changes in the flow and quality of freshwater emanating from the Everglades resulted in the overproduction of seagrass throughout much of the western basin. Density-dependent declines in the health of seagrasses coupled with high temperature and an outbreak of a pathogenic slime mould (Labyrinthula sp.) resulted in the die-off of thousands of hectares of seagrass. The release of nutrients from decaying seagrass and the suspension of sediments in the water column is thought to have fuelled the subsequent and repeated harmful algal blooms, which persisted for months. The blooms loomed over hundreds of kilometres of seagrass and tropical hard-bottom habitat, and at times were swept out to sea threatening the coral reefs (Butler et al., 1995; Philips et al., 1999). The cyanobacterial blooms triggered a massive mortality of sponges, resulting in the decimation of the sponge community over much of the affected region (Butler et al., 1995; Herrnkind et al., 1997; Lynch & Philips, 2000). In turn, the rapid loss of seagrass and sponges resulted in a reconfiguration of nursery habitat for spiny lobster on a grand scale.

 (\blacklozenge)

Approximately 20% of the area used by *P. argus* as a nursery in Florida was destroyed, and the result was significant local declines in lobster recruitment (Herrnkind *et al.*, 1997).

8.2.3 Effect of spiny lobsters on benthic community structure

Lobsters are simultaneously predators and prey throughout their benthic life. Gut-content analysis on many species shows the ubiquitous presence of molluscs, crustaceans, echinoderms, and other invertebrates, but also coralline and fleshy algae (Joll & Phillips, 1984; Herrnkind et al., 1987; Edgar 1990; Jernakoff et al., 1993; Díaz-Arredondo & Guzmán-del-Próo, 1995; Lozano-Álvarez, 1996; Cox et al., 1997; Mayfield et al., 2000; Castaneda et al., 2005). Prey size generally increases with lobster growth, reflecting changes in mandible size and other constraints to handling, accessibility, and durophagy. Throughout life, palinurids are highly opportunistic foragers and consume the same types of prey, although the size and species composition may vary widely with habitat (Briones-Fourzán et al., 2003). Although we know much about the array of prey consumed by lobsters in various habitats, less is known about the effects of lobsters on prey communities.

The large size, predatory habits, and often great local abundance of spiny lobsters suggests that their impact on benthic prey communities should be profound, yet evidence of their influence on prey community structure appears limited largely to rocky, temperate ecosystems. The most extensive evidence that spiny lobsters alter prey communities with cascading effects on benthic community structure comes from studies of P. interruptus in southern California. Tegner and Dayton (1981) found that *P. interruptus* together with a predatory fish (sheepshead; Semicossyphus pulcher) controlled the abundance and distribution of two species of sea urchin (red sea urchin, Strongylocentrotus franciscanus; purple sea urchin, S. purpuratus). The grazing activities of the urchins, in turn, altered the abundance of giant kelp (Macrocystis pyrifera), the defining species in California kelp forests. Later modelling studies suggested that predation by P. interruptus also probably controls the

 (\blacklozenge)

bimodality in size structure observed in red sea urchins that dwell in different habitats that vary in accessibility to lobster (Botsford et al., 1994). Predation by P. interruptus, along with that by octopuses and whelks, also controls the joint distribution of bivalve and gastropod prey on rocky reefs in Southern California (Schmidt, 1982, 1987), resulting in 'apparent competition' between prey that is in fact due to dissimilar patterns of predation. Other investigations of P. interruptus demonstrated its similar role in structuring sessile benthic communities via its consumption of a competitively dominant mussel (Robles et al., 1995; Robles 1997), although physical disturbance (i.e. wave surge) and prey recruitment patterns moderate lobster impacts. A similar picture has emerged in temperate, subtidal rocky communities on the opposite side of the globe in South Africa and New Zealand.

In South Africa, predation by J. lalandii and P. homarus alters the abundance and size structure of their mussel, urchin, and gastropod prey, whose availability may limit lobster growth (Newman & Pollock, 1974; Pollock, 1979; Griffiths & Seiderer, 1980; Berry & Smale, 1980; Barkai & McQuaid, 1988; Mayfield et al., 2000). Much as in southern California, predation by lobsters and fishes on these benthic invertebrates is thought to have cascading effects in the ecosystem, including impacts on macroalgal community structure and abalone recruitment (Branch, in prep.). A peculiar role reversal has also been reported in South Africa on isolated islands long devoid of lobsters (Barkai & McQuaid, 1988). On those islands, predatory whelks freed from lobster predation, after low dissolved oxygen events had decimated the lobsters, have reached extraordinary densities and have assumed benthic predatory primacy. Lobster immigrants to those islands are quickly consumed by marauding whelks, which prevent the reestablishment of lobster populations in the area.

Studies in New Zealand also suggest that lobsters (*J. edwardsii*) together with predatory fishes control the abundance of sea urchins that in turn alter macroalgal structure in subtidal rocky communities (Andrew & MacDiarmid, 1991; Shears & Babock, 2002). For example, when urchins (*Evechinus chloroticus*) were removed from urchin barrens

4/11/2006 11:06:47 AM

dominated by crustose coralline algae, those areas were transformed into macroalgal-dominated habitat within 12 months. Indeed, macroalgaldominated areas are more abundant in marine protected areas where lobsters and large fishes abound (Babcock *et al.*, 1999).

Each of these studies is one step removed from actually manipulating predator abundance (lobster or fish) experimentally so that the response of the community without confounding influences can be observed. Nonetheless, their observations provide compelling evidence of top-down control of community structure by spiny lobster in rocky subtidal temperate ecosystems. In contrast, there is little evidence to indicate that palinurids have the same defining effect on benthic community structure in tropical or soft-sediment habitats. Predation by spiny lobsters can reduce prey densities and alter prey-size structure and species composition in seagrass and soft-sediment habitats adjacent to dens where lobsters are aggregated, but the effects are localised and diminish with distance from the den (Joll & Phillips, 1984; Jernakoff, 1987; Jernakoff et al., 1987; Edgar, 1990; Nizinski, 1998). The prey that spiny lobsters seek in seagrass and soft-bottom habitats are presumably sufficiently cryptic and sparse that lobsters cannot pinpoint them, and so lobsters must forage over wide areas in search of prey, and the severity of their predatory activities is diminished.

8.2.4 Spiny lobsters and marine protected areas

Marine protected areas (MPAs) have taken marine science by storm in the past decade. Their potential for preserving ecosystem biodiversity and their utility as management tools for protecting unique or sensitive habitats, species, or cultural sites is real and generally unquestioned, but many are less sanguine about their appropriate design or usefulness in fishery management. Ironically, spiny lobsters are often touted as a success story in the burgeoning literature on MPAs. In a 1997 review of the effects of marine reserves on spiny lobster populations, Childress (1997) concluded that the evidence was convincing that palinurid abundance, mean size, and spawning-stock biomass are typically greater within MPAs where removal of lobster is prohibited than in surrounding fished areas. He also noted that the magnitude of this difference was a function of the size of the MPA, the suite of habitats encompassed by the MPA, and the movement patterns of the lobsters. Those themes recur in recent studies, which continue to yield evidence that the population abundance, individual size, and egg production of palinurid lobsters generally increase in no-take MPAs.

Some of the best recent examples come from studies of J. edwardsii in New Zealand. Using linear models, Kelly et al. (2000) estimated the temporal patterns of change in lobster population structure at a series of marine reserves that differed in age. Their results show that change can indeed be rapid. Lobster density increased by ~4% per year in shallow areas (<10 m) and ~10% in deeper regions of the MPAs. The size of lobsters observed in the reserves increased by an average of 1.14 mmCL per year, and by coupling patterns in size and abundance, the authors estimated that lobster biomass increased by ~5% per year in shallow areas and ~11% per year in deeper reserve areas. Egg production increases mirrored those of biomass. Strikingly similar patterns in MPA effects on J. edwardsii were observed by other researchers using similar methods at another MPA (Tonga Island MPA) in New Zealand (Davidson et al., 2002). Five years after establishment of the Tonga Island MPA, the abundance of J. edwardsii had increased by 22% (~4% per year), and change was greater at deeper sites. Lobsters were nearly three times more abundant in the MPA than in adjacent fished sites, they were 19-28 mm CL larger (shallow-deep sites, respectively), large males were an order of magnitude more abundant, and fecundity in the MPA was nearly nine times greater than that in the fished area. These results are consistent with the findings of earlier studies conducted in the same region (Cole et al., 1990; MacDiarmid & Breen, 1993).

Similar differences in spiny lobster population structure or egg production between MPAs and fished areas have been noted in studies of other palinurid species in Spain (*Palinurus elephas*; Goñi *et al.*, 2001), Florida (*P. argus*; Bertlesen & Cox, 2000; Bertelsen & Mathews, 2001), and

France (P. elephas; Secci et al., 1999) among others. In fact, P. elephas has been identified as an important indicator species for measuring the success of MPAs in the Mediterranean (Mouillot et al., 2002). Not every MPA in the world has experienced the same blossoming of spiny lobster populations, however. Notable exceptions are studies of MPA effectiveness in Florida and the Bahamas where the small size of MPAs, habitat differences between MPAs and fished sites, or lack of enforcement and resultant poaching within MPAs have precluded the development of noticeable differences in P. argus populations (Lipcius et al., 2001; Bertelsen et al., in press). Although commercial fishing is undeniably the primary cause of differences in lobster population attributes between MPAs and unprotected areas, substantial recreational fisheries also contribute to this difference in some areas (Davis, 1977; Eggleston & Dahlgren, 2001).

Despite recent advances, we are still uncertain whether the effects documented within MPAs produce any measurable impact on spiny lobster populations outside the reserves. For lobsters, as well as other species subject to fishing, this is one of the most pressing issues related to MPAs - and also perhaps the most difficult one to answer. The long larval period of palinurid lobsters poses a formidable obstacle to empirical investigation of the benefits of MPAs to recruitment and population replenishment outside of reserves. Simulation modelling has thus far been the tool of choice for building at least a heuristic understanding of the potential importance of larval and postlarval retention and transport in MPA design (Stockhausen et al., 2000; Griffin et al., 2001; Lipcius et al., 2001; Stockhausen & Lipcius, 2001). There is little or no empirical evidence to support the idea that the build-up of lobsters and spawning stocks within MPAs has had any impact outside the reserves.

Even the importance of adult 'spill-over' into adjacent fisheries is questionable (Chiappone & Sealey, 2000; Kelly *et al.*, 2002). In perhaps the best study to date of adult lobster movement and spill-over, Kelly and MacDiarmid (2003) detailed how size-specific differences in male and female lobster movements contribute to population buildup within MPAs. During their eight year mark–

 (\blacklozenge)

recapture study of J. edwardsii in Leigh Marine Reserve in northern New Zealand, over 20% of the over 1300 adults they tagged were re-sighted on a small, 15 ha rocky reef in the reserve. Philopatry increased with size for females and among the larger males (>130 mm CL), but adult lobsters also participated in seasonal movements back and forth across the reserve boundary and were thus susceptible to capture by the fishery (i.e. spilled over). These same patterns were evident in the adjacent fishery catch. More large individuals were indeed captured by the fishery adjacent to the Leigh MPA, but the catch was seasonally variable - more so than in nearby fished populations (Kelly et al., 2002). That seasonality, together with differences in the catch of smaller, legal-sized lobsters, resulted in non-significant differences in catch-per-uniteffort (i.e., kg /trap haul) of J. edwardsii between areas adjacent to reserves and those further away.

Rates of movement, MPA area and habitat structure, and fishing intensity along the MPA boundary are all critical factors governing the spill-over from MPAs, as well as the equilibrium density of spiny lobsters within MPAs. Acosta (2002) examined these factors in detail using a simple logistic rate model and empirical data for P. argus and queen conch from an isolated MPA (Glover's Atoll) in Belize. The model predicted that the lobster population within the MPA would increase 2.5 fold within five years of MPA establishment, in close agreement with the observed data. Changes in the modelled reserve size led to predictable changes in lobster population size, but changes in fishing intensity along the MPA border resulted in equally dramatic changes in lobster density in the MPA because of nomadic foraging by adult P. argus outside the reserve.

Research on spiny lobsters in MPAs is still in its infancy, but the need for new tools for better management of lobster populations subject to fishing could not be direr. Like the majority of fishery stocks worldwide, lobster stocks are nearly all fully- or over-exploited (National Research Council, 1994; US Ocean Commission, 2004). In southern California, for example, the fishery for *P. interruptus* began in the late 1880s when landings in only 260 traps was about 105000kg annually with lobsters averaging 150 mm CL (Dayton *et al.*, 1998). By 1976, it took 19000 traps to land an equivalent biomass of lobsters that by then averaged only about half (88 mm CL) their former size. That fishery is virtually non-existent today. Yet lobsters may be good model organisms for studying the efficacy of MPAs as tools for fishery replenishment. Their long larval period sets an upper bound on the potential for long-distance oceanic dispersal of marine organisms, yet the vertical migratory behaviour of palinurid larvae and the remarkable swimming and olfactory responses of the pueruli (see Chapter 7) leave open the seemingly unlikely possibility of local retention and recruitment. Similarly, adult lobsters, although capable of extraordinary excursions, are often place-bound. Yet benthic lobsters are also more tractable than fishes, so more studies of adult spill-over from MPAs are certain to appear soon. Coming to grips with these possibilities is likely to require a melding of approaches, including modelling, molecular genetics, and some ingenious empirical studies.

8.3 Clawed lobsters

Clawed lobsters (Homaridae) are phylogenetically diverse (Chapter 4), abundant, and ecologically important in coastal zones and continental shelves of the temperate to subarctic regions of the North Atlantic (Fig. 8.7A). The most abundant species are Homarus americanus, H. gammarus and Nephrops norvegicus. Based on commercial landings, that reflect the magnitude of relative abundance, H. americanus is the most abundant, N. norvegicus next, and *H. gammarus* a distant third (Fig. 8.7B; FAO, 2004). Nephrops and H. gammarus are distributed from northern Norway (Lofoten Islands) south to the Atlantic coast of Morocco and throughout much of the Mediterranean (Holthuis, 1995). In contrast, H. americanus has greater landings over a relatively small geographic range from northern Newfoundland south to the mid-Atlantic coast of North America (Holthuis, 1995).

Direct, *in situ* measurement of clawed lobster population densities scale with their fisheriesdependent abundances (i.e. Fig. 8.7B). Average population densities of *H. americanus* range between one and two per square metre (Fig. 8.8A, B) over hundreds of kilometres of the US coast of Maine (Steneck & Wilson 2001). In contrast, H. gammarus is so rare, that we could find no published population densities from the field. The population density of N. norvegicus is also lower than that of H. americanus, though its landings are high (Fig. 8.7B) because it is distributed in sedimentary habitats over vast areas of the continental shelf (Chapman, 1980; Tuck et al., 1997; Maynou et al., 1998) (Fig. 8.7A) from 20-800 m (Holthuis, 1995). Its maximum population densities range between 0.006/m² in the Mediterranean near Spain (Maynou *et al.*, 1998) to $0.125/m^2$ for Scotland (Chapman & Rice, 1971). These population densities are one to three orders of magnitude lower than those reported for H. americanus in Maine, USA (Fig. 8.8B; Steneck & Wilson, 2001).

Although good ecological observations have been made on *N. norvegicus* (e.g. Chapman & Rice, 1971; Chapman, 1980; Cobb & Wahle, 1994), our knowledge of the ecology of *H. americanus* is far greater. The American lobster is abundant and occurs within depths that are easily studied. In contrast, the average depth of occurrence for *N. norvegicus* is 300–400 m (Maynou *et al.*, 1998), a range that is difficult and expensive to study. For these reasons, *H americanus* has received the most attention in ecological research, and its treatment therefore dominates our review.

There are numerous physiological and behavioural similarities shared by clawed lobsters beyond their obvious large chelipeds, which they use for prey capture and mate selection. For example, clawed lobsters are solitary crevice dwellers that defend their space against others of their species and each other (Cobb, 1971). They carry developing eggs for nearly a year, before the eggs hatch at about 10°C (18-12°C, H. americanus, Aiken & Waddy, 1989; 5-15°C, H. gammarus, Tully et al., 2001; 7-11°C, N. norvegicus, Thompson & Ayers, 1989). They all have relatively short larval durations: three larval stages before they metamorphose into postlarvae (reviewed by Cobb & Wahle, 1994). Once they become established in benthic habitats, they pass through three ecological phases (early benthic, adolescent and reproductive phases; sensu Cobb & Wahle, 1994). The timing and duration of each phase varies geographically



Fig. 8.7 (A) The North Atlantic distribution of American lobster Homarus americanus (US and Canada), European lobster H. gammarus and the Norway lobster Nephrops norvegicus (Holthuis, 1995). (B) Landings for all three species since 1950. Open squares are H. americanus, open circles are H. gammarus, and closed squares are N. norvegicus. (Data from FAO (2004), National Marine Fisheries Service and Canada Department of Fisheries and Oceans.)

and oceanographically among and within the three species (e.g. Wahle *et al.*, 2004). Despite these similarities, these species differ strikingly in patterns of distribution, abundance, agility (their propensity to move), habitat use, and key aspects of the ecology of the habitats in which they live.

8.3.1 Limits to recruitment

Several studies concluded that successful settlement to the benthos drives the demography of lobsters (e.g. spiny: Butler & Herrnkind, 1997; Parrish & Polovina, 1994; and clawed: Cobb & Wahle, 1994). For the American lobster, settlement and early benthic phase (juveniles <40 mm CL) subpopulations are strongly bound to the interstices of their cobblestone shelter (Steneck, 1989; Wahle & Steneck, 1991). Their strong habitat-selection behaviour for small shelter-providing substrata (Able *et al.*, 1988; Wahle & Steneck, 1991) at the time of settlement coupled with the demonstrably low post-settlement mortality measured in the field (Wahle & Steneck, 1992; Palma *et al.*, 1999; Wahle *et al.*, 2004) may explain why successful settlement drives the demography of this species today (Palma *et al.*, 1999; Steneck & Wilson, 2001). As lobsters grow, their dependency on shelters for protection declines (Wahle & Steneck, 1991; Wahle, 1992),



()

()

4/11/2006 11:06:48 AM

۲

and their annual migration range increases (Krouse, 1980). Specifically, young of the year lobsters remain only a metre or two from where they settled (Incze *et al.*, 1997; Palma *et al.*, 1999).

Recruitment to the benthos may therefore be the gateway to population growth among at least some clawed lobsters. Successful settlement for lobsters requires three sequential steps (Fig. 8.9): (1) available competent larvae (which requires sufficient

broodstock, larval production and connectivity via oceanographically driven dispersal), (2) the larval behaviour contributing to its propensity to settle, and (3) available nursery habitat (i.e. microhabitats where post-settlement mortality is low). Most of what we know about clawed lobster recruitment comes from studies of *H. americanus* in the Gulf of Maine. The Gulf of Maine is a good laboratory in which to study lobster ecology because larvae



Fig. 8.9 Conceptual model of variable demographic bottlenecks for clawed lobsters leading to recruitment limitation. Three sequential steps related to larval availability, propensity to settle and available nursery habitats lead to recruitment to the benthos. Arrows to the right represent possible bottlenecks. Examples of those bottlenecks are given to the right of the arrows.

 (\blacklozenge)

and young of the year lobsters are abundant and easy to sample (Incze & Wahle, 1991; Wahle & Steneck, 1991; Miller & Reeves, 2000).

Postlarval availability and settlement

The abundance of larvae and settlement to the benthos are invariably greatest in outer coastal habitats and decline up estuaries and in deep embayments (Palma et al., 1999; Steneck & Wilson, 2001). At very coarse levels, therefore, connectivity must exist between outer coastal regions where larvae and postlarvae develop (Incze et al., 1997) and nearshore shallow (Wilson, 1999) nursery habitats. Oceanographic control of lobster larval transport and availability for settlement is evident at several scales. For example, larval 'shadows' occur on the lee sides of small islands, where winddriven advection significantly reduces settlement (Incze & Wahle, 1991; Palma et al., 1999). The absence of available larvae for settlement is also thought to create settlement 'cold spot' patches up estuaries such as Maine's Penobscot Bay, (Fig. 8.8C, Steneck & Wilson, 2001) and elsewhere (Palma et al., 1999). Advection of larvae and postlarvae offshore into deep-water regions probably causes considerable pre-settlement mortality (Incze & Naimie, 2000; Wahle, 2003) and may explain why lobster settlement in the Gulf of Maine declined from 1995 to 2000 (Wahle et al., 2004) despite reproductive populations in the region increasing over that same period of time (ASMFC, 2000; Steneck, 2006). Larval mortality as a result of oceanic transport away from nursery habitats has also been reported for H. gammarus (Nichols & Lovewell, 1987) and Nephrops (White et al., 1988; Hill, 1990; Cobb & Wahle, 1994) of the western Irish Sea. Simple passive advection by ocean currents (Incze & Namie, 2000) together with wind-driven surface currents, may explain a considerable proportion of the variance in settlement, but long-distance directional swimming by postlarvae could also affect larval availability (Fig. 8.9) (Katz et al., 1994). Nevertheless, arrival of postlarvae in waters over potential nursery grounds does not alone assure successful settlement.

Once competent postlarvae arrive at a potential settlement site, their propensity to settle is control-

led by several factors that operate hierarchically (Boudreau et al., 1990). Water temperature controls larval development and possibly recruitment of postlarvae to the benthos (Cobb & Wahle, 1994) by limiting the diving behaviour of pelagic postlarvae (Boudreau et al., 1990, 1991; Annis, 2004). Although laboratory studies by Boudreau et al. (1990, 1991) concluded that compressed temperature gradients with depth (i.e. thermoclines) exceeding 6°C will limit settlement of American lobsters, other studies concluded that a specific temperature or 'thermal threshold' mediates settling behaviour among postlarvae (Annis, 2004). Annis (2004) followed sounding postlarvae in the field and observed that water temperatures of 12°C or more limited their diving. This is the same temperature that Huntsman (1923) hypothesised controlled recruitment along the north shore of the Gulf of Maine. Similarly, Wilson (1999) found a marked increase in lobster settlement both in areas and at depths having temperatures warmer than 11.5°C. This result conformed to observations from large regional studies that found high rates of settlement in warm stratified water in Maine (e.g. west of Penobscot Bay, Maine, Fig. 8.8A, C; Steneck & Wilson, 2001) but low settlement in eastern Maine where water is cold but not stratified (Wahle & Steneck, 1991; Cobb & Wahle, 1994). These observations do not contradict the laboratory findings of Boudreau et al. (1992) because all of their control chambers in which the highest rates of lobster settlement were observed were warmer than the 12°C threshold temperature. Nevertheless, several lines of evidence point to seawater temperatures as controlling the propensity to settle in American lobsters (Fig. 8.8).

Olfactory cues may also contribute to recruitment success among settling lobsters. Laboratory studies on the behaviour of competent American lobster postlarvae with respect to odour plumes, found that at the time of settlement, they swim toward adult lobsters, other postlarvae and benthic algae, but away from potential predators (Boudreau *et al.*, 1993). This behaviour is likely to increase post-settlement survival by attracting lobsters to the shallow photic zone where water warms during the summer months and their growth rates will be high (Wahle *et al.*, 2004) but will allow them to

avoid predators (Wahle, 1992; Boudreau *et al.*, 1993). This illustrates the rather elaborate metre-scale habitat selection behaviour evident in this species at the time of settlement.

Nursery habitats and demographic bottlenecks

Lobster settlement is largely limited to shallow, cobble, nursery grounds (Wahle & Steneck, 1991; Cobb & Wahle, 1994) where early benthic phase lobsters live for the first several years of their lives. Because this substrate comprises no more than 2–10% of coastal substrates in Maine (Kelley, 1987) it has been described as the primary 'demographic bottleneck' for the American lobster (Wahle & Steneck, 1991; Wahle, 1992; Cobb & Wahle, 1994). As such, this substrate at this life history phase may set the carrying capacity for this species.

Little is known about recruitment to the benthos by European lobster, H. gammarus, because they are exceedingly rare. Newly-settled, young of the year and early benthic phase lobsters have never been found subtidally (Mercer et al., 2001). This, despite experienced researchers using techniques proven effective for H. americanus (e.g. Wahle, 1998) and a large team of European researchers sampling broadly in four countries (Norway, Ireland, UK and Italy) (Linnane et al., 2001; Mercer et al., 2001; and discussed below). A few early benthic phase and adolescent phase European lobsters (20-50mmCL) were found in an intertidal zone near a source of fresh water (Linnane et al., 2000a, 2001), but little can be concluded from that rare encounter. It does indicate, however, that European lobsters can live in the intertidal zone but that they do so at a small fraction of the densities common for American lobsters in that zone (Cowen et al., 2001). For example, the four-year study by Cowen et al. (2001) reported 1934 lobsters from 4490 quadrates from New England, or an average density of 0.4/m² with maximum site averages exceeding one per square metre.

Observations of laboratory-reared European lobsters indicates that their settlement and early post-settlement ecology is similar to that of *H. americanus*. They preferentially select cobble habitat and sustain themselves by suspension feeding (Linnane *et al.*, 2000b). Theories advanced

to explain why European early benthic phase lobsters have not been found include simple rarity of the species, avoidance of sampling gear, preference for habitats distinct from those of juvenile and adult lobsters, and preference for specialised nursery grounds that are yet to be sampled. Although Mercer et al. (2001) favoured the last thesis, others argued simply that they are too rare to be detected (Wahle, 1998). Overall population density estimates of early benthic phase European lobsters, based on landings, range from 0.01 to $0.001/m^2$ (R. Bannister & S. Lovewell personal communication in Mercer et al., 2001). If these estimates were correct, then suction sampling of areas between 100 and $1000 \,\mathrm{m}^2$ per site would be necessary (although admittedly impractical on the high side). To date, a total area of 94.5 m² has been suction sampled among four countries (Ireland, 23 m²; UK, $6.5 \,\mathrm{m}^2$; Norway, $41 \,\mathrm{m}^2$; Italy, $24 \,\mathrm{m}^2$), and some sampling was devoted to substrates such as Zostera eelgrass (Norway), which are generally considered poor settlement and early benthic phase habitats (Cobb & Wahle 1994). In comparison, 280 m² of cobble substrate is sampled annually at seven locations as part of Maine's lobster settlement monitoring programme.

Clearly, newly-settled and all subsequent phases of European lobsters are much less abundant than their American counterparts (e.g., Fig. 8.7B). Accordingly, larval availability is likely to be relatively low because of the low densities of reproductive-phase populations. European lobsters may therefore be reproductively limited; the demographic bottleneck limiting their overall density may be at the first step of the recruitment sequence (Fig. 8.9). Despite low larval availability however, the other steps may also be important for recruitment. Recent advances in methods for aging European lobsters (Sheehy et al., 1999) allow high-resolution cohort analyses, which can determine interannual variations in recruitment strength (Sheehy & Bannister, 2002). Analysis by these methods showed that onshore winds (driving larval availability) and local sea temperatures at the time of settlement (affecting the propensity to settle) correspond to reconstructed annual settlement strength for H. gammarus (Sheehy & Bannister, 2002).

4/11/2006 11:06:49 AM

	Gulf of Maine	Norway	Ireland	UK	Italy
Lobster (no./m ²)	1.5	0	0	0	0
Decapod density (no./m ²)	8.6	146.5	86.5	85.5	32
No. decapod families	4	12	14	13	12
No. decapod species	5	17	32	15	20
Dominant genus/family	Homarus	<i>Galathea</i> sp.	Porcellanidae	Porcellanidae	Alpheus
No. m ² quadrats	40	74	46	13	48

Table 8.1 Regional comparison of decapod populations from suction sampling of cobblestone habitat at 5–10 m depth. (Europe data from Linnane *et al.* (2001) and Mercer *et al.* (2001). Gulf of Maine data from Steneck – unpublished data from Damariscove Island, Maine 2003.)

Experimental and field evidence indicate that early post-settlement processes such as competition and predation may also be important to recruitment of this species. For example, tethering studies showed that attack rates on small, unprotected lobsters were very high (Ball et al., 2001; Mercer et al., 2001), as they are for the American lobster (Wahle & Steneck, 1992), but competition for interstitial space among cobblestones is likely to be much greater for European than for American lobsters (Wahle, 1998). Suction samples of cobblestone nursery habitats yielded densities of decapods nearly an order of magnitude greater in Europe than at a rich site in the Gulf of Maine (Table 8.1). The diversity of decapod families and species were also considerably higher in Europe than that found in America.

Interactions between these two early postsettlement processes could have synergistic effects. Settling lobsters select the habitat into which they recruit by probing spaces with their claws and exploring entry into small shelters. The high density of other decapods in Europe (Table 8.1) may lead to much longer searches for unoccupied shelters by European than by American lobsters and therefore higher per capita predation rates on them. In contrast, American lobsters more often encounter vacant cobblestone habitats resulting in rapid occupation of predator-free refuges (Wahle & Steneck, 1992).

Recruitment dynamics for *N. norvegicus* differ from those of *Homarus* spp. because it lives in deeper water and recruits to and lives in cohesive mud habitats (Chapman & Rice, 1971; Cobb, 1977; Cobb & Wahle, 1994). Larval availability in the western Irish Sea is related to the biophysics of oceanographic connectivity, which are under climatological control (Hill, 1990; Hill & White, 1990). Relatively little is known about the settlement behaviour of *N. norvegicus* (see Cobb & Wahle, 1994), but they are thought to be most abundant in fine sediment near the lower limit of the photic zone (Chapman, 1980), where visual predators are probably less effective (Cobb & Wahle, 1994). In contrast to *H. americanus, N. norvegicus* is believed to settle into small holes in the same habitat where adults live.

Bottleneck variability

The limits to recruitment described above are reasonable proximate explanations for the differences we see today in the abundances of clawed lobsters. The series of events leading to successful recruitment may be 'pinched' at any of several successive nodes, with significant demographic consequences (Fig. 8.9). Demographic bottlenecks are variable, therefore, and depend upon key input parameters that operate on several scales (Palma *et al.*, 1999). For example, in warmer-than-average years, the bottleneck could widen if a thermal threshold that limits the sounding depth of competent postlarvae deepens, exposing more potential nursery habitats to settlement (Sheehy & Bannister, 2002; Annis,

۲

2004; Steneck, 2006). Year class strength is often set by chance encounter of postlarvae oceanographically-driven to coastal zones that happen to have nursery habitats. At the scale of embayments, a very high percent of American lobster postlarvae find, settle and survive in cobblestone habitats (Incze *et al.*, 1997, 2000), whereas a very high percentage of the same number of postlarvae entering an otherwise identical sandy bay would die. Thus, the large, bay-scale area of available nursery habitats may well be more important as a demographic bottleneck for this species than simply the availability of settlement space within any given square metre of cobblestone.

We stress the *demographic* consequences of ecological processes such as settlement, habitat selection, competition, and predation because only some of those processes result in death of the settlers (thereby having demographic effects). Intense competition at the time of settlement could cause postlarval lobsters to continue searching for available nursery habitat, which may affect their distribution but will not affect the year class strength unless this behaviour also increases their per capita mortality rates. This was determined for postlarvae entering small embayments in Maine in which most eventually found and settled into cobblestone nursery habitats without significant post-larval mortality (Incze & Wahle, 1991; Incze et al., 1997).

Intraspecific competition at the time of settlement has modest demographic effects. Even in areas with the highest density of newly-settled lobsters, space within nursery habitats does not appear to be demographically limiting. When Wahle et al. (2001) artificially over-saturated cobblestone habitats with postlarval lobsters, the equilibrium densities were much greater than that ever found in the field, so cobble habitats are probably rarely limiting in nature. A similar cobble-stocking experiment was conducted for H. gammarus under predatorfree conditions, with results similar to those of Wahle (2003). After a year, a high percentage of the experimentally introduced individuals remained (Linnane et al., 2000a). Thus successful settlement may well drive the demography of lobsters but many ecological factors regulate it in complex and variable ways.

8.3.2 Post-recruitment patterns and processes

Distribution, abundance and body size

The American lobster undergoes an 'ecological niche shift' during its ontogeny; different ecological phases segregate into different habitats (Fig. 8.10). Over 80% of settlement occurs at depths less than 20 m (Wilson, 1999) and primarily in cobblestone habitats (Wahle & Steneck, 1991; Palma *et al.*, 1999). As lobsters grow toward harvestable size (83 mm CL), their annual migration range is on the order of 1–5 km (Krouse, 1980). By the time they reach large, reproductive-phase sizes (\geq 90 mm CL), they migrate 20–30 km annually, and a few tagged individuals have been observed to roam for hundreds of kilometres in less than a year (Campbell & Stasko, 1985; Campbell, 1986, 1989; Estrella & Morrissey, 1997).

Interestingly, 'No similar migrations of *H. gammarus* have been reported' (Cobb & Wahle, 1994). Bannister *et al.* (1994) found that most microwire-tagged hatchery-reared European lobsters remained near their points of release at least until reaching harvestable size. Electromagnetic telemetry studies revealed that relatively small-scale (≤ 10 km) migrations among adjacent reefs were common but few or no long-distance migrations were reported (Jensen *et al.*, 1994; Smith *et al.*, 1998). The longest reported *H. gammarus* migration is about 20 km (Bannister *et al.*, 1994), less than the average seasonal migration (>30 km/year, Campbell 1986) and an order of magnitude less than that of the longest-migrating *H. americanus*.

Recruitment cells of *H. gammarus* are so closed that little gene flow occurs among northern populations of this lobster (Jørstad *et al.*, 2004). Using allozyme, microsatellite, and mtDNA analyses, Jørstad *et al.*, (2004) found that genetically distinct subpopulations of *H. gammarus* persist, that are separated by only 142 km. Oceanographic conditions prevent larval exchange among coastal populations, but this genetic separation shows that migration of reproductive stocks must also be virtually nil (Jørstad *et al.*, 2004). In sharp contrast, the American lobster migrates long distances and shows no measurable stock differentiation within



Fig. 8.10 Lobster population segregation among habitats and with distance from shore. Diagrammatic representation of shallow nearshore settlement into cobble habitat, diffusion to coastal boulder fields with increasing size and age, and eventual diffusion of larger reproductive-phase size classes to offshore habitats.

its range (including the Gulf of St Lawrence, southwest Nova Scotia, and Georges Bank; Harding *et al.*, 1997). Similarly, *N. norvegicus* does not migrate (Chapman, 1980). Since they settle and live in adult habitats, there is no segregation by size or sex resulting in rather discrete patches in abundance (Maynou *et al.*, 1998).

Because lobsters settle in shallow coastal zones (Wilson, 1999) and diffuse offshore at a large size (Fig. 8.10), their size frequency modes shift to progressively larger size with distance from the coast (which is also distance from their nursery habitats; Fig. 8.11). Small early benthic phase lobsters (<40 mmCL, Figs 8.8C, 8.11A, C) dominate rocky substrata in the shallowest coastal zones, and cobble nursery habitats harbour the smallest size classes (Fig. 8.11A). A few metres away, in sediment substrata, lobsters are significantly larger (Fig. 8.11B). Lobsters smaller than harvestable size (83 mm CL) dominate most shallow subtidal coastal zones. Distinctly larger lobsters (50-80 mm CL mode, Fig. 8.11E) are trawled from deeper inshore habitats within Maine state waters and have sizestructure more similar to that of trap-caught lobsters (ASMFC, 2000). Trawl surveys conducted in adjacent offshore habitats in Maine yielded significantly larger lobsters (80–90 mm CL; Fig. 8.11G). These correspond to the size frequencies from the National Marine Fisheries Service (NMFS) semiannual trawl surveys (Steneck, 2006). The ontogenetic segregation in some areas is so complete that almost no overlap exists between populations of seasonally migrating reproductive-phase lobsters (\geq 90 mm CL, Fig. 8.11F) and distinct but more stationary adjacent juvenile populations in the coastal zone (Fig. 8.11D; Campbell & Pezzack, 1986). Large reproductive-phase lobsters dominate all of the most distant offshore canyons of the Gulf of Maine's Georges Bank (Fig 8.11H; Skud & Perkins, 1969).

The ecological consequences of segregated reproductive populations may be profound. Connectivity studies between broodstock and settlement 'hotspots' (Fig. 8.8C) suggest the existence of a long-distance larval source–sink dynamic (Harding *et al.*, 1983; Incze & Naimie, 2000; Annis, 2004). This pattern has management consequences both for stock–recruitment relations (Wahle, 2003) and as a postlarval subsidy in coastal zones from reproductive lobsters living in offshore refugia where fishing pressure is low (Fogarty, 1998). This long-distance larval source–sink rela-

 $(\mathbf{0})$



Fig. 8.11 Size structure of lobsters illustrating ontogenetic segregation illustrated in Fig. 8.10. The elongate vertical rectangle isolates adolescent phase (AP) lobsters 40–89mmCL from smaller early benthic phase lobsters (5–39mmCL) and larger reproductive phase lobsters (≥90mmCL). (A) and (B) illustrate shallow nearshore nursery habitat-related segregation of early benthic phase in cobblestone habitats (A) as distinct from adjacent sediment (B) (adapted from Wahle & Steneck, 1991). (C) Adjacent boulder habitat contains intermediate-sized individuals (Steneck, unpublished data). Segregation among size classes at larger spatial scales is evident around Grand Manan Island in New Brunswick, Canada where migratory reproductive-phase lobsters congregate seasonally in shallow northern coves (F, adapted from Campbell & Pezzack, 1986) whereas much smaller nonmigratory lobsters reside in southern coves at the same depths (D, adapted from Campbell & Pezzack, 1986). Maine State trawl surveys from inshore habitats (E, Maine DMR) show significantly fewer reproductive-phase lobsters than do the same surveys from adjacent sites somewhat farther offshore (<5.6 km) (G). Farthest offshore on Georges Bank (278 km) (H) virtually all lobsters are reproductive-phase.

۲

tionship enables lobster stock to withstand higher levels of fishing mortality in coastal zones (Fogarty, 1998; Steneck, 2006).

Competition and predation

In a significant review paper, Wahle (2003) concluded for lobsters in general that, 'Post-settlement survival is strongly influenced by the three-way interaction of predation risk, habitat quality and body size. As a result, refuge habitat is more often a limiting factor than food, especially among small individuals still vulnerable to predators'. For this reason we will focus primarily on the ecological processes of competition and predation, which drive habitat selection, survival, and the demography of clawed lobsters.

Most clawed lobsters are solitary, shelterpreferring organisms by day and active foragers by night (Cobb & Wahle, 1994). Evidence exists of shelter competition for all three species. Homarus gammarus is known to compete for space during mating (Debuse et al., 2003), but the demographic consequences are likely to be low because of the species' rarity so it is probably not shelter-limited. Population density and body size are inversely correlated for N. norvegicus (Tuck et al., 1997), possibly because larger ones in competition for shelter space displace small lobsters. Although this pattern may affect local small-scale size structure, no evidence indicates that it influences overall population densities. In fact, throughout much of its deepwater range, population densities (maximum 0.006/ m²; Maynou et al., 1998)(Fig. 8.7B) are three orders of magnitude lower than that of the American lobster. Higher population densities averaging $0.125/m^2$ (one order of magnitude less than that of the American lobster) were studied at 30m depths in Scotland (Chapman & Rice, 1971). At that density, active territorial fights over shelters were observed, consistent with the notion that intraspecific competition increases with population density. The competitive interactions were remarkably similar in detail to those observed in H. americanus (e.g. by Cobb, 1971), but the difficulties of scuba diving at 30m leave many ecological questions about N. norvegicus unanswered. Conversely, because H. americanus is found both at high population densities and at depths amenable to protracted *in situ* study, considerably more has been published about its post-recruitment ecology.

Size-specific habitat space can be limiting and can drive intraspecific space competition among clawed lobsters living at relatively high population densities. In most cases, such competition has some effect on the size structure and/or the habitat in which they live. Size-specific habitat availability therefore controls local carrying capacity (e.g. Caddy, 1986), but depending largely on the predator environment, it may also control the demography of the species. That is, the consequences of competitive displacement in a predator-free environment merely redistribute individuals because competitively subordinate lobsters do not die. However, the per capita mortality rate increases significantly if competitive displacement occurs in a predator-rich environment (Wahle et al., 2004). Size-mediated predator vulnerability therefore accounts for much of the variance in the postsettlement survival of lobsters.

Predation is a highly size-specific ecological process (Wahle, 1992), and even under pristine conditions (before human influence) the largest individuals (those over 20 kg) would probably have been immune to predation. The rate at which predation declines with body size relative to the availability of shelters is therefore likely to determine local and regional carrying capacity.

Today's fish predators are primarily small (<5 cm long), commercially unimportant species such as juvenile cunners (Tautogolabrus adsperus), sculpins (Myoxocephalus spp.), and shannies (Ulvaria spp). This guild of small predatory fishes is ubiquitous in shallow coastal zones, where average densities of nearly 1/m² have been recorded (Malpass, 1992). Attack rates on lobsters in coastal Maine decline precipitously with increasing body size (Fig. 8.12A). At settlement size (5–7 mm CL), tethered lobsters suffered up to 60 attacks per hour, but the rate decreased to 10 by the time they reached 8-9 mm and fell below detectable levels by the time they reached 20 mm CL (Wahle & Steneck, 1992; Fig. 8.12A). In parallel studies, lobsters up to 80 mm CL were tethered for as long as 45 days over a three year period, and not a single predator attack was recorded (Steneck, 1997; Steneck & Carlton,



 $(\mathbf{0})$

Fig. 8.12 Changes in ecological processes as a function of body size over space (e.g. inshore as opposed to offshore) and time. (A) The importance of predation and competition. Predator attack rates decline precipitously with size at 'inshore' shallow coastal sites (adapted from Wahle & Steneck, 1992) whereas they increase with size at 'offshore' sites where large predators persist (adapted from Steneck, 1997; Steneck & Carlton, 2001). The percentage of individuals competing for shelter space increased markedly above 60 mm CL (adapted from Steneck 1989). (B) Rates of predator-induced mortality in modern coastal and offshore regions based on tethering studies (Steneck & Carlton, 2001; see text). 'Pristine' conditions are those before measurable human effects. The size of large predators is estimated from archaeological studies (see text). Horizontal lines indicate the estimated predator size based on archaeological records (4000 to 500 years before present, Jackson *et al.*, 2001), modern offshore habitats and under pristine conditions (all extrapolated from attack rates and reflected in B).

2001). This rapid decline in predation rates (Fig. 8.12A; Wahle & Steneck, 1992) with increasing size produces the low post-settlement predatorinduced mortality rates (Fig. 8.12B) and high postsettlement survival (Fig. 8.12C) reported for *H. americanus* (Wahle & Incze, 1997; Palma *et al.*, 1998, 1999). Competition for shelter space is conspicuous in *H. americanus* (Cobb, 1971). Arguably, intraspecific competition occurs among all size classes, but habitat limitations (e.g. shelter space; Caddy, 1986), aggression and range of detection all increase for lobsters larger than about 60 mmCL (Steneck, 1989; Fig. 8.11A). Early benthic phase lobsters

BMA08.indd 293

۲

settle into small shelter-providing habitats such as cobble (Fig. 8.11A) but with time, they outgrow cobble habitat and occupy adjacent sediment (Fig. 8.11B) and boulder (Fig. 8.11C) habitats. Shelter size and spacing regulates competition pressure. By experimentally reducing shelter separation, Steneck (1989) showed intraspecific competition among lobsters over 60mmCL increased (Fig. 8.12A). Surprisingly, with increased population density and competition, large lobsters vacated the area diffusing to habitats with lower population densities. This 'demographic diffusion' (sensu Steneck, 1989) is evident in the decline of pre-harvestable sized lobsters (i.e. 60-83 mmCL) in shallow coastal zones (Figs 8.11B, C, E) and results in size-mediated habitat segregation (Figs. 8.10, 8.11). Since lobsters over 60mmCL are virtually immune to predation (Steneck, 1997; Fig. 8.12A), this demographic diffusion only redistributes larger size classes from high-population-density, shelter-rich shallow coastal boulder habitats (see, e.g. Figs 8.9, 8.10C) with little consequence to overall lobster abundance. This demographic diffusion may contribute to the accumulation of larger, competitively aggressive lobsters in nearshore deep water (Fig 8.11 E, G) and on offshore banks (e.g. Fig. 8.11H).

Currently, the predation risk for American lobsters greater than 60mmCL in size is too low to measure (Wahle & Steneck, 1992; Steneck, 1997), so reproductive-phase lobsters (usually >90 mm CL) can accumulate in offshore habitats (i.e. to the right of the vertical rectangle in Fig. 8.11). This size segregation occurs upon the onset of sexual maturity (Campbell & Stasko, 1985), allowing these lobsters to increase in abundance (Steneck, 2006) and to migrate seasonally into shallow coastal zones (e.g. North Head, Grand Manan Island in New Brunswick; Campbell & Pezzack, 1986; Fig. 8.11F) in the summer. The fishery-induced decline in coastal predators (Steneck, 1997; Jackson et al., 2001) allows for the unprecedented accumulation of reproductive-phase lobsters (Steneck, 2006) that fuels the settlement-driven (Palma et al., 1999) population explosion of American lobsters today (Fig. 8.7B).

On Cashes Ledge, a small, shallow kelp-forested ledge 80 km offshore in the Gulf of Maine, a relict population of large predatory finfishes persists

(Steneck & Carlton, 2001). There the dominant predators are cod (Gadus morhua), wolfish (Anarhichas lupus), and large cunner. Interestingly, the guild of small predatory fishes such as sculpins, shannies, and rock gunnels are rare at offshore sites where large predators persist, consistent with the idea that they too were food for large apex predators such as cod (Fig. 8.12A-C; labelled 'offshore'). When early benthic phase lobsters were tethered at Cashes Ledge, they were not attacked (R. Wahle & R. Steneck unpublished data), but the attack rate increased with size of tethered lobsters at this offshore site (Steneck, 1997; Fig. 8.12A; labelled 'offshore'). This trend suggests that predatory fish forage optimally, seeking the greatest energy value per attack. They do not attack small lobsters because their food value is not worth the effort. Instead the moderately large predators (40-55 cm; Fig. 8.12B) eat larger size classes at increasing frequency, and the largest tethered size class (70-78 mm CL; Steneck, 1997) was attacked at the highest rate. Thus there exist entirely different size-dependent survivorship trajectories resulting from differences in the ecological importance of predation early in the life of lobsters (Fig. 8.12C). Inshore, where attacks by large predators are rare, high mortality rates are limited to the time of settlement. In contrast, where large predators persist today (e.g. 'offshore', Fig. 8.12A), early post-settlement mortality is low but it increases with size and thus remains an important agent of mortality (Fig. 8.12B) and survival (Fig. 8.12C) for a protracted period of time.

8.3.3 Ghosts of predators past: a topdown to bottom-up transition

'Next to man with his traps, the codfish is probably the most destructive enemy of the lobster, for it not only takes in the soft and hard shell animals alike up to 8 inches or more in length, but is very partial to the young from 2 to 4 inches long.' – Herrick, 1909.

Demographically important changes in natural mortality and ecosystem structure and function

 (\blacklozenge)

have occurred at an accelerating rate in recent years (Steneck *et al.*, 2004). Rapidly changing ecosystems can change the recruitment potential and the predation potential of the benthos (*sensu* Steneck & Dethier, 1994) such that the present is neither indicative of distant past or future ecosystem states.

The American lobster is endemic to the western North Atlantic where it evolved under intense predation from large predatory ground fish such as cod (Steneck, 1997; Steneck & Carlton, 2001; Steneck et al., 2004). Evidence for this comes from archaeological midden deposits that indicate that cod and other large predatory ground fish dominated coastal zones for thousands of years to as recently as the last half century (Jackson et al., 2001; Steneck et al., 2002, 2004; Lotze & Milewski, 2004). Significantly, while cod bones comprise as much as 85% of the bone mass of some coastal Indian middens (Steneck, 1997), no lobster or crab exoskeletons have ever been found (Spiess & Lewis, 2001; Lotze & Milewski, 2004; Steneck et al., 2004). Because lobsters produce massive exoskeletons when they are large, and large decapods including lobsters have an impressive fossil record (Feldman et al., 1977; Bishop, 1986), had they been abundant and harvested, some should have been preserved in middens, as did happen with such chronically poorly-preserved invertebrates as sea urchins (Steneck et al., 2004).

When cod were abundant in coastal zones, lobsters were often found in their stomachs (e.g. Herrick, 1909 quotation above). The cod that were abundant in coastal zones of Maine for thousands of years (4500-500 years before present, Steneck et al., 2004) were large. Their reconstructed size averaged about one metre in length (Jackson et al., 2001; Fig. 8.12B). At a unique offshore site in the Gulf of Maine where large ground fish persisted through the 1980s (Witman & Sebens, 1992), they were shown to attack the largest size class of tethered lobsters (70-78 mm CL) at the highest frequency, choosing to ignore the smallest lobsters (30-38 mmCL) (Steneck, 1997; Fig. 8.12A, see ascending curve labelled 'offshore'). This result contrasted with the attack rate on tethered lobsters in coastal zones where only the smallest size class was attacked at high frequency (Wahle & Steneck,

1992; Steneck, 1997; Fig. 8.12A see descending curve labelled 'inshore').

The abundance of large coastal predatory finfish probably maintained high rates of natural mortality among larger pre-harvestable and harvest-sized lobsters (Fig 8.12B labelled 'pristine'). The 'bust' period, when lobster stocks in Maine collapsed between 1920–1940 (Acheson & Steneck, 1997) may have resulted from the combined effects of the harvesting of large lobsters (i.e. those immune to even the largest predators) and consumption by predators of most smaller lobsters at or below harvestable size (Steneck, 1997; Fig 8.12B, C 'pristine'). Large predatory ground fish were shown to have been abundant in Maine's coastal zone through the 1920s (Rich, 1929), but they were rapidly extirpated from nearshore areas during the 1930s when cod and haddock spawning stocks were targeted (Ames, 2004). In 1939, Maine's Department of Sea and Shore Fisheries declared that coastal ground fish stocks 'have been depleted' (Steneck, 1997). Immediately following the extirpation of coastal ground fish stocks, landings increased rapidly to a new high plateau (Steneck, 1997, 2006, Fig. 8.7), perhaps due to release from demographic control by predators. Thus predator-induced mortality has probably declined significantly over the past several decades due to the decline of predator abundance and size (Fig. 8.12B) and as a result only a narrow range of small lobsters remain vulnerable to predators today (Fig. 8.12 A-C).

As 'top-down' (sensu Power, 1992) forces such as predation lose control in regulating lobster populations in coastal habitats, 'bottom-up' forces such as settlement-driven demography (e.g. Palma et al., 1999) probably have become more important (Steneck & Sala, 2005). This represents a fundamental change in how coastal ecosystems are structured, but more importantly, how they function. Predator loss may help explain why this species remains so resilient to fishing pressure. American and probably the other clawed lobsters of the North Atlantic, evolved in an environment of high predator-mediated adolescent and adult mortality. The persistence of *H. americanus* and its ability to thrive today, even under intense fishing pressure, may result from its highly efficient biology having a higher than average per egg survival (Wahle,

4/11/2006 11:06:51 AM

2003) and lower than average post-settlement mortality (Palma *et al.*, 1998).

The loss of large predatory finfish is not restricted to the Gulf of Maine. Apex predators have been extirpated globally (Pauly *et al.*, 1998; Jackson *et al.*, 2001; Myers & Worm, 2003). Given the susceptibility of large, slow, clawed lobsters, their evolution of shelter-seeking behaviour is not surprising. Their reproductive efficiency and relatively short larval life may reflect traits that succeeded over evolutionary time under conditions of high adult predator-induced mortality rates. This pressure has been relaxed due to overfishing of predators (Steneck *et al.*, 2002; Steneck & Sala, 2005) perhaps resulting in a world with a significantly greater carrying capacity (Fig. 8.12C) than had existed in the past. This may help explain why these species have either persisted (*H. gammarus*, Fig. 8.7B) or even thrived (*H. americanus* and *N. norvegicus*, Fig. 8.7B) in recent years despite decades of intense fishing on them.

References

- Able, K.W., Heck, K.L., Jr, Fahay, M.P. & Roman, C.T. (1988) Use of salt-marsh peat reefs by small juvenile lobsters on Cape Cod, Massachusetts. *Estuaries*, **11**, 83–6.
- Acheson, J. & Steneck, R.S. (1997) Bust and then boom in the Maine lobster industry: perspectives of fishers and biologists. North American Journal of Fisheries Management, 17, 826–47.
- Acosta, C. (1999) Benthic dispersal of Caribbean spiny lobsters among insular habitats: implications for the conservation of exploited marine species. *Conservation Biology*, **13** (3), 603–12.
- Acosta, C. (2002) Spatially-explicit dispersal dynamics and equilibrium population sizes in marine harvest refuges. *ICES Journal of Marine Science*, **59** (3), 458–68.
- Acosta, C.A. & Butler, M.J., IV (1997) The role of mangrove habitat as nursery for juvenile spiny lobster, *Panulirus argus*, in Belize. *Marine and Freshwater Research*, **48**, 721–8.
- Acgsta, C.A. & Butler, M.J., IV (1999) Adaptive strategies that reduce predation on spiny lobster postlarvae during onshore transport. *Limnology and Oceanography*, 44, 494–501.
- Acosta, C.A. & Robertson, D.N. (2002) Comparative spatial ecology of fished spiny lobster *Panulirus argus* and an unfished congener *P. guttatus* in an isolated marine reserve at Glover's Reef, Belize. *Coral Reefs* (published online 5 December 2002).
- Aiken, D. & Waddy, S. (1989) Interaction of temperature and photoperiod in the regulation of spawning by American lobsters (*Homarus americanus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **46** (1), 145–8.
- Ames, E.P. (2004) Atlantic cod stock structure in the Gulf of Maine. Fisheries, 29, 10–28.
- Andree, S.W. (1981) Locomotory Activity Patterns and Food items of Benthic Postlarval Spiny Lobsters, *Panulirus argus*. MS thesis, Florida State University.
- Andrew, N.L. & MacDiarmid, A.B. (1991) Interrelations between sea urchins and spiny lobsters in northeastern New Zealand. *Marine Ecology Progress Series*, **70**, 211–22.
- Annis, E.R. (2004) Temperature effects on vertical distribution of lobster postlarvae (Homarus americanus). In: Biology and Ecology of Larval Lobsters (Homarus americanus): Implications for Population Connectivity and Larval Transport. PhD dissertation, Oceanography Program, School of Marine Sciences, University of Maine. pp. 31–98.
- Arango, L., Manrique, M.L. & Jaimes, J.C. (2001) Juvenile recruitment of the lobster (*Panulirus argus*) with artificial shelters in the Colombian Caribbean. *Revista Investigaciones Marinas*, 22 (3), 221–8.
- Arce, A.M., Aguilar-Davila, W., Sosa-Cordero, E. & Caddy, J.F. (1997) Artificial shelters (casitas) as habitats for juvenile spiny lobsters *Panulirus argus* in the Mexican Caribbean. *Marine Ecology Progress Series*, 158, 217–24.
- ASMFC (Atlantic States Marine Fisheries Commission) (2000) American Lobster Stock Assessment Report. Stock Assessment Report No. 00–01 (Supplement), ASMFC American Lobster Stock Assessment Sub-Committee, Washington.

- Atema, J. & Cobb, J.S. (1980) Social behaviour. In: J.S. Cobb & B.F. Phillips (Eds) *The Biology and Management* of Lobsters, *1*, Physiology and Behavior. Academic Press, New York. pp. 409–50.
- Babcock, R.C., Kelly, S., Shears, N.T., Walker, J.W. & Willis, T.J. (1999) Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series*, **189**, 125–34.
- Bach, S.D. & Beardsley, G.L. (1976) A disease of Florida spiny lobster. Sea Frontiers, 22, 52-3.
- Ball, B., Linnane, A., Munday, B., Brown, R. & Mercer, J.P. (2001) The effect of cover on *in situ* predation on early benthic phase European lobster *Homarus gammarus*. *Journal of the Marine Biological Association of the United Kingdom*, **81**, 639–42.
- Bannister, R.C.A., Addison, J.T. & Lovewell, S.R.J. (1994) Growth, movement recapture rate and survival of hatchery-reared lobsters (*Homarus gammarus* Linnaeus, 1758) released in the wild on the English east coast. *Crustaceana*, 67, 156–72.
- Barkai, A. & McQuaid, C. (1988) Predator-prey role reversal in a marine benthic ecosystem. Science, 242, 62-4.
- Barshaw, D.E., Lavalli, K.L. & Spanier, E. (2003) Offense versus defense: responses of three morphological types of lobsters to predation. *Marine Ecology Progress Series*, **256**, 171–82.
- Behringer, D.C., Jr (2003) The Ecological Ramifications of Disease and Density in the Caribbean Spiny Lobster, *Panulirus argus*. PhD dissertation, Old Dominion University, Norfolk, VA.
- Behringer, D.C., Jr & Butler, M.J., IV. Density-dependent population dynamics in juvenile *Panulirus argus*: the impact of artificial enhancement. *Journal of Experimental Marine Biology and Ecology* (in press).
- Bell, R.S., Channells, P.W., MacFarlane, J.W., Moore, R. & Phillips, B.F. (1987) Movements and breeding of the ornate rock lobster, in Torres Strait and the northeast coast of Queensland. *Australian Journal of Marine and Freshwater Research*, **38**, 197–210.
- Berger, D.K. & Butler, M.J., IV (2001) Do octopuses influence den selection by juvenile Caribbean spiny lobster? *Marine and Freshwater Research*, **52**, 1049–54.
- Berrill, M. (1975) Gregarious behavior of juveniles of the spiny lobster, *Panulirus argus* (Crustacea: Decapoda) *Bulletin of Marine Science*, **25**, 515–22.
- Berrill, M. (1976) Aggressive behaviour of post-puerulus larvae of the western rock lobster *Panulirus longipes* (Milne-Edwards). *Australian Journal of Marine and Freshwater Research*, **27**, 83–8.
- Berry, P.F. (1971) The spiny lobsters (Palinuridae) of the east coast of southern Africa. Distribution and ecological notes. *South African Oceanographic Research Institute Investigations Report*, **27**, 1–23.
- Berry, P.F. & Smale, M.J. (1980) An estimate of production and consumption rates in the spiny lobster *Panulirus homarus* on a shallow littoral reef off the Natal coast, South Africa. *Marine Ecology Progress Series*, **2**, 337–43.
- Bertelsen, R.D. & Cox, C. (2000) Sanctuary roles in population and reproductive dynamics of Caribbean spiny lobster. *Spatial Processes and Management of Marine Populations*, Lowell Wakefield Fisheries Symposium Series No. 17, pp. 591–605.
- Bertelsen R.D, Cox C., Beaver R. & Hunt J.H. Changes in local spiny lobster (*Panulirus argus*) population size structure, abundance and fecundity in different sized sanctuaries in south Florida. *Proceedings of the Symposium on Aquatic Protected Areas as Fisheries Management Tools*, American Fisheries Society (in press).
- Bertelsen, R.D. & Matthews, T.R. (2001) Fecundity dynamics of female spiny lobster (*Panulirus argus*) in a south Florida fishery and Dry Tortugas National Park sanctuary. *Marine and Freshwater Research*, **52**, 1559–66.
- Bishop, G. (1986) Taxonomy of the North American decapods. Journal of Crustacean Biology, 6 (3), 326-55.
- Boles, L. & Lohman, K. (2003) True navigation and magnetic maps in spiny lobsters. Nature, 421, 60-3.
- Booth, J.D. (1979) Settlement of the rock lobster, *Jasus edwardsii* (Decapoda: Palinuridae), at Castlepoint, New Zealand. *New Zealand Journal Marine Freshwater Research*, **13**, 395–406.
- Booth, J.D. (1986) Recruitment of packhorse rock lobster *Jasus verreauxi* in New Zealand. *Canadian Journal of Fisheries and Aquatic Science*, **43**, 2212–27.
- Booth, J.D. (1988) Rock lobster farming in New Zealand: problems and possibilities. *Proceedings AQUANZ '88, National Conference on Aquaculture*, Wellington, NZ. pp. 100–4.
- Booth, J.D. (2001) Habitat preferences and behavior of newly settled *Jasus edwardsii* (Palinuridae). *Marine and Freshwater Research*, **52**, 1055–66.

- Booth, J.D. & Bowring, L.D. (1988) Decreased abundance of the puerulus stage of the rock lobster *Jasus edwardsii*, at Kaikoura, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **22**, 613–16.
- Booth, J.D. & Kittaka, J. (2000) Spiny lobster growout. In: B.F. Phillips and J. Kittaka (Eds) *Spiny Lobsters: Fisheries and Culture* (2nd edn). Blackwell Science, Oxford. pp. 556–85.
- Booth, J.D., Carruthers, A.D., Bolt, C.D. & Stewart, R.A. (1991) Measuring depth of settlement in the red rock lobster, Jasus edwardsii. New Zealand Journal of Marine Freshwater Research, 25, 123–32.
- Booth, J.D., Stotter, D.R., Forman, J.S. & Bradford, E. (2001) Juvenile abundance both mirrors and masks a settlement pulse of the rock lobster *Jasus edwardsii*. *Marine and Freshwater Research*, **52**, 1067–75.
- Botsford, L.W., Smith, B.D. & Quinn, J.F. (1994) Bimodality in size distributions: the red sea urchin *Stronglyocentrotus franciscanus* as an example. *Ecological Applications*, **4**, 42–50.
- Boudreau, B., Bourget, E. & Simard, Y (1990) Benthic invertebrate larval response to substrate characteristics at settlement: shelter preferences of the American lobster *Homarus americanus*. *Marine Biology*, **106**, 191–8.
- Boudreau, B., Simard, Y. & Bourget, E. (1991) Behavioral responses of the planktonic stages of the American lobster Homarus americanus to thermal gradients and ecological implications. Marine Ecology Progress Series, 76, 12–23.
- Boudreau, B., Simard, Y. & Bourget, E. (1992) Influence of a thermocline on vertical distribution and settlement of post-larvae of the American lobster *Homarus americanus* Milne-Edwards. *Journal of Experimental Marine Biology and Ecology*, **162**, 35–49.
- Boudreau, B., Bourget, E. & Simard, Y. (1993) Effect of age, injury, and predator odors on settlement and shelter selection by lobster *Homarus americanus* postlarvae. *Marine Ecology Progress Series*, **93**, 119–29.
- Breen, P.A. & Booth, J.D. (1989) Puerulus and juvenile abundance in the rock lobster *Jasus edwardsii* at Stewart Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **23**, 519–23.
- Briones-Fourzán, P. (1995) Diferencias y similitudes enter *Panulirus argus* y *P. guttaus*, does especies communes en el Caribe mexicano. *Revista Cubanos Investigaciones Pesquderos*, **19**, 14–20.
- Briones-Fourzán, P. & Lozano-Álvarez, E. (2001) Effects of artificial shelters (casitas) on the abundance and biomass of juvenile spiny lobsters *Panulirus argus* in a habitat-limited tropical reef lagoon. *Marine Ecology Progress Series*, 221, 221–32.
- Briones-Fourzán, P., Lara, V.C.F. de, Lozano-Álvarez, E. & Estrada-Olivo, J. (2003) Feeding ecology of the three juvenile phases of the spiny lobster *Panulirus argus* in a tropical reef lagoon. *Marine Biology*, **142**, 855–65.
- Butler, M.J., IV (2003) Incorporating ecological process and environmental change into spiny lobster population models using a spatially-explicit, individual-based approach. *Fisheries Research*, **65**, 63–79.
- Butler, M.J., IV & Herrnkind, W.F. (1992a) Are artificial Witham surface collectors adequate indicators of Caribbean spiny lobster recruitment? *Proceedings Gulf Caribbean Fisheries Institute*, 42, 135–8.
- Butler, M.J., IV & Herrnkind, W.F. (1992b) Spiny lobster recruitment in south Florida: quantitative experiments and management implications. *Proceedings Gulf Caribbean Fisheries Institute*, 41, 508–15.
- Butler, M.J., IV & Herrnkind, W.F. (1997) A test of recruitment limitation and the potential for artificial enhancement of spiny lobster populations in Florida. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 452–63.
- Butler, M.J., IV, Hunt, J.H., Herrnkind, W.F., Matthews, T., Childress, M., Bertelsen, R., Sharp, W., Field, J.M. & Marshall, H. (1995) Cascading disturbances in Florida Bay, USA: cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobster *Panulirus argus. Marine Ecology Progress Series*, **129**, 119–25.
- Butler, M.J., IV, Herrnkind, W.F & Hunt, J.H. (1997) Factors affecting the recruitment of juvenile Caribbean spiny lobsters dwelling in macroalgae. *Bulletin of Marine Science*, **61**, 3–19.
- Butler, M.J., IV, MacDiarmid, A.B. & Booth, J.D. (1999) Ontogenetic changes in social aggregation and its adaptive value for spiny lobsters in New Zealand. *Marine Ecology Progress Series*, 188, 179–91.
- Butler, M.J., IV, Dolan, T., Herrnkind, W. & Hunt, J. (2001) Modeling the effect of spatial variation in postlarval supply and habitat structure on recruitment of Caribbean spiny lobster. *Marine and Freshwater Research*, **52**, 1243–53.
- Butler, M.J., IV, Dolan, T., Hunt, J.H., Herrnkind, W.F. & Rose, K. (2005) Recruitment in degraded marine habitats: a spatially-explicit, individual-based model for spiny lobster. *Ecological Applications*, **15**, 902–18.

- Caddy, J. (1986) Modelling stock-recruitment processes in crustacea: some practical and theoretical perspectives. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 2330–44.
- Campbell, A. (1986) Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, Eastern Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 2197–205.
- Campbell, A. (1989) Dispersal of American lobsters, *Homarus americanus*, tagged off southern Nova Scotia. *Cana*dian Journal of Fisheries and Aquatic Sciences, 46, 1842–4.
- Campbell, A. & Pezzack, D. (1986) Relative egg production and abundance of berried lobsters, *Homarus americanus*, in the Bay of Fundy and off southwestern Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 2190–6.
- Campbell, A. & Stasko, A.B. (1985) Movements of tagged American lobsters, *Homarus americanus*, off southwestern Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences*, **42**, 229–38.
- Caputi, N., Brown, R.S. & Chubb, C.F. (1995) Regional prediction of the western rock lobster, *Panulirus cygnus*, commercial catch in Western Australia. *Crustaceana*, **68** (2), 245–56.
- Caputi, N., Chubb, C., Melville-Smith, R., Pearce, A. & Griffin, D. (2003) Review of relationships between life history stages of the western rock lobster, *Panulirus cygnus*, in Western Australia. *Fisheries Research*, **65**, 47–61.
- Castaneda-Fernadez, V., Butler, M.J., IV, Hernandez-Vazquez, S., del Próo, S.G. & Serviere-Zaragoza, E. (2005) Determination of preferred habitats of early benthic juvenile California spiny lobster *Panulirus interruptus* on the Pacific coast of Baja California Sur, Mexico. *New Zealand Journal of Marine and Freshwater Research*, **56**, 1–9.
- Chapman, C.J. (1980) Ecology of juvenile and adult *Nephrops*. In: J.S. Cobb & B.F. Phillips (Eds) *The Biology and Management of Lobsters*. Academic Press, New York. pp. 143–78.
- Chapman, C.J. & Rice, A.L. (1971) Some direct observations on the ecology and behavior of the Norway lobster Nephrops norvegicus. Marine Biology, 10, 321–9.
- Chiappone, M. & Sealey, K.M.S. (2000) Marine reserve design criteria and measures of success: lessons learned from the Exuma Cays Land and Sea Park, Bahamas. *Bulletin Marine Science*, **66** (3), 691–705.
- Childress, M.J. (1995) Ontogeny and Evolution of Gregarious Behavior in Juvenile Caribbean Spiny Lobster, *Panulirus argus*. PhD dissertation, Florida State University, Florida.
- Childress, M.J. (1997) Marine reserves and their effects on lobster populations: report from a workshop. *Marine and Freshwater Research*, **48**, 1111–14.
- Childress, M.J. & Herrnkind, W.F. (1994) The behaviour of juvenile Caribbean spiny lobster in Florida Bay: seasonality, ontogeny, and sociality. *Bulletin Marine Science*, **54**, 819–27.
- Childress, M.J. & Herrnkind, W.F. (1996) The ontogeny of social behaviour among juvenile Caribbean spiny lobsters. *Animal Behaviour*, **51**, 675–87.
- Childress, M. & Herrnkind, W.F. (1997) Den sharing by juvenile spiny lobsters (*Panulirus argus*) in nursery habitat. *Marine and Freshwater Research*, **48**, 751–8.
- Childress, M. & Herrnkind, W.F. (2001a) The guide effect influence on the gregariousness of juvenile Caribbean spiny lobsters. *Animal Behaviour* **62**, 465–72.
- Childress, M. & Herrnkind, W.F. (2001b) The influence of conspecifics on the ontogenetic habitat shift of juvenile Caribbean spiny lobsters. *Marine and Freshwater Research*, **52** (8), 1077–84.
- Chiswell, S.M. & Booth, J.D. (1999) Rock lobster *Jasus edwardsii* larval retention by the Wairarapa Eddy off New Zealand. *Marine Ecology Progress Series*, **183**, 227–40.
- Chittleborough, R.G. & Phillips, B.F. (1975) Fluctuations of year-class strength and recruitment in the western rock lobster *Panulirus longipes* (Milne-Edwards). *Australian Journal of Marine and Freshwater Research*, 26, 317–28.
- Chubb, C.F. (2000) Reproductive biology: issues for management. In: B.F. Phillips and J. Kittaka (Eds) *Spiny Lobsters: Fisheries and Culture* (2nd edn). Blackwell Science, Oxford. pp. 245–77.
- Cobb, J. (1971) The shelter-related behaviour of the lobster, Homarus americanus. Ecology, 52, 108-15.
- Cobb, J.S. (1977) Review of the habitat behaviour of the clawed lobsters (*Homarus* and *Nephrops*). In: B.F. Phillips & J.S. Cobb (Eds) *Division of Fisheries and Oceanography Circular 7*. Commonwealth Scientific and Industrial Research Organization, Melbourne, Australia. pp. 143–57.

- Cobb, J.S. & Phillips, B.F. (Eds) (1980) *The Biology and Management of Lobsters*, Vols 1 and 2. Academic Press, New York.
- Cobb, J.S. & Wahle, R.A. (1994) Early life history and recruitment processes of clawed lobsters. *Crustaceana*, **67**, 1–25.
- Cobb, J.S. & Wang, D. (1985) Fisheries biology of lobsters and crayfishes. In: A.J. Provenzano (Ed.) The Biology of Crustacea, Vol. 10. Academic Press, New York. pp. 167–247.
- Cockcroft, A.C. (2001) *Jasus lalandii* 'walkouts' or mass strandings in South Africa during the 1990's: an overview. *Marine and Freshwater Research*, **52**, 1085–94.
- Cole, R.G., Ayling, T.M. & Creese, R.G. (1990) Effects of marine reserve protection at Goat Island, northern New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **24** (2), 197–210.
- Connell, J.H. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist*, **122**, 661–96.
- Cowen, D.F., Solow A.R. & Beet, A. (2001) Patterns in abundance and growth of juvenile lobster, *Homarus americanus*. *Marine and Freshwater Research*, **52**, 1085–94.
- Cox, C., Hunt, J.H., Lyons, W.G. & Davis, G.E. (1997) Nocturnal foraging of the Caribbean spiny lobster (*Panulirus argus*) on offshore reefs of Florida, USA. *Marine and Freshwater Research*, **48**, 671–9.
- Cruz, R., Brito, R., Diaz, E. & Lalana, R. (1986) Ecology of the lobster (*Panulirus argus*) at the Southeast of the Juventud Island. 1. Settlement of artificial reefs. *Revisita Investigaciones Marinas*, **7** (3), 3–17.
- Cruz, R., Leon, M.E. de & Puga, R. (1995a) Prediction of commercial catches of the spiny lobster *Panulirus argus* in the Gulf of Batabano, Cuba. *Crustaceana*, **68**, 238–44.
- Cruz, R., Puga, R. & Leon, M.E. (1995b) Catch forecast of lobster *Panulirus argus* by fishing regions, Cuba. *Revisita Cubano Investigaciones Pesqueros*, **19** (1), 51–9.
- Cruz, R., Diaz, E., Baez, M. & Adriano, R. (2001) Variability in recruitment of multiple life stages of the Caribbean spiny lobster, *Panulirus argus*, in the Gulf of Batabano, Cuba. *Marine and Freshwater Research*, **52**, 1263–71.
- Davidson, R.J., Villouta, E., Cole, R.G. & Barrier, R.G.F. (2002) Effects of marine reserve protection on spiny lobster (*Jasus edwardsii*) abundance and size on Tonga Island Marine Reserve, New Zealand. Aquatic Conservation Marine Freshwater Ecosystems, 12 (2), 213–27.
- Davis, G.E. (1977) Effects of recreational harvest on a spiny lobster, *Panulirus argus*, population. *Bulletin Marine Science*, 27, 223–36.
- Dayton, P.K., Tegner, M.J., Edwards, P.B. & Riser, K.L. (1998) Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecological Applications*, **8**, 309–22.
- Deblock, S., Williams, A. & Evans, L.H. (1990) Contribution a l'etude des Microphallidae Travassos 1920 (Trematoda). Description de *Thulakiotrema genitale* n. gen., n. sp., metacercaire parasite de langoustes australiennes. *Bulletin of the Museum of Natural History, Paris*, 12, 563–76.
- Debuse, V.J., Addison, J.T. & Reynolds, J.D. (2003) Effects of breeding site density on competition and sexual selection in the European lobster. *Behavioral Ecology*, 14, 396–402.
- DeMartini, E.E., Ellis, D.M. & Honda, V.A. (1993) Comparisons of spiny lobster, *Panulirus marginatus*, fecundity, egg size, and spawning frequency before and after exploitation. *Fisheries Bulletin*, **91**, 1–7.
- Dennis, D.M., Skewes, T.D. & Pitcher, C.R. (1997) Habitat use and growth of juvenile ornate rock lobsters, *Panulirus ornatus* (Fabricius, 1798), in Torres Strait, Australia. *Marine and Freshwater Research*, 48, 663–70.
- Diaz, D., Mari, M., Abello, P. & Demestre, M. (2001) Settlement and juvenile habitat of the European spiny lobster Palinurus elephas (Crustacea: Decapoda: Palinuridae) in the western Mediterranean Sea. Science Marinas Barcelona, 65 (4), 347–56.
- Díaz-Arredondo, M.A. & Guzmán-del-Próo, S.A. (1995) Feeding habits of the spiny lobster (*Panulirus interruptus* Randall, 1840) in Bahía Tortugas, Baja California Sur. *Ciencias Marinas*, **21**, 439–62.
- Diggles, B.K., Moss, G.A., Carson, J. & Anderson, C.D. (2000) Luminous vibriosis in rock lobster *Jasus verreauxi* (Decapoda: Palinuridae) phyllosoma larvae associated with infection by *Vibrio harveyi*. *Diseases of Aquatic Organisms*, **43**, 127–37.

- Edgar, G.J. (1990) Predator-prey interactions in seagrass beds. I. The influence of macrofaunal abundance and sizestructure on the diet and growth of the Western rock lobster *Panulirus cygnus* George. *Journal of Experimental Marine Biology and Ecology*, **139**, 1–22.
- Edmunds, M. (1995) The Ecology of the Juvenile Southern Rock Lobster, *Jasus edwardsii* (Hutton 1875)(Palinuridae). PhD dissertation, University of Tasmania, Hobart, Australia.
- Eggleston, D.B. & Dahlgren, C.P. (2001) Distribution and abundance of Caribbean spiny lobsters in the Key West National Wildlife Refuge: relationship to habitat features and impact of an intensive recreational fishery. *Marine and Freshwater Research*, **52**, 1567–76.
- Eggleston, D.B. & Lipcius, R.N. (1992) Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. *Ecology*, 73, 992–1011.
- Eggleston, D., Lipcius, R., Coba-Centina, L., & Miller, D. (1990) Shelter scaling regulates survival of juvenile spiny lobster, *Panulirus argus. Marine Ecology Progress Series*, 62, 79–88.
- Eggleston, D., Lipcius, R. & Grover, J.J. (1997) Predator and shelter-size effects on coral reef fishand spiny lobster prey. *Marine Ecology Progress Series*, **149**, 43–59.
- Eggleston, D.B., Lipcius, R.N., Marshall, L.S., Jr & Ratchford, S.G. (1998) Spatiotemporal variation in postlarval recruitment of the Caribbean spiny lobster in the central Bahamas: lunar and seasonal periodicity, spatial coherence, and wind forcing. *Marine Ecology Progress Series*, **174**, 33–49.
- Engle, J.M. (1979) Ecology and Growth of Juvenile California Spiny Lobster, *Panulirus interruptus* (Randall). PhD dissertation, University of Southern California, Los Angeles.
- Estrella, B.T. & Morrissey, T.D. (1997) Seasonal movement of offshore American lobster, *Homarus americanus*, tagged along the eastern shore of Cape Cod, Massachusetts. *Fishery Bulletin*, **95**, 466–76.
- Evans, L.H., Jones, J.B. & Brock, J.A. (2000) Diseases of spiny lobsters. In: B.F. Phillips and J. Kittaka (Eds) *Spiny Lobsters: Fisheries and Culture* (2nd edn). Blackwell Science, Oxford. pp. 586–600.
- Factor, J.R. (Ed.) (1995) Biology of the Lobster, Homarus americanus. Academic Press, San Diego.
- FAO (Food and Agriculture Organization) (2004) FAOSTAT data, 2004. http://faostat.fac.org/faostat (last updated February 2005).
- Feldman, R., Bishop, G. & Kammer, T.W. (1977) Macrurous decapods from the Bearpaw Shale (Cretaceous: Campanian) of Northeastern Montana. *Journal of Paleontology*, **51**, 1161–80.
- Field, J.M. & Butler, M.J., IV (1994) The influence of temperature, salinity, and larval transport on the distribution of juvenile spiny lobsters, *Panulirus argus*, in Florida Bay. *Crustaceana*, **67**, 26–45.
- Fogarty, M.J. (1998) Implications of migration and larval interchange in American lobster (*Homarus americanus*) stocks: spatial structure and resilience. *Canadian Special Publications Fisheries and Aquatic Sciences*, **125**, 273–83.
- Fitzpatrick, J.F., Jernakoff, P. & Phillips, B.F. (1989) An Investigation of the Habitat Requirements of the Juvenile Stocks of the Western Rock Lobster. Final Report to the Fisheries Industrial Research and Development Council, Grant 86/83.
- Forcucci, D.M., Butler, M.J., IV & Hunt, J.H. (1994) Growth and population dynamics of juvenile Caribbean spiny lobster, *Panulirus argus*, in Florida Bay, FL (USA). *Bulletin of Marine Science*, **54**, 805–18.
- Ford, R.F., Phillips, B.F. & Joll, J.M. (1988) Experimental manipulation of population density and its effects on growth and mortality of juvenile western rock lobsters, *Panulirus cygnus* George. *Fishery Bulletin*, 86, 773–87.
- Fourqurean, J.W. & Robblee, M.B. (1999) Florida Bay: a history of recent ecological changes. *Estuaries*, **22**, 345–57.
- Gardner, C., Frusher, S.D., Kennedy, R.B. & Cawthorn, A. (2001) Relationship between settlement of southern rock lobster pueruli, *Jasus edwardsii*, and recruitment to the fishery in Tasmania, Australia. *Marine and Freshwater Research*, **52**, 1271–5.
- George, R.W. (1968) Tropical spiny lobsters, *Panulirus* spp., of Western Australia (and the indo-west Pacific). *Journal Royal Society of Western Australia*, **51**, 33–8.
- George, R.W. & Main A.R. (1967) The evolution of spiny lobsters (Palinuridae): a study of evolution in the marine environment. *Evolution*, **21**, 803–20.

302 Lobsters: Biology, Management, Aquaculture and Fisheries

- Goñi, R., Renones, O. & Quetglas, A. (2001) Dynamics of a protected Western Mediterranean population of the European spiny lobster *Palinurus elephas* (Fabricus, 1787) assessed by trap surveys. *Marine and Freshwater Research*, 52, 1577–87.
- Gregory, D.R. & Labisky, R.F. (1986) Movements of the spiny lobster *Panulirus argus* in south Florida. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 2228–34.
- Griffin, D.A., Wilkin, J.L., Chubb, C.B., Pearce, A.F. & Caputi, N. (2001) Ocean currents and the larval phase of Australian western rock lobster, *Panulirus cygnus. Marine and Freshwater Research*, **52**, 1187–99.
- Griffiths, C.L. & Seiderer, J.L. (1980) Rock-lobsters and mussels limitations and preferences in a predator-prey interaction. *Journal of Experimental Marine Biology and Ecology*, 44, 95–109.
- Groeneveld, J.C. (2000) Stock assessment, ecology and economics as criteria for choosing between trap and trawl fisheries for spiny lobster *Palinurus delagoae*. *Fisheries Research*, **48**, 141–55.
- Groeneveld, J.C. & Branch, G.M. (2002) Long-distance migration of South African deep-water rock lobster *Palinurus gilchristi. Marine Ecology Progress Series*, 232, 225–38.
- Harding, G.C., Drinkwater, K.F. & Vass, W.P. (1983) Factors influencing the size of American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St Lawrence, and Gulf of Maine: a new synthesis. *Canadian Journal of Fisheries and Aquatic Sciences*, 40, 168–84.
- Harding, G.C., Kenchington, E.L., Bird, C.J., Pezzack, D.S. & Landry, D.C. (1997) Genetic relationships among subpopulations of the American lobster (*Homarus americanus*) as revealed by random amplification polymorphic DNA. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 1762–71.
- Heck, K.L., Jr, Hays, G. & Orth, R.J. (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series*, 253, 123–36.
- Heisig, J.S. (2003) Male Reproductive Dynamics in the Caribbean Spiny Lobster, *Panulirus argus*. MS thesis, Department of Biological Sciences, Old Dominion University, Norfolk, VA.
- Herrick, F.H. (1909) Natural history of the American lobster. Bulletin of the Bureau of Fisheries, 29, 153-408.
- Herrnkind, W.F. (1980) Spiny lobsters: patterns of movement. In: J.S. Cobb & B.F. Phillips (Eds) *The Biology and Management of Lobsters*, *1, Physiology and Behavior*. Academic Press, New York. pp. 349–407.
- Herrnkind, W. (1983) Movement patterns and orientation of Crustacea. In: F. Vernberg & W. Vernberg (Eds) Biology of Crustacea, 5, Behavior and Ecology of Crustacea. Academic Press, New York. pp. 41–105.
- Herrnkind, W. (1985) Evolution and mechanisms of mass single-file migration in spiny lobster: synopsis. Contributions in Marine Science (Special Symposium Volume), University of Texas, 27, 197–211.
- Herrnkind, W.F. & Butler, M.J., IV (1986) Factors regulating settlement and microhabitat use by juvenile spiny lobsters, *Panulirus argus. Marine Ecology Progress Series*, 34, 23–30.
- Herrnkind, W.F. & Butler, M.J., IV (1994) Settlement of spiny lobsters, *Panulirus argus* in Florida: pattern without predictability. *Crustaceana*, 67, 46–64.
- Herrnkind, W.F. & Cummings, W.C. (1964) Single file migrations of the spiny lobster *Panulirus argus. Bull Mar Sci Gulf and Carib*, **14** (1), 123–5.
- Herrnkind, W.F. & McLean, R. (1971) Field studies of orientation, homing, and mass emigration in the spiny lobster, *Panulirus argus. Annals of the New York Academy of Sciences*, **188**, 359–77.
- Herrnkind, W.F., VanDerwalker, J. & Barr, L. (1975) Population dynamics, ecology and behaviour of spiny lobster, *Panulirus argus*, of St John, US Virgin Islands: habitation and pattern of movements. Results of the TEKTITE Program, Vol. 2, *Bulletin of Natural History Museum of Los Angeles Count*, **20**, 31–45.
- Herrnkind, W.F., Butler, M.J., IV, Hunt, J.H. & Childress, M. (1997) The role of physical refugia: implications from a mass sponge die-off in a lobster nursery. *Marine and Freshwater Research*, **48**, 759–70.
- Herrnkind, W.F., Butler, M.J., IV & Tankersley, R.A. (1988) The effects of siltation on the recruitment of spiny lobsters (*Panulirus argus*) in south Florida. *Fisheries Bulletin*, 86, 331–8.
- Herrnkind, W.F., Butler, M.J., IV & Hunt, J.H. (1999) A case for shelter replacement in a disturbed spiny lobster nursery in Florida: why basic research had to come first. *Fish Habitat: Essential Fish Habitat and Rehabilitation*, *American Fisheries Society Symposium*, 22, 421–37.
- Herrnkind, W.F., Childress, M. & Lavalli, K. (2001) Cooperative defence and other benefits among exposed spiny lobsters: inferences from group size and behaviour. *Marine and Freshwater Research*, **52** (8), 1113–24.

- Hill, A.E. (1990) Pelagic dispersal of Norway lobster (*Nephrops norvegicus*) larvae examined using an advectiondiffusion-mortality model. *Marine Ecology Progress Series*, **64**, 217–26.
- Hill, A.E. & White, R.G. (1990) The dynamics of Norway lobster (*Nephrops norvegicus* L.) populations on isolated mud patches. *Journal of Conservation and International Exploration*, **46**, 167–74.
- Holthius, L.B. (1991) *Marine Lobsters of the World*. FAO Species Catalogue, Vol. 13. FAO Fisheries Synopsis, No. 125. FAO, Rome.
- Holthuis, L.B. (1995) *Marine Lobsters of the World of Interest to Fisheries*. FAO Species Catalogue 13. UNESCO Publishing, Paris, France.

Howard, R.K. (1988) Fish predators of western rock lobster (*Panulirus cygnus* George) in nearshore nursery habitat. *Australian Journal of Marine and Freshwater Research*, **39**, 307–16.

Huntsman, A.G. (1923) Natural lobster breeding. Bulletin of the Biological Board of Canada, 5, 3–11.

- Incze, L.S. & Naimie, C.E. (2000) Modelling the transport of lobster (*Homarus americanus*) larvae and postlarvae in the Gulf of Maine. *Fisheries Oceanography*, **9**, 99–113.
- Incze, L.S. & Wahle, R.A. (1991) Recruitment from pelagic to early benthic phase in lobsters *Homarus americanus*. *Marine Ecology Progress Series*, **79**, 77–87.
- Incze, L.S., Wahle, R.A. & Cobb, J.S. (1997) Quantitative relationships between postlarval production and benthic recruitment in lobsters, *Homarus americanus. Marine and Freshwater Research*, **48**, 729–44.
- Incze, L., Wahle, R. & Palma, A.T. (2000) Advection and settlement rates in a benthic invertebrate: recruitment to the first benthic stage *Homarus americanus*. *ICES Journal Marine Sciences*, **57**, 430–7.
- Iversen, E.S. & Beardsley, G.L. (1976) Shell disease in crustaceans indigenous to South Florida. Progressive Fish-Culturist, 38, 195–6.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J. & Bradbury, R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, **293**, 629–38.
- Jennings, S. & Kaiser, M.J. (1998) Effect of fishing on marine ecosystems. Advances in Marine Biology, 34, 203–354.
- Jensen, A.C., Collins, K.J., Free, E.K. & Bannister, R.C.A. (1994) Lobster (*Homarus gammarus*) movement on an artificial reef: the potential use of artificial reefs for stock enhancement. *Crustaceana*, **67**, 198–211.
- Jernakoff, P. (1987) Foraging patterns of juvenile western rock lobsters *Panulirus cygnus* George. *Journal of Experimental Marine Biology and Ecology*, **113**, 125–44.
- Jernakoff, P. (1990) Distribution of newly settled western rock lobsters *Panulirus cygnus*. *Marine Ecology Progress* Series, **66**, 63–74.
- Jernakoff, P., Phillips, B.F. & Maller, R.A. (1987) A quantitative study of nocturnal foraging distances of the western rock lobster *Panulirus cygnus* George. *Journal of Experimental Marine Biology and Ecology*, **113**, 9–21.
- Jernakoff, P., Phillips, B.F. & Fitzpatrick J.J. (1993) The diet of post puerulus Western rock lobster *Panulirus cygnus* (George) at seven Mile Beach, Western Australia. *Australian Journal of Marine and Freshwater Research*, **44**, 649–55.
- Jernakoff, P., Phillips, B.F. & DeBoer, E. (1994) Density and growth in populations of juvenile western rock lobsters, *Panulirus cygnus* (George). *Australian Journal of Marine and Freshwater Research*, **45**, 69–81.
- Joll, L.M. & Phillips, B.F. (1984) Natural diet and growth of juvenile Western rock lobster *Panulirus cygnus. Journal* of *Experimental Marine Biology and Ecology*, **75**, 145–69.
- Jørstad, K.E., Prodöhl, P.A., Agnalt, A.-L., Hughes, M., Apostolidis, A.P., Triantafyllidis, A., Farestveit, E., Kristiansen, T.S., Mercer, J. & Svåsand, T. (2004) Sub-arctic populations of European lobster, *Homarus gammarus*, in Northern Norway. *Environmental Biology of Fishes*. 69, 223–31.
- Kanciruk, P. (1980). Ecology of juvenile and adult Palinuridae (spiny lobsters). In: J.S. Cobb & B.F. Phillips (Eds) The Biology and Management of Lobsters, 2, Ecology and Management. Academic Press, New York. pp. 59–96.
- Katz, C.H., Cobb, J.S. & Spaulding M. (1994) Larval behaviour, hydrodynamic transport and potential offshore recruitment in the American lobster, *Homarus americanus. Marine Ecology Progress Series*, **103**, 265–73.
- Kelley, J. (1987) Sedimentary environments along Maine's estuarine coastline. In: D.M. Fitzgerald & P.S. Rosen (Eds) A Treatise on Glaciated Coasts. Academic Press, New York. pp. 151–76.

- Kelly, S. & MacDiarmid, A.B. (2003) Movement patterns of mature spiny lobsters, *Jasus edwardsii*, from a marine reserve. *New Zealand Journal of Marine and Freshwater Research*, **37** (1), 149–58.
- Kelly, S., MacDiarmid, A.B. & Babcock, R.C. (1999) Characteristics of spiny lobster, *Jasus edwardsii*, aggregations in exposed reef and sandy areas. *Marine and Freshwater Research*, **50**, 409–16.
- Kelly, S., Scott, D., MacDiarmid, A.B. & Babcock, R.C. (2000) Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. *Biological Conservation*, **92** (3), 359–69.
- Kelly, S., Scott, D. & MacDiarmid, A.B. (2002) The value of a spillover fishery for spiny lobsters around a marine reserve in northern New Zealand. *Coastal Management*, **30** (2), 153–66.
- Kensler, C.B. (1967) Notes on laboratory rearing of juvenile spiny lobsters, Jasus edwardsii (Hutton) (Crustacea: Decapoda: Palinuridae). New Zealand Journal Marine Freshwater Research, 1, 71–5.
- Kittaka, J. & Abrunhosa, F.A. (1997) Characteristics of palinurids (Decapoda: Crustacea) in larval culture. *Hydrobiologia*, 358, 305–11.
- Krouse, J.S. (1980) Summary of lobster, *Homarus americanus*, tagging studies in American waters (1898–1978). *Canadian Technical Report Fisheries Aquatic Sciences*, **932**, 135–51.
- Kuthalingam, M.D.K., Luther, F. & Lazarus, S. (1980) Rearing of early juveniles of spiny lobster *Panulirus versicolor* (Latrielle) with notes on lobster fishery in Vizhinjam area. *Indian Journal of Fisheries*, **27**, 17–23.
- Lear, J.A. (2004) Strong Interactions Between Juvenile Caribbean Spiny Lobster (*Panulirus argus*) and Caribbean Reef Octopus (*Octopus briareus*) in the Florida Keys, FL. MS thesis, Old Dominion University, Norfolk, VA.

Lewis, R.K. (1977) Rock lobster puerulus settlement in the southeast. SAFIC, 13, 9-10.

- Lindberg, R.G. (1955) Growth, population dynamics and behavior in the spiny lobster, *Panulirus interruptus* (Randall). University of California Berkeley Publications in Zoology, **59**, 157–248.
- Linnane, A., Ball, B., Munday, B. & Mercer, J.P. (2000a) On the occurrence of juvenile lobster *Homarus gammarus* in intertidal habitat. *Journal of the Marine Biological Association of the United Kingdom*, **80**, 375–6.
- Linnane, A., Mazzoni, D. & Mercer, J.P. (2000b) A long-term mesocosms study on the settlement and survival of juvenile European lobster *Homarus gammarus* L. in four natural substrata. *Journal of Experimental Marine Biology and Ecology*, 249, 51–64.
- Linnane, A., Ball, B., Mercer, J.P., Browne, R., van der Meeren, G., Ringvold, H., Bannister, C., Mazzoni, D. & Munday, B. (2001) Searching for the early benthic phase (EBP) of the European lobster: a trans-European study of cobble fauna. *Hydrobiologia*, 465, 63–72.
- Lipcius, R.N., Stockhausen, W.T., Eggleston, D.B., Marshall, L.S., Jr & Hickey, B. (1997) Hydrodynamic decoupling of recruitment, habitat quality, and adult abundance in the Caribbean spiny lobster: source-sink dynamics? *Marine* and Freshwater Research, 48, 807–16.
- Lipcius, R.N., Eggleston, D.B., Miller, D.L. & Luhrs, T.C. (1998) The habitat-survival function for Caribbean spiny lobster: an inverted size effect and non-linearity in mixed algal and seagrass habitats. *Marine and Freshwater Research*, 49, 807–16.
- Lipcius, R.N., Stockhausen, W.T. & Eggleston, D.B. (2001) Marine reserves for Caribbean spiny lobster: empirical evaluation and theoretical metapopulations recruitment dynamics. *Marine and Freshwater Research*, **52**, 1589–98.
- Losada-Torteson, V. & Posada, J.M. (2001) Using tyres as shelters for the protection of juvenile spiny lobsters, *Panulirus argus*, or as a fishing gear for adults. *Marine and Freshwater Research*, **52**, 1445–50.
- Lotze, H.K. & Milewski, I. (2004) Two centuries of multiple human impacts and successive changes in a North Atlantic food web. *Ecological Applications*, 14, 1428–77.
- Lozano-Álvarez, E. & Aramoni-Serrano, G. (1996) Alimentación y estado nutricional de las langostas Panulirus inflatus y Panulirus gracilis (Decapoda: Palinuridae) en Guerrero, México. Revista de Biología Tropical, 44, 453–61.
- Lozano-Álvarez, E. & Briones-Fourzán, P. (2001) Den choice and occupation patterns of shelters by two sympatric lobster species, *Panulirus argus* and *Panulirus guttatus*, under experimental conditions. *Marine and Freshwater Research*, 52, 1145–55.
- Lozano-Álvarez, E., Briones-Fourzán, P. & Negrete-Soto, F. (1994) An evaluation of concrete block structures as shelter for juvenile Caribbean spiny lobsters, *Panulirus argus. Bulletin of Marine Science*, **55**, 351–62.

- Lozano-Álvarez, E., Briones-Fourzán, P. & Ramos-Aguilar, M.E. (2003) Distribution, shelter fidelity and movements of subadult spiny lobsters (*Panulirus argus*) in areas with artificial shelters (casitas). *Journal of Shellfish Research*, 22, 533–40.
- Lynch T.C. & Philips, E.J. (2000) Filtration of the bloom-forming cyanobacteria *Synechococcus* by three sponge species from Florida Bay, USA. *Bulletin of Marine Science*, **67**, 923–1213.
- MacDiarmid, A.B. (1989) Moulting and reproduction of the spiny lobster *Jasus edwardsii* (Decapoda; Palinuridae) in northern New Zealand. *Marine Biology*, **103**, 303–10.
- MacDiarmid, A.B. (1994) Cohabitation in the spiny lobster Jasus edwardsii. Crustaceana, 66, 341-55.
- MacDiarmid, A.B. & Breen, P.A. (1993) Spiny lobster population changes in a marine reserve. In: C.N. Battershil, D.R. Schiel, G.P. Jones, R.G. Creese, & A.B. MacDiarmid (Eds) *Proceedings of the Second International Temperate Reef Symposium*. NIWA Marine Publications, Wellington, New Zealand. pp. 47–56.
- MacDiarmid, A.B. & Butler, M.J., IV (1999) Sperm economy and limitation in spiny lobsters. *Behavioral Ecology* and Sociobiology, 46, 14–24.
- MacDonald, C.D., Jazwinski, S.C. & Prescott, J.H. (1984). Queuing behaviour of the Hawaiian spiny lobster Panulirus marginatus. Bulletin of Marine Science, 35, 111–14.
- Malpass, W. (1992) The Role of Small Predatory Finfish in the Structure of Coastal Benthic Communities in Maine. MS thesis, Department of Oceanography, University of Maine.
- Marx, J.M. & Herrnkind, W.F. (1985a) Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for juvenile spiny lobsters, *Panulirus argus. Bulletin of Marine Science*, **36**, 423–31.
- Marx, J. & Herrnkind, W.F. (1985b) Factors regulating microhabitat use by young juvenile spiny lobsters, *Panulirus argus:* food and shelter. *Journal of Crustacean Biology*, **5**, 650–7.
- Mayfield, S., Branch, G.M. & Cockcroft, A.C. (2000) Relationships among diet, growth rate, and food availability for the South African rock lobster, *Jasus lalandii* (Decapoda; Palinuridea). *Crustaceana*, **73**, 815–34.
- Maynou, F.X., Sardà, F. & Conan, G.Y. (1998) Assessment of the spatial structure and biomass evaluation of *Nephrops norvegicus* (L.) populations in the northwestern Mediterranean by geostatistics. *ICES Journal of Marine Science*, 55, 102–20.
- McAleer, R. (1983) Black shell disease of the western rock lobster caused by *Fusarium solani*. Proceedings of the International Society of Human and Animal Mycology, **34**, 378–82.
- Melville-Smith, R., Cheng, Y.W. & Thomson, A.W. (2003) Factors affecting the colour change in 'white' western rock lobsters, *Panulirus cygnus. Journal of Experimental Marine Biology and Ecology*, **291**, 111–29.
- Mercer, J.P., Bannister, R.C.A., van der Meeren, G.I., Debuse, V., Mazzoni, D., Lovewell, S., Browne, R., Linnane, A. & Ball, B. (2001) An overview of LEAR (Lobster Ecology and Recruitment) project: results of field and experimental studies on the juvenile ecology of *Homarus gammarus* in cobble. *Marine and Freshwater Research*, 52, 1291–301.
- Miller, C.F. & Reeves, A. (2000) Efficient sampling design for larvae of American lobster. *Journal of Plankton Research*, 22, 1299–309.
- Mintz, J.D., Lipcius, R.N., Eggleston, D.B. & Seebo, M.S. (1994) Survival of juvenile Caribbean spiny lobster: effects of shelter size, geographic location, and conspecific abundance. *Marine Ecology Progress Series*, **112** (3), 255–66.
- Mouillot, D., Culioli, J-M. & Chi, T.D. (2002) Indicator species analysis as a test of non-random distibution of species in the context of marine protected areas. *Environmental Conservation*, **29** (3), 385–90.
- Myers, R.A. & Worm, B. (2003) Rapid worldwide depletion of predatory fish communities. *Nature*, 423, 280-3.
- National Research Council (1994) *Priorities for Coastal Ecosystem Science*. National Academy Press, Washington, DC.
- Nevitt, G., Pentcheff, N.D., Lohmann, K.J. & Zimmer, R.K. (2000) Den selection by the spiny lobster *Panulirus argus*: testing attraction to conspecifics odours in the field. *Marine Ecology Progress Series*, **203**, 225–31.
- Newman, G.G. & Pollock, D.E. (1974) Growth of the rock lobster *Jasus lalandii* and its relationship to benthos. *Marine Biology*, **24**, 339–46.
- Nichols, J.H. & Lovewell, S.J. (1987) Lobster larvae (*Homarus gammarus* L.) investigations in Bridlington Bay. Can quantitative sampling be confined to the neuston layer? *Journal of Natural History London*, **21**, 825–41.

- Nizinski, M. (1998) Caribbean Spiny Lobster and their Molluscan Prey: Are Top-Down Forces Key in Structuring Prey Assemblages in a Florida Bay Seagrass System? PhD dissertation, College of William and Mary, Williamsburg, VA.
- Norman, C.P. & Morikawa, Y. (1996) Rock face incline and height above seabed of holes used as shelters by pueruli and juvenile Japanese spiny lobsters *Panulirus japonicus*. *Crustacean Research*, **25**, 121–8.
- Norman, C.P., Yamakawa, H. & Yoshimura, T. (1994) Habitat selection, growth rate and density of juvenile *Panulirus japonicus* (Von Seibold, 1824) (Decapoda, Palinuridae) at Banda, Chiba Prefecture, Japan. *Crustaceana*, **66** (3), 366–83.
- Olsen, D.A. & Koblick, I.G. (1975) Population dynamics, ecology and behaviour of spiny lobster, *Panulirus argus*, of St John, US Virgin Islands: II Growth and mortality. Results of the TEKTITE Program, Vol. 2, *Bulletin of Natural History Museum Los Angeles County* 20, 17–21.
- Palma, A.T., Wahle, R.A. & Steneck, R.S. (1998) Different early post-settlement strategies between American lobsters *Homarus americanus* and rock crabs *Cancer irroratus* in the Gulf of Maine. *Marine Ecology Progress Series*, 162, 215–25.
- Palma, A.T., Steneck, R.S. & Wilson, C. (1999) Settlement-driven, multiscale demographic patterns of large benthic decapods in the Gulf of Maine. *Journal of Experimental Marine Biology and Ecology*, **241**, 107–36.
- Parrish, F.A. & Polovina, J.J. (1994) Habitat thresholds and bottlenecks in production of the spiny lobster (*Panulirus marginatus*) in the northwestern Hawaiian Islands. *Bulletin of Marine Science*, **54**, 151–63.
- Pauly, D., Christensen, V., Dalsgarrd, J., Froese, R. & Torres, F., Jr (1998). Fishing down Maine food webs. *Science*, **279**, 860–3.
- Philips, E.J., Badylak, S. & Lynch, T.C. (1999) Blooms of the picoplanktonic cyanobacterium *Synechococcus* in Florida Bay, a subtropical inner-shelf lagoon. *Limnology Oceanography*, **44**, 1166–75.
- Phillips, B.F. (1972) A semi-quantitative collector of the puerulus larvae of the western rock lobster *Panulirus lon-gipes cygnus* George (Decapoda, Palinuridae). *Crustaceana*, **22**, 147–54.
- Phillips, B.F. (1983) Migrations of pre-adult western rock lobsters, *Panulirus cygnus*, in Western Australia. *Marine Biology*, 76, 311–18.
- Phillips, B.F. (1986). Prediction of commercial catches of the western rock lobster *Panulirus cygnus* George. *Cana*dian Journal of Fisheries and Aquatic Sciences, 43, 2126–30.
- Phillips, B.F. (1990) Estimating the density and mortality of juvenile western rock lobsters (*Panulirus cygnus*) in nursery reefs. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 1330–8.
- Phillips, B.F. & Booth, J.D. (1994) Design, use and effectiveness of collectors for catching the puerulus stage of spiny lobsters. *Reviews Fish Biology*, 2, 255–89.
- Phillips, B.F. & Cobb, J.S. (1977) Workshop on Lobster and Rock Lobster Ecology and Physiology. Division of Fisheries and Oceanography Circular No. 7. CSIRO, Melbourne, Australia.
- Phillips, B.F. & Kittaka, J. (Eds) (2000) Spiny Lobsters: Fisheries and Culture (2nd edn). Blackwell Science, Oxford.
- Phillips, B.F., Melville-Smith, R. & Cheng, Y.W (2003) Measuring the effects of pueruli removals and habitat improvement in assessing sustainability of spiny lobster populations. *Fisheries Research*, **65**, 89–101.
- Pitcher, C.R., Skewes, T.D. & Dennis, D.M. (1992) *Research for Management of the Ornate Rock Lobster*, Panulirus ornatus, *Fishery in Torres Strait*. Report on CSIRO Research, 1987–1990. CSIRO, Australia.
- Pollock, D.E. (1973) Growth of juvenile rock lobster Jasus lalandii. Investigation Reports Sea Fisheries Branch South Africa, **106**, 1–16.
- Pollock, D.E. (1979) Predator-prey relationships between the rock lobster *Jasus lalandii* and the mussel *Aulacomya ater* at Robben Island on the Cape West Coast of Africa. *Marine Biology*, **52**, 347–56.
- Pollock, D.E. (1995) Changes in maturation sizes and ages in crustacean and fish populations. *South African Journal* of Marine Science, **5**, 99–103.
- Polovina, J.J. & Mitchum, G.T. (1994) Spiny lobster recruitment and sea level: results of a 1990 forecast. *Fishery Bulletin*, **92** (1), 203–5.
- Polovina, J.J., Haight, W.R., Moffitt, R.B. & Parrish, F.A. (1995) The role of benthic habitat, oceanography, and fishing on the population dynamics of the spiny lobster, *Panulirus marginatus* (Decapoda, Palinuridae) in the Hawaiian archipelago. *Crustaceana*, **68**, 203–12.

- Polovina, J.J., Kleiber, P. & Kabayashi, D.R. (1999) Application of Topex/Poseidon satellite altimetry to simulate transport dynamics of larvae of the spiny lobster (*Panulirus marginatus*) in the northwestern Hawaiian Islands, 1993–96. *Fishery Bulletin*, 97, 132–43.
- Porter, L., Butler, M. & Reeves, R.H. (2001) Normal bacterial flora of the spiny lobster *Panulirus argus* and its possible role in shell disease. *Marine and Freshwater Research*, **52**, 1401–6.
- Power, M.E. (1992) Top-down and bottom-up forces in food webs: do plants have primacy? Ecology, 73, 1733–46.

Prescott, J.H., Phillips, B.F. & Bell, R.S. (1986) Rock lobster research in Torres Strait. Australian Fisheries, 45, 2–4.

- Ratchford, S.G. & Eggleston, D.B. (1998) Size- and scale-dependent chemical attraction contribute to an ontogenetic shift in sociality. *Animal Behavior*, **56**, 1027–34.
- Rich, W.H. (1929) Fishing grounds of the Gulf of Maine. *Report of the United States Commissioner of Fisheries*, **1929**, 51–117.
- Robertson, D. (2001) Implications of the Target Area Hypothesis for the Population Dynamics of the Spotted Spiny Lobster, *Panulirus guttatus*. PhD dissertation, Old Dominion University, Norfolk, VA.
- Robertson, D.N. & Butler, M.J., IV (2003) Growth and size at maturity of the spotted spiny lobster, *Panulirus gut*tatus. Journal of Crustacean Biology, 23, 265–72.
- Robles, C.D. (1997) Changing recruitment in constant species assemblages: implications for predation theory in intertidal communities. *Ecology*, **78**, 1400–14.
- Robles, C.D., Sherwood-Stevens, R. & Alvarado, M. (1995) Responses of a key intertidal predator to varying recruitment of its prey. *Ecology*, 76, 565–79.
- Schmidt, R.S. (1982) Consequences of dissimilar defenses against predation in a subtidal marine community. *Ecology*, **63**, 1588–601.
- Schmidt, R.S. (1987) Indirect interactions between prey: apparent competition, predator aggregation, and habitat segregation. *Ecology*, **68**, 1887–97.
- Schratwieser, J. (1999) The Impact of Resident and Transient Predators on the Population Dynamics of Juvenile Caribbean Spiny Lobster (*Panulirus argus*) in Florida Bay, Florida. MS thesis, Old Dominion University, Norfolk, VA.
- Secci, E., Cuccu, D., Follesa, M.C., Sabatini, A. & Cau, A. (1999) Restocking of *Palinurus elephas* (Fabr. 1787) in a western central Sardinian area. *Biologica Marinas Mediterrean*, **6** (1), 614–16.
- Serfling, S.A. & Ford, R.F. (1975) Ecological studies on the puerulus larval stage of the California spiny lobster *Panulirus interruptus. US National Marine Fishery Service Bulletin*, **73**, 360–77.
- Sharp, W.C., Hunt, J.H. & Lyons, W.G. (1997) Life history of the spotted spiny lobster, *Panulirus guttatus*, an obligate reef dweller. *Marine and Freshwater Research*, 48, 687–98.
- Sharp, W.C., Lellis, W.A., Butler, M.J., Herrnkind, W.F., Hunt, J.H., Pardee-Woodring, M. & Matthews, T.R. (2000) The use of coded microwire tags for mark-recapture studies of juvenile Caribbean spiny lobster, *Panulirus argus*. *Journal of Crustacean Biology*, **20**, 510–21.
- Shears, N.I. & Babcock, R.I. (2002) Marine reserves demonstrate top-down control of community structure on temperature reefs. *Oecologia*, **132** (1), 131–42.
- Sheehy, M.R.J. & Bannister, R.C.A. (2002) Year-class detection reveals climatic modulation of settlement strength in the European lobster, *Homarus gammarus. Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1132–43.
- Sheehy, M.R.J., Bannister, R.C.A., Wickins, J.F. & Shelton, P.M. (1999) New perspectives on the growth and longevity of the European lobster (*Homarus gammarus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 1904–15.
- Shields, J.D. & Behringer, D.C. (2004) A new pathogenic virus in the Caribbean spiny lobster, *Panulirus argus*, from Florida. *Diseases of Aquatic Organisms*, **59**,109–18.
- Sindermann, C.J. & Rosenfield, A. (1967) Principal diseases of commercially important marine bivalve Mollusca and Crustacea. *Fisheries Bulletin*, 66, 335–85.
- Skewes, T.D., Dennis, D.M., Pitcher, C.R. & Long, B.G. (1997) Age structure of *Panulirus ornatus* in two habitats in Torres Strait, Australia. *Marine and Freshwater Research*, 48, 745–50.
- Skud, B.E. & Perkins, H.C. (1969) Size composition, sex ratio, and size at maturity of offshore northern lobsters. US Fish and Wildlife Service Special Scientific Report, **598**, 1–10.

- Smith, I.P., Collins, K.J. & Jensen, A.C. (1998) Electromagnetic telemetry of lobster (*Homarus gammarus* (L.)) movements and activity: preliminary results. *Hydrobiologia*, **372**, 133–41.
- Smith, K.N. & Herrnkind, W.F. (1992) Predation on early juvenile spiny lobsters, *Panulirus argus* (Latreille): influence of size and shelter. *Journal of Experimental Marine Biology and Ecology*, **157**, 3–18.
- Sosa-Cordero, E., Arce, A.M., Aguilar-Davila, W. & Ramierz-Gonzalez, A. (1998) Artificial shelters for spiny lobster Panulirus argus (Latreille): an evaluation of occupancy in different benthic habitats. Journal of Experimental Marine Biology and Ecology, 229, 1–18.
- Spiess, A.E. & Lewis, R. (2001) The Turner Farm fauna: five thousand years of hunting and fishing in Penobscot Bay, Maine. *Occasional Publications in Maine Archeology*, **11**, 1–120.
- Steneck, R.S. (1989) The ecological ontogeny of lobsters: in situ studies with demographic implications. In: I. Kornfield (Ed.) Proceedings Lobster Life History Workshop. University of Maine. pp. 130–3.
- Steneck, R.S. (1997) Fisheries-induced biological changes to the structure and function of the Gulf of Maine Ecosystem. Plenary Paper. In: G.T. Wallace & E.F. Braasch (Eds) Proceedings of the Gulf of Maine Ecosystem Dynamics Scientific Symposium and Workshop. RARGOM Report, 97 – 1. Regional Association for Research on the Gulf of Maine, Hanover, NH. pp. 151–65.
- Steneck, R.S. (2006) Is the American lobster, *Homarus americanus* overfished? A review of overfishing with an ecologically-based perspective. *Bulletin of Marine Science* (in press).
- Steneck, R.S. & Carlton, J.T. (2001) Human alterations of marine communities: students beware! In: M. Bertness, S. Gaines & M. Hay (Eds) *Marine Community Ecology*. Sinauer Press, Sunderland, Massachusetts. pp. 445–68.
- Steneck, R.S. & Dethier, M.N. (1994) A functional group approach to the structure of algal-dominated communities. *Oikos*, **69**, 476–98.
- Steneck, R.S. & Sala, E.A. (2005) Large marine carnivores: trophic cascades and top-down controls in coastal ecosystems past and present. In: J. Ray, K. Redford, R. Steneck & J. Berger (Eds) Large Carnivores and the Conservation of Biodiversity. Island Press, Washington. pp. 110–37.
- Steneck, R.S. & Wilson, C.J. (2001) Large-scale and long-term, spatial and temporal patterns in demography and landings of the American lobster, *Homarus americanus*, in Maine. *Marine and Freshwater Research*, 52, 1303–19.
- Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M, Estes, J.A. & Tegner, M.J. (2002) Kelp forest ecosystem: biodiversity, stability, resilience and their future. *Environmental Conservation*, 29, 436–59.
- Steneck, R.S., Vavrinec, J. & Leland, A.V. (2004) Accelerating trophic level dysfunction in kelp forest ecosystems of the western North Atlantic. *Ecosystems*, 7, 323–31.
- Stockhausen, W.T. & Lipcius, R.N. (2001) Single large or several small marine reserves for the Caribbean spiny lobster? *Marine and Freshwater Research*, **52**, 1605–14.
- Stockhausen, W.T., Lipcius, R.N. & Hickey, B.H. (2000) Joint effects of larval dispersal, population regulation, marine reserve design, and exploitation on production and recruitment in the Caribbean spiny lobster. *Bulletin of Marine Science*, 66, 957–90.
- Sutherland, J.P. (1974) Multiple stable points in natural communities. American Naturalist, 108, 839–73.
- Tegner, M.J. & Dayton, P.K. (1981) Population structure, recruitment and mortality of two sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. *Marine Ecology Progress Series*, **5**, 255–68.
- Thompson, B.M. & Ayers, R.A. (1989) Laboratory studies on the development of *Nephrops norvegicus* larvae. *Journal of the Marine Biological Association of the United Kingdom*, **69**, 795–801.
- Trendall, J.T., Bell, R.S. & Phillips, B.F. (1988) Growth of the spiny lobster, *Panulirus ornatus*, in the Torres Strait. *Proceedings of a Workshop on Pacific Inshore Fisheries*. South Pacific Commission, Noumea. pp. 1–17.
- Tuck, I.D., Chapman, C.J. & Atkinson, R.J.A. (1997) Population biology of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland – I: Growth and density. *ICES Journal of Marine Science*, 54, 125–35.
- Tully, O., Roantree, V. & Robinson, M. (2001) Maturity, fecundity and reproductive potential of the European lobster (*Homarus gammarus*) in Ireland. *Journal of the Marine Biological Association of the United Kingdom*, **81**, 61–8.
- US Ocean Commission (2004) An Ocean Blueprint for the 21st Century. Final Report of the US Commission on Ocean Policy, Washington, DC. http://oceancommission.gov/documents/prepub_report/welcome.html.

- Vianna, M.L. (1986) On the ecology and intraspecific variation in the spiny lobster *Panulirus echinatus* Smith, 1869, (Decapoda, Palinuridae) from Brazil. *Crustaceana*, **51**, 25–37.
- Wahle, R.A. (1992) Body-size dependent antipredator mechanisms of the American lobster. Oikos, 63, 1-9.
- Wahle, R. (1997) Consequences of fishing, with regard to lobster fisheries: report from a workshop. *Marine and Freshwater Research*, **48**, 1115–20.
- Wahle, R.A. (1998) A trans-Atlantic perspective on *Homarus* recruitment and enhancement. In: G.I. Van der Meeren & O. Soldal (Eds) *The European Lobster* Homarus gammarus (L.): *Proceedings from the Seminar at Kvitsoy* 1995. *Fisken og havet 1998*, No. 18, Havforskningsinstituttet, Bergen, Norway. pp. 36–43.
- Wahle, R.A. (2003) Revealing stock-recruitment relationships in lobsters and crabs: is experimental ecology the key? *Fisheries Research*, **65**, 3–32.
- Wahle, R. & Incze, L. (1997) Pre- and post-settlement processes in recruiment of the American lobster. *Journal of Experimental Marine Biology and Ecology*, 217, 179–207.
- Wahle, R.A. & Steneck, R.S. (1991) Recruitment habitats and nursery grounds of the American lobster, *Homarus americanus*: a demographic bottleneck? *Marine Ecology Progress Series*, **69**, 231–43.
- Wahle, R.A. & Steneck, R.S. (1992) Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. *Journal of Experimental Marine Biology and Ecology*, **157**, 991–1114.
- Wahle, R.A., Tully, O. & O'Donovan, V. (2001) Environmentally mediated crowding effects on growth, survival and metabolic rate of juvenile American lobsters (*Homarus americanus*). *Marine and Freshwater Research*, 52, 1157–66.
- Wahle, R.A., Incze, L.S. & Fogarty, M.J. (2004) First projections of American lobster fishery recruitment using a settlement index and variable growth. *Bulletin of Marine Science*, **74**, 101–14.
- White, R.G., Hill, A.E. & Jones, D.A. (1988) The distribution of *Nephrops norvegicus* (L) larvae in the western Irish Sea: an example of advective control on recruitment. *Journal of Plankton Research*, **10**, 735–47.
- Wilson, C.E. (1999) Bathymetric and Spatial Patterns of Settlement in American Lobster, *Homarus americanus*, in the Gulf of Maine: Insights into Processes Controlling Abundance. Masters thesis, Department of Oceanography, University of Maine.
- Witham, R., Ingle, R.M. & Joyce, E.A. (1968) Physiological and ecological studies of *Panulirus argus* from the St Lucie estuary. *Florida Board of Conservation Marine Laboratory Technical Series*, **53**.
- Witman, J.D. & Sebens, K.P. (1992) Regional variation in fish predation intensity: a historical perspective in the Gulf of Maine. *Oecologia*, **90**, 305–15.
- Yoshimura, T. & Yamakawa, H. (1988) Ecological investigations of settled puerulus and juvenile stages of the Japanese spiny lobster *Panulirus japonicus* at Kominato, Japan. *Journal of Crustacean Biology*, **8**, 524–31.
- Yoshimura, T., Yamakawa, H. & Norman, C.P. (1994) Comparison of hole and seaweed habitats of post-settled pueruli and early benthic juvenile lobsters, *Panulirus japonicus* (Von Siebold, 1824). *Crustaceana*, **66** (3), 356–65.
- Zimmer-Faust, R.K., Tyre, J.E. & Case, J.F. (1985) Chemical attraction causing aggregation in the spiny lobster, *Panulirus interruptus* (Randall), and its probable ecological significance. *Biological Bulletin*, **169**, 106–18.

BMA08.indd 309