ABUNDANCE, INTERACTION AND MOVEMENT IN A EUROPEAN LOBSTER STOCK

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Abstract

European lobsters form one of the most economically valuable portions of UK landings, yet they are little regulated, despite stocks being considered fully exploited. Biological and behavioural knowledge is lacking, managerial effort is low and understanding is often inferred from other species. To ensure continued productivity of this important fishery, improved data on fishing activity, population dynamics, catchability, recruitment, movement and distribution are urgently required. Through analysis of capture-mark-recapture data, fishery-independent catches, behavioural-interaction studies and acoustic telemetry tracking, this thesis aims to provide a basis for future research and management.

Capture-mark-recapture (CMR) and fishery-independent catch data established estimates of density, proportionate distribution, movements and site-fidelity and catchability parameters. These revealed high site fidelity and catchability differences between sexes leading to female-skewed density estimates. If these findings are corroborated, the effect and causes of disproportionate sex ratios must be addressed.

The mixed-species nature of UK shellfisheries led to studies recording the impact of inter-specific and intra-specific interactions on catchability and catch rates. Lobster presence significantly lowered catchability of crab species and occurrences of same-sex lobster pairings were lower than expected. Findings highlight both the inconsistency of using catch per unit effort (CPUE) as a direct index of abundance and the danger of analysing crab and lobster catch data in isolation from each other.

The final study employed an acoustic telemetry array to quantify *in situ* lobster movement, providing unique information on short-term home-ranges and habitat-utilisation. There were both transient and resident portions of the population, not predictable by sex or size. Males had significantly larger home-ranges than females,

which could explain their increased catchability estimated in the CMR study. In contrast to trap catch data, most lobsters were recorded using soft substrate outwith their home-range. Movement behaviour changed accordingly, from 'searching' behaviour on mixed and hard substrates to 'exploratory' behaviour on soft. This highlighted a potential connectivity between isolated rocky habitats.

The present study reveals the importance of undertaking local lobster studies in order to elucidate behavioural traits and highlight sampling uncertainties that can have important impacts on methods of stock assessment. Findings provide an initial baseline for further data collection, allowing changes in the population to be monitored.

Acknowledgements

I took on the challenge of this PhD under no illusions of the task at hand; I never underestimated the amount of hard work that would be involved. However, the three years have also been a great deal of fun and was an experience I am unlikely to forget. Since moving to Newcastle in 2005, I have regarded it as my home, therefore this study has had a particular resonance with me. Working alongside fishermen and managers within Northumberland, with focus on this relatively understudied population of lobster within such close vicinity to my doorstep, has been a rare privilege. I would like to think that the findings, outcomes and working relationships built during this study will prove useful for years to come.

Numerous people have provided help, advice and support during the three years of planning and implementing of fieldwork and writing this thesis. Unfortunately I do not have space to thank them all, but I am grateful for the experience that each one has shared with me. I would first like to thank my supervisors Dr Clare Fitzsimmons and Prof. Nicholas Polunin for all their help throughout the PhD. They have offered support, guidance and plenty of patience. I have learnt a great deal and enjoyed every aspect of working together over the past five years.

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Special thanks must go to the NIFCA officers, without their help I could never have begun to gain samples to study these animals. Particularly, I would like to thank those

who helped with fieldwork and the painting of hundreds of lobsters and thousands of crabs during 2010, the coldest winter since records began. I know some mornings you despaired, but it was all good fun in the end. Without the NIFCA officers most of this PhD would not have been possible. I would also like to thank Robert Oliver for first showing me how to rig traps and tie an eye-splice; Peter Berney and all other volunteers during this study, for tirelessly helping during field work. Finally I must thank all those involved with the RV Princess Royal. Especially, Dr Ben Wigham for helping to make time in the schedule for my work and Neil Armstrong and Barry Pearson for helping with the planning and conducting of the final two years of field work. I learnt a vast amount from these two, although to their annoyance I often forgot some of it too.

This PhD was made possible by initial funding and belief from Natural England and the NIFCA. Further investment from Newcastle University and the MMO helped it expand into a PhD. Hopefully this financial investment and personal involvement will help to begin to increase our knowledge and understanding of lobster in the North East, and help to prepare for the continued sustainability of this regionally important species. I am proud to have had the opportunity to conduct research within Northumberland, alongside the great people I have worked with.

I am also incredibly grateful to all my family and friends for the support and love they have offered me throughout, particularly, Dr Paul Woods for affording me the opportunity to remain within academia. Finally, and most importantly, I would like to thank Chloe. Thank you for your patience while I have completed this thesis. Thank you for your support, encouragement and love, I could not have completed this without your inspiration.

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1.1 Clawed lobsters

Lobsters are found throughout most temperate and tropical marine waters and the demand for clawed (Nephropidae), spiny (Palinuridae) and slipper lobsters (Scyllaridae), has resulted in major fisheries around the world (Frusher and Gardner 2005; Phillips 2005). Due to the focus on lobster as a valuable resource, collectively they are among the most researched animals in the world. Yet there is expanding need for their study due to changing pressures and concern for their management.

Clawed lobsters have a global distribution with over 50 species occurring on most substrates, from the sub-littoral to depths of 3,000m (Holthuis 1974; Cobb 1997). Management occurs at different scales and draws from a wide understanding, including: larval ecology, behaviour, genetics, stock assessment, effects of fishing, post-harvest practices, economics, and more recently aquaculture and enhancement. In many cases new priorities for research arise because of changing fisheries, developing technology and disease, as well as managerial developments such as marine protected areas (MPAs).

The American lobsters' (*Homarus americanus*) biology and fishery are well studied (Incze and Naimie 2000; Tremblay and Smith 2001; Rowe 2002; Wahle 2003), however, for European lobster (*Homarus gammarus*), knowledge is often derived from *ex situ* or outdated studies (Van der Meeren 2005), inferred from work on *H. americanus* (Fig. 1.1), or is unavailable. There is a danger in freely interpreting results from one species to another (Mercer, Bannister *et al.* 2001), especially considering the dichotomy between abundances and landings of the two species (Phillips 2013). Due to the reliance on the continued productivity of their stocks and in the light of reported failures of many finfish stocks (Pauly, Christensen *et al.* 1998; Myers and Worm 2003), increased data on *H. gammarus* are urgently required.

This introductory chapter aims to appraise the current state of knowledge regarding clawed lobsters, with focus on *H. gammarus*; its biology, behaviour, distribution, extraction and management are outlined and the objectives of the thesis stated.

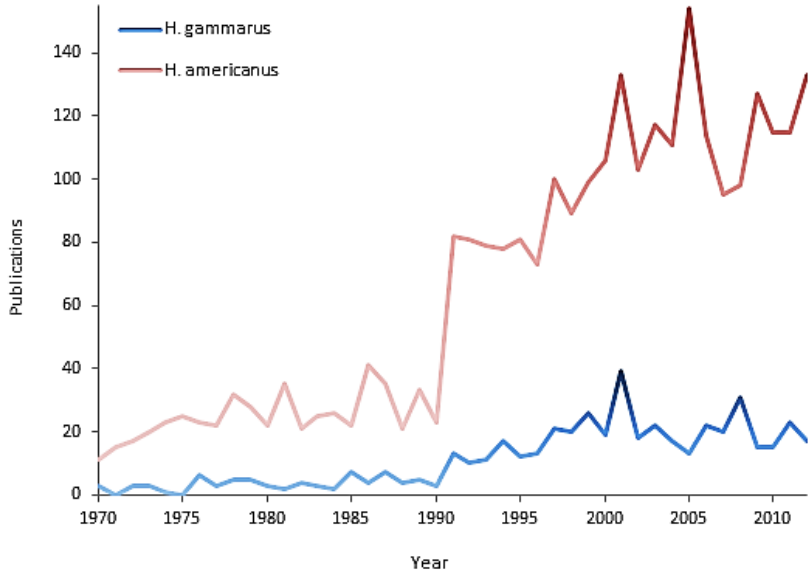


Figure 1.1 Number of publications per year for *H. gammarus* (blue) and *H. americanus* (red). Figures based on search results in Web of Knowledge for *"Homarus gammarus"* and "*Homarus americanus*" respectively.

1.2 Biology, reproduction and larval ecology

Homarus spp mature sexually at 5 to 8 years; maturation time is influenced by ambient water temperature and individual fitness. Males often mature earlier than females (Jørstad, Farestveit *et al.* 2005), however, size at first maturity can vary significantly. Growth via exoskeleton ecdysis occurs incrementally; carapace length (CL) increase per moult in adults varies significantly between regions and individuals (Laurens, Fifas *et al.* 2009). As skeletal structure is shed and a lack of correlation between annual cohorts and size exists (Bennett 1974; Matsuda and Yamakawa 1997), no precise ageing method for crustacean is currently routinely available (Bannister and Addison 1998; Wahle, Tully et al. 2001; Sheehy and Bannister 2002; Hopkins 2012). However, the recent detection of growth bands in calcified regions of the eyestalk and gastric mill, has the potential to provide estimates of age (Kilada, Sainte-Marie *et al.* 2012).

In the UK, mating occurs in the summer during or after the moulting cycle is complete and recently ovigerous (berried) females appear from September to December (Pawson 1995). Often females show a two year reproductive cycle (ovigerous, moult, ovigerous again), however, variation exists (Agnalt, Kristiansen *et al.* 2007); females may mate during moult (Waddy and Aiken 1986; Waddy and Aiken 1990), moult and

subsequently mate (Atema, Jacobson *et al.* 1979; Karnofsky and Price 1989), or forfeit moulting and fertilise eggs using sperm from a previous season (Waddy and Aiken 1986). Some *H. gammarus* females spawn each year (Latrouite, Léglise *et al.* 1981) and about half of these also moult each year; these are so called 'super-females' (Campbell and Robinson 1983; Comeau and Savoie 2002). Male behaviour may also vary between forfeiting moulting and mating or being subordinate and moult without mating (Cowan and Atema 1990). It remains unclear what determines an individual's reproductive cycle, but diet and health are likely to contribute. Genetic data suggest females in the wild mostly mate with a single male (Ferguson and Danzmann 1998), while *ex situ* tank studies demonstrate that males are capable of fertilising several females in one season (Jørstad, Farestveit *et al.* 2005). Polyandry is likely common in the wild, and recent unpublished genetic data suggests male abundance and fitness play a role in determining the number of partners.

Lobsters produce large eggs in relatively small numbers, carried beneath the female's abdomen for up to one year, before hatching and beginning a pelagic stage of development for 2-3 weeks, the duration depending on water temperature, timing of settlement and nutrition (Cobb and Wahle 1994; Cowan, Solow *et al.* 2001). Knowledge of larval dispersion for *H. gammarus* is largely limited to model simulation (Cobb 1997; Cobb, Booth *et al.* 1997); winds, currents and larval behaviour play significant roles (Incze, Wahle *et al.* 1997). During this pelagic period larvae pass through four recognised stages of development before final metamorphosis and settlement on the seabed (Cobb, Wang *et al.* 1989; Cobb, Wang *et al.* 1989a; Incze and Wahle 1991) (Fig. 1.2). Newly settled *H. americanus* are found in shallow, rocky habitats, primarily cobble (Hudon 1987; Wahle and Steneck 1991; Cobb and Wahle 1994). However, the larval form of *H. gammarus* has only been identified in the wild (Tully and Ceidigh 1987), and the benthic habitat to which it recruits remains uncertain, despite significant and widespread investigations (Linnane, Mazzoni *et al.* 2000; Linnane, Ball *et al.* 2001; Mercer, Bannister *et al.* 2001).

The lack of early benthic phase (EBP) *H. gammarus* observations causes difficulties for stock assessment and creates problems ascertaining the success of management and enhancement programmes (Sheehy and Bannister 2002). Hatchery-reared *H. gammarus* are therefore often used for studies (Mercer, Bannister *et al.* 2001), or

inferences are made based on observations of EBP *H. americanus*. Mesocosm studies show recruits of both *Homarus* spp have similar reliance on shelter-providing substrate such as mussel beds, cobble or gravel (Linnane, Mazzoni *et al.* 2000). The settlement stage in many marine species is considered a 'bottleneck'; density-dependent growth, mortality and ultimately recruitment strength are constrained by shortages of shelter and food, and increased predation (Incze, Wahle *et al.* 1997; Wahle, Tully *et al.* 2001; Phillips 2005). After settlement, *H. americanus* remain cryptic and sedentary within cobble patches for one or two years before moving out to seek larger shelters and to forage (Hovel and Wahle 2010), however, individuals remain vulnerable to predation during their juvenile phase (Wahle and Steneck 1991).

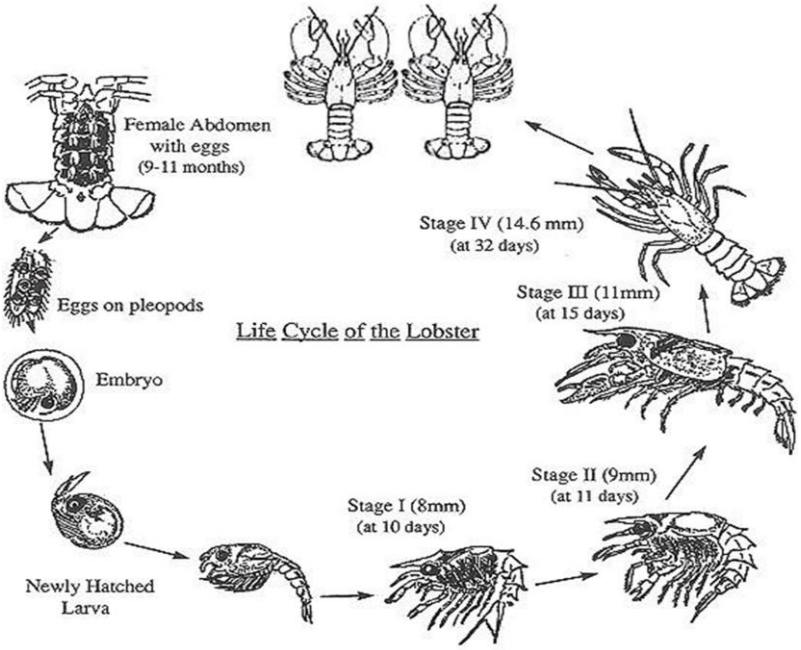


Figure 1.2 The life cycle of *Homarus* spp. Newly hatched larva are the beginning of the pelagic stage, and stage III represents the ontogenetic shift to a benthic stage. Image: http://njscuba.net.

Population genetics of *H. gammarus* is better understood than many other marine species, however, there is conflicting evidence for long-distance adult dispersal and the potential for high gene flow because of uncertainty about the larval planktonic period (Aiken and Waddy 1986; Aiken and Waddy 1986). In Europe low levels of genetic exchange among local populations occur (Ferguson and Danzmann 1998; Jørstad, Farestveit *et al.* 2005; Triantafyllidis, Apostolidis *et al.* 2005), fitting an 'island' model consisting of discrete populations with little or limited exchange (Ulrich, Muller *et al.* 2001). Taking into consideration the potential for migratory behaviour and larval

dispersion, genetic exchange between European lobster populations seems unexpectedly restricted.

1.3 Behaviour and distribution

Homarus gammarus has a broad distribution throughout coastal Europe, but is absent from the Baltic Sea, probably due to environmental extremes (e.g. salinity) and is much less abundant throughout the coastal areas of the Mediterranean. Southern distribution extends along mainland Europe to a limit of about 30^{o} latitude on the Atlantic coast of Morocco; its northern limit is the Lofoten Islands, Norway (Fig. 1.3). Found from low water mark to depths of around 150m, most catches are taken in less than 35m. Primarily nocturnal (Smith, Collins *et al.* 1998), it is a slow periodic feeder (Mente, Houlihan *et al.* 2001), targeting bivalves, small crustaceans and polychaetes, and it also scavenges. Mixed substrate and cobble is usually preferred foraging ground, because of its abundant and accessible prey (Cox, Hunt *et al.* 1997). Spatial variability in the abundance or diversity of prey may influence distribution and spatial variability in growth, morphology and behaviour (O'Malley, Drazen *et al.* 2012).

Figure 1.3. Approximate distribution of *Homarus gammarus*, highlighted by the dark grey line surrounding the coast. Image: http://www.imr.no.

Most behavioural studies are conducted on *H. americanus*, under controlled laboratory conditions (Phillips 2005) and primarily concerned with aggression, dominance and shelter use (Scrivener and Terhune 1971; Sastry and Ehinger 1980; Finley and Haley 1983; Miller and Addison 1995). However, *in situ* or large-mesocosm experiments have become increasingly preferred, but remain predominantly confined to *H. americanus* (Linnane, Mazzoni *et al.* 2000; Mercer, Bannister *et al.* 2001; Bowlby, Hanson *et al.* 2008; Geraldi, Wahle *et al.* 2009; Watson, Golet *et al.* 2009; Hovel and Wahle 2010; Moland, Olsen *et al.* 2011).

1.3.1 Movement

Movement data are vital for determining stock structure of mobile species (Smith, Jensen *et al.* 2001; Bowlby, Hanson *et al.* 2008); seasonal-, sex- and age-driven distributions must be understood in order to observe and predict population changes (Harwood and Stokes 2003; Fogarty and Gendron 2004), set management limitations (Frank and Brickman 2001; Bowlby, Hanson *et al.* 2008) and monitor the success of enhancement projects (Addison and Bannister 1994; Bannister and Addison 1998; Kelly, Scott *et al.* 2000).

Lobsters are capable of fast propulsion using their telson, but cannot maintain this momentum, relying on walking for sustained movements. *H. americanus* typically walks in five minute bouts (Taylor 1982); with a mean walking speed of 0.9m min^{-1}, increasing to 2.5m min^{-1} (O'Grady, Jury *et al.* 2001). It was assumed that all adult *H. americanus* underwent seasonal migration shortly before mating.However, diver observations, tagging and telemetry studies suggest the majority move 100-300m, usually during foraging excursions at night, before returning to their home-shelter (Krouse 1980; Karnofsky, Atema *et al.* 1989; Watson, Vetrovs *et al.* 1999). CMR found that 60% of marked *H. americanus* were recaptured within the immediate vicinity of their original location over three years (Rowe 2001); of those that moved 80% travelled less than 1km, but no relationship between movement and sex-, size- or duration was found. There is evidence that portions of the population do undertake migrations, reportedly walking 1-4km day^{-1}, covering 30-100km in one season (Pezzack and Duggan 1986). Yet it is unclear why this occurs and why only portions of the population appear to undertake it; in the case of ovigerous females, they may migrate along waters of

certain temperatures, to help maximise egg development (Ennis 1984; Crossin, Al-Ayoub *et al.* 1998).

In the Gulf of Maine, New Hampshire and Canadian waters, some lobsters make inshore migrations in the spring and then into deeper waters in late autumn, covering 30-100km (Krouse 1980; Munro and Therriault 1983; Chen, Sherman *et al.* 2006), suggesting control by environmental variables such as temperature and salinity. Small *H. americanus* are more likely to be found in inshore waters, whereas large lobsters are more common offshore (Cooper, Clifford *et al.* 1975); attributable to size-specific responses to the environment (Jury, Kinnison *et al.* 1994; Jury, Kinnison *et al.* 1994), this could also be a result of higher fishing pressure in inshore waters. In contrast, there are few recorded fisheries of *H. gammarus* near the continental shelf margin, but large specimens are found several tens of kilometres offshore in isolated patches of suitable habitat (Smith, Jensen *et al.* 2001). There is a severe lack of data regarding *H. gammarus* (Smith, Jensen *et al.* 2001); most behavioural studies are conducted using CMR with the primary goal of estimating fishing mortality or growth rates while providing limited movement data. European lobsters are generally regarded as sedentary animals with small home ranges (Bannister, Addison *et al.* 1994; Jørstad, Prodöhl *et al.* 2004), and the few studies conducted support this; most recaptures occur within 3km of release (Jensen, Collins *et al.* 1994; Smith, Collins *et al.* 1999; Smith, Jensen *et al.* 2001), and only a small proportion have been observed to travel up to 15km in a season (Thomas 1954; Simpson 1961). However, there is evidence that *H. gammarus* can quickly colonise new habitat; the rapid colonisation of the Poole Bay artificial reef, some 3km from known lobster habitat supports this (Jensen, Collins *et al.* 1994; Jensen 2002). While anecdotal evidence suggests small inshore movement of adult lobsters during the spring and summer months occur (largely concluded from increased inshore catch rates), extensive seasonal migrations by *H. gammarus* have not been clearly defined. In general it is believed to make small random movements prompted by local competition for food, the search for suitable mates, or the need to change habitats as size increases (Pawson 1995). Smith *et al.* (2001) found that short movements appeared to be largely influenced by the spatial distribution of suitable habitat (often reflected in the distribution of trapping effort) (Smith, Jensen *et al.* 2001).

1.3.2 Habitat

Habitat type, quality and location are considered key determinants of animal movements, distributions and abundances (Geraldi, Wahle *et al.* 2009). The greatest concentrations of adult *H. americanus* occur on substrate with overlaying rock, boulders and cobble (Lawton and Lavalli 1995; Tremblay, Smith *et al.* 2009). The presence of shelter-providing refuge, along with suitable prey items, cause local increases in density, as lobsters are dependent upon shelters, spending most of the time within them (Howard 1980). Adult *Homarus* spp may excavate shelter under vegetation and boulders or shelter in crevices (Karnofsky, Atema *et al.* 1989); however, type of shelter is often less important than its availability and size (Caddy 1986; Steger 1987; Caddy and Stamatopoulos 1990; Hernkind, Butler Iv *et al.* 1997). Where boulders rest on substrate there is a limit to the size of burrow that can be excavated beneath it before it collapses, creating size-specific distributions (Howard 1980), with location of shelters appearing to be clustered (Cobb 1971).

Habitat type, shelter size and availability at fine spatial scales clearly influence distribution (Poff 1997; Chang, Chen *et al.* 2010), but temporal consistencies in crustacean distribution at large scales suggest distribution is also regulated by environmental factors (e.g. temperature, salinity, depth and habitat) (Ungaro, Marano *et al.* 2005). Abundances of animals are therefore the result of several multi-scale ecological factors (Barbaresi, Cannicci *et al.* 2007). At regional scales, the role of historical and anthropogenic pressures, recruitment strength and temperature are likely to prevail, but locally the composition of a community may well be explained by environmental variables alone (Irlandi, Ambrose Jr *et al.* 1995; Eggleston, Elis *et al.* 1999; Hovel and Lipcius 2001; Townsend, Dolédec *et al.* 2003; Hovel and Wahle 2010).

Within areas composed of a mosaic of habitat types, animals commonly live near interfaces of several types, with each habitat uniquely influencing behaviour, growth, distribution or survival (Selgrath, Hovel *et al.* 2007). Movement between habitats involves a trade-off between benefits and risks (Werner and Gilliam 1984); certain habitats may act as corridors, facilitating access to preferred areas (Micheli and Peterson 1999). As crustaceans have pelagic stages leading to wide dispersal, maintaining connections among habitat patches has been generally regarded as

unimportant for management (Hedgecock 1986; Palumbi 1992); this is an assumption challenged however by recent larval and genetic studies. As lobsters grow they gain a size-refuge from predators, and in turn their association with shelter tends to relax. Therefore, smaller lobsters are more common in the middle of cobble patches, whereas large lobsters are more common on edges (Selgrath, Hovel *et al.* 2007) and isolated habitats. However, outgrowing local supply of shelter before outgrowing predation could potentially cause a shelter 'bottleneck' (Wahle and Steneck 1991; Parrish and Polovina 1994; Wahle 2003). As the influence of habitat changes with spatial scale, the choice of scale for a study greatly influences the interpretation of the ecological system being studied (Andren 1994; With and Crist 1995; Eggleston, Elis *et al.* 1999).

Habitat may also significantly affect lobster catchability, due to increased shelter availability (Karnofsky, Atema *et al.* 1989; Lawton and Lavalli 1995) or topography; as lobsters locate bait by odour, bottom complexity can influence the hydrodynamics of bait odour plumes, altering the area of bait influence (Weissburg and Zimmer-Faust 1993; Watson, Golet *et al.* 2009). Diver studies of *H. americanus* found that densities of lobster were highest on rocky habitat, but trap catch rates were highest on unstructured sediment (Tremblay and Smith 2001; Geraldi, Wahle *et al.* 2009), suggesting that lobsters' utilisation of a habitat alters catchability; complex, hard habitat is used primarily for shelter during periods of vulnerability, such as ecdysis or juvenile stages, and homogenous sediment habitats used for foraging. These discrepancies in catchability can lead to misinterpretation of catch rates, and lead to erroneous estimates of abundance.

1.4 Fishing

The range of habitats used by lobsters creates difficulties when conducting surveys of abundance. For complex inshore habitats, diver surveys are often considered the best approach (Pitcher, Dennis *et al.* 1997), but are restricted by depth, time, cost and environmental conditions. Trawling is sometimes used in low complexity habitats, but is easily avoided by lobsters (Roddick and Miller 1992). Most lobster fisheries deploy stationary baited parlour traps that attract animals (Fig. 1.4). Used extensively in commercial shellfisheries, and as a tool for population studies, traps are

relatively inexpensive, can be deployed from small vessels in any habitat and in any configuration, with relatively little damage to catch or habitat compared to mobile gear. However, indices of abundance are based on the assumption that the catch of the trap is representative of the surrounding population.

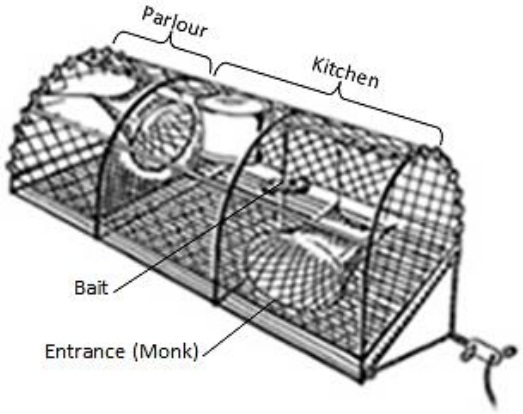


Figure 1.4 Standard design of a parlour trap.

Previous studies have demonstrated that the catchability of an individual animal depends on size, sex, moult status, and environmental factors such as water temperature and currents. Miller (1990) has provided a comprehensive review of factors governing trap efficiency. Understanding trends in catchability is fundamental to improved assessments of stock status that rely on trap data (Tremblay and Smith 2001), but catch rates are subject to uncertainties due to additional factors, such as escapements, gear design (Montgomery 2005), selectivity and saturation effects, species interactions, changing area of bait influence or attractiveness and seasonality (Bennett 1974a; Miller 1990; Fogarty and Addison 1997; Bell, Addison *et al.* 2001; Ziegler, Frusher *et al.* 2003). Often summarised as catch probability and effort, it is important to understand how external factors influence observed catch, so that data can be standardised and more representative of the abundance of the target species.

1.4.1 Seasonality

Homarus gammarus catch per unit effort (CPUE) is relatively low, previous studies estimate it at 1% that of *Cancer pagurus* (Bennett 1974a), with two seasonal peaks generally observed; there is a spring peak, lasting three to four months, when effort changes to target lobsters inshore and rising water temperature increases lobster

activity, and a shorter peak in the autumn, possibly following the emergence of newly moulted lobsters, including those recruiting into the fishable stock for the first time (Fig. 1.5). This seasonal pattern is reflected in the majority of UK shellfish studies, landing data and anecdotal evidence, and must be taken into account during fishery-independent studies or when using commercial catch data.

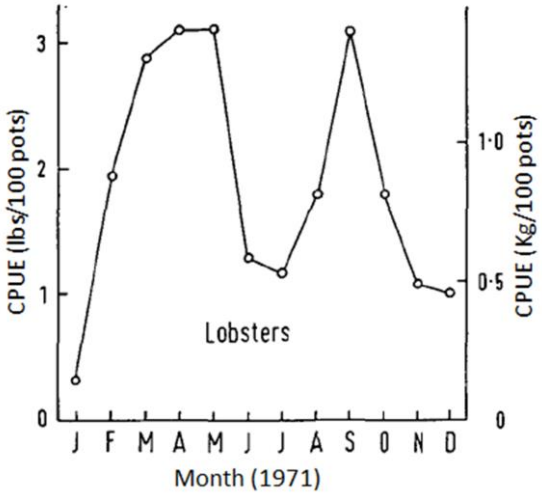


Figure 1.5 Monthly changes in lobster catch per unit effort during 1971 (Bennett 1974).

1.4.2 Soak-time

Over the past 40 years, the effect of soak- or immersion-time on CPUE has been studied by several authors (Bennett 1974a; Montgomery 2005), but expressing this process quantitatively is difficult. The process of trap saturation, the reduction in catch rate with increasing catch (Miller 1979), has long been recognised, and a number of models have been developed to describe the process (Fogarty and Addison 1997). However, gaining sufficient data by experimental fishing can be time-consuming; therefore much of the available data are derived from commercial records.

Trap catches generally increase over the soak period, but do not necessarily increase linearly (Bennett and Brown 1979). Catch rates of *Jasus verreauxi* in New Zealand are not affected by soak-times between 1 and 3 days as traps often saturate within 24 hours (Montgomery 2005). However, traps do not have fixed saturation levels, but vary

with season (Munro and Therriault 1983), choice of bait, target species, trap design and location. Most studies of saturation for *C. pagurus*, *H. americanus* and *H. gammarus*, found that catch rates begin to plateau after 24 hours (Dow 1961; Bennett 1974a; Fogarty and Borden 1980; Fogarty and Addison 1997). At high densities, saturation could limit catches in less than 12 hours (Miller and Rodger 1996), but as few fisheries lift traps more frequently than daily, and as lobsters feed more actively at night, greatest catches are generally obtained after soaks of 24 hours. In some instances, after an initial decline in rate of catch increase, a second increase in catch may be seen after 4 or 5 days. This could be due to escapements making the trap attractive again, or animals within the trap dying, acting as fresh bait (Breen 1989). In addition, with extended soak times the attractiveness of the bait diminishes, resulting in reduced catch rates. Conversely after four or five days the reported increase in catch rate may be due to the decomposition of the bait and further release of attractive substances.

The swimming ability and manoeuvrability of lobsters, which is much greater than that of crabs, can allow for easy escape from traps, particularly those with 'hard-eyed' or 'fixed' entrances. Jury *et al.* (2001) analysed videotapes to reveal that traps caught about 6% of lobsters that entered; allowing 94% to escape (Jury, Howell *et al.* 2001). This high rate of escapement means that the observed catch of a trap is only the catch at the time of hauling, and not necessarily representative of the animals that have entered the trap over the course of the soak.

1.4.3 Effective area fished

When estimating abundance or density by any method, it is essential to know the area of habitat being sampled and the efficiency with which individuals are detected within this area. Unlike direct sampling devices such as quadrats that are characterised in terms of area or volume covered per unit, sampling properties of baited traps are not easily estimated. The key property is the effective area fished, which is the notional area of seafloor containing as many animals as were trapped (McQuinn, Gendron *et al.* 1988; Miller 1989). It can be defined as a catchability coefficient, allowing for the conversion of CPUE to population density (Miller 1990). However, effective area fished is also the most difficult property to measure (Bell,

Addison *et al.* 2001). Animals are attracted to traps by the bait odour plume (Reidenbach, George *et al.* 2008; Reidenbach and Koehl 2011), therefore, independent of interactions or trap spacing, the shape of the fished area will be dictated by water currents, foraging behaviour and seafloor topography, and constrained by certain habitats or obstructions (McQuinn, Gendron *et al.* 1988; Watson, Golet *et al.* 2009). The difficulties of estimating the area being sampled by baited traps causes it to be overlooked in the majority of trap-based studies, but can have dramatic effects, particularly when converting abundance to density (Bell, Eaton *et al.* 2003).

1.4.4 Species interaction

In most trap fisheries several species are caught by the same gear and competitive interactions inside and outside traps are likely to influence the capture process and affect ingress and egress (Rossong, Williams *et al.* 2006; Williams, Floyd *et al.* 2006). Interactions between individuals of the same species (intra-specific) and different species (inter-specific) influence the catchability of portions of the population (Miller 1979; Richards, Cobb *et al.* 1983). Reduced entry of *Cancer productus* and *Cancer magister* has been linked to behavioural interactions causing significant reductions in catch (Miller 1979); in addition avoidance of dead conspecifics can also alter catchability (Richards, Cobb *et al.* 1983; Addison 1995).

Agonistic interactions between *H. gammarus* within a trap and animals approaching reportedly inhibit catch rates of both *H. gammarus* and *C. pagurus* (Addison 1995). The presence of one or two *H. americanus* in a trap also significantly reduced subsequent catch rates of both conspecifics (Smolowitz 1978) and *Cancer* spp (Richards, Cobb *et al.* 1983). In particular, aggressive intraspecific interactions over control of the bait, appear to be the dominant factor limiting both rate of entry and rate of escape of *H. americanus* (Jury, Howell *et al.* 2001).

Without understanding the relationship between trap catch and the population present around the trap, assessments based on catch data will have unknown biases. Catchability, variable both seasonally, temporally and between portions of the population (Dunnington, Wahle *et al.* 2005), can also be influenced by physiological, behavioural and environmental factors and variations in gear design. Therefore, numbers and distributions of animals among traps may not represent the relative

abundance and distribution (Addison and Bell 1997), leading to complex relationships with CPUE. These issues have been reviewed for baited fisheries as a whole (Stoner 2004) and for lobster fisheries specifically (Fogarty and Addison 1997; Addison and Bannister 1998; Bell, Addison et al. 2001; Cobb and Castro 2006).

Improving understanding of catchability is essential, as traps are currently almost exclusively used for sampling, especially where the substrate is complex, heavily vegetated, deep, or visibility low (Tremblay and Smith 2001). Given the large number of potentially interacting factors that can affect trap catches, many authors agree that trap-based measures of abundance should be based on controlled fishing experiments rather than commercial catch data (Miller 1990; Fogarty and Addison 1997).

1.5 Management

Worldwide, marine fisheries are under increasing pressure from fishing effort, pollution, temperature change and acidification; increasing the threat of stock collapse. Fisheries managers are tasked with monitoring these pressures as well as the stocks themselves and implement a variety of regulations, such as effort and catch limitations, temporal and spatial closures, limited entry to the fishery and minimum landing sizes (MLS).

In contrast with many other shellfisheries worldwide (e.g. *H. americanus* and *Panulirus Cygnus*), *H. gammarus* in the UK is only lightly regulated by MLS, supported in some regions by national or local bans on landing ‘v-notched’ or ovigerous individuals. From January 2002, the EU-wide MLS of 87mm CL, close to the mean size of first maturity in many areas, came into force. The objective is to improve yield per recruit and avoid landing functionally immature animals (Gendron 2005). As mean size at first maturity varies spatially, the level of protection will vary accordingly (Lizarraga-Cubedo, Tuck *et al.* 2003). Populations under high size-specific exploitation rates, have been shown to increase fitness by decreasing size at sexual maturity relative to less exploited populations (Abrams and Rowe 1996; Landers, Keser *et al.* 2001); a process well documented in finfish populations (Cardinale and Modin 1999; Domínguez-Petit, Korta *et al.* 2008). Smaller breeding individuals could cause a reduction in eggs per recruit or reduce the health of future recruits (Moland, Olsen *et al.* 2010).

Unexploited stocks naturally fluctuate over time (Soutar and Isaacs 1969; Botsford and Hobbs 1995), changing size via four fundamental processes: birth (recruitment), death (mortality), immigration and emigration. The first two processes tend to be local, whereas the second two probably operate on larger spatial scales (Pulliam 1988). Additional mortality due to fishing and disease (Wahle, Gibson *et al.* 2009) can lead to high mortality rates, which if uncontrolled may become economically and biologically detrimental. Simplistically, as fishing effort and overall catch increase, stock abundance and average catch decline. This relationship between fishing effort and catch is the first fundamental theory of fisheries management (Fig. 1.6). Two main explanations for this decline exist, that can occur independently or simultaneously: firstly, if fish are continuously removed prior to reaching average adult weight, the average individual weight will decline and subsequent catch by weight will decrease. This is known as 'growth-overfishing'. Secondly, if the breeding stock is reduced to such low abundances it cannot produce sufficient recruitment to replace the removed catch. This is termed 'recruitment overfishing' and is potentially the most serious form of overfishing. Lobster stocks are generally considered robust, however, but although extinctions due to fishing are rare, they have occurred in some *H. gammarus* stocks (Cobb and Castro 2006). Therefore it should not be assumed that productive *H. gammarus* fisheries will necessarily continue in the absence of proper data collection, stock assessment, or regulation.

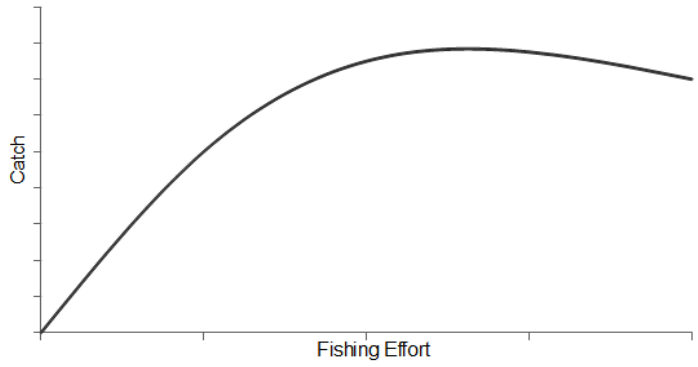


Figure 1.6 The theoretical relationship between catch and fishing effort.

The principle of fisheries management is '*to obtain the best possible sustainable utilisation of the stock for the benefit of the community*'; this could be interpreted as aiming for greater yields, increased profits, or a more abundant stock (Saetersdal

1984). In order for fisheries managers to effectively manage a stock, they must first have an understanding of the status of the stock concerned, in the form of a stock assessment. This assessment can be interpreted as relating catch to fishing effort and determining the present position of the fishery on the curve (Fig. 1.6). Fundamentally this involves; calculating the number (or an index) of individuals within the stock, and forecasting how many individuals there will be in the future. This process is complex, requiring appropriate data and analyses of them, short- and long-term projections of the yield and biomass, determined biological reference points and estimates of short- and long-term effects on yield and biomass of fishery exploitation.

1.5.1 Stock assessment

Scientific advice for fisheries management is generally based on the results of some form of stock monitoring, or assessment (Hilborn and Walters 1992), however, there are four key complications that commonly arise (Gulland 1983):

1) Species rarely form single, homogeneous populations, and the 'unit stock' being exploited by the fishery under assessment needs to be identified

2) Few fisheries operate on a single species or stock, the interactions between these species/stocks need to be considered

3) Several fisheries may operate in the same region on different species, so interactions between different fisheries need to be considered

4) Many factors other than fishing affect stocks

These complications plague lobster stock monitoring, yet are often overlooked. Arguably the first question for all fisheries management, therefore, is to identify the stock itself, which "…*describes characteristics of semi-discrete group of fish with some definable attributes which are of interest to fishery managers*" (Begg, Friedland *et al.* 1999). In some instances geographical or habitat boundaries clearly define the stock, but this is often not the case (Smith, McKoy *et al.* 1980; Phillips 2005), highlighting the need for improved data on catch location, habitat distribution, and movement, distribution and exchange of the target species. Although having some understanding of stock distribution is essential, boundaries are often inferred through political or

jurisdictional limits. Interactions between species or stocks are also often overlooked, especially considering that much of the *C. pagurus* and *H. gammarus* catch comes from the same gear, but assessments are often conducted in isolation.

Despite evidence that population densities can be determined from calibrated fishery-dependent data (Steneck and Wilson 2001), adequate estimation requires accurate and large time-series. Ideally indices of abundance are based on fishery-independent data, to allow for tighter control of the uncertainties of trap fishing (Smith and Tremblay 2003). However, fishery-independent data are often expensive and spatially limited, therefore stock monitoring is typically confined to catch and effort data reported by commercial fishers. Often in the form of CPUE, these indices can be misleading due to changes in catch occurring for many reasons other than those merely in abundance.

Maunder and Punt (2004) reviewed methods for standardizing catch and effort data for fisheries in general, noting that the use of catch rate as an index of abundance assumes that at small spatial scales, catch (*C*) is proportional to the product of fishing effort and density:

1) $$C = qEN$$

Where E is fishing effort, N is density or population abundance and q the proportion of the abundance that is captured by one unit of effort, referred to as the catchability coefficient. Rearranging equation (1) leads to the fundamental relationship between catch and density:

2) $$\frac{C}{E} = qN$$

However, q is only constant when the conditions are constant and in reality they change spatially, temporally and between sectors of the population. Therefore, to appropriately use catch rate as an index of abundance, adjustments for the impact of changes in catchability over time and in space are required, referred to as 'catch-effort standardisation'. Methods often involve fitting statistical models to the catch and effort data (Gavaris 1980; Kimura 1981), the last few decades have seen an increase in the number of new methods. However, even if catch and effort data are appropriately

standardised, there is still no guarantee that the resultant index of abundance is linearly proportional to abundance.

There are four general approaches to estimating stock abundance: depletion methods, reconstruction from past-catch data, capture-mark-recapture and the simplest methods based on direct counts. Various other stock monitoring methods have been applied to crustacean fisheries: Smith and Addison (2003) reviewed and evaluated biomass dynamics models, delay-difference models, depletion methods, yield and egg per recruit models and dynamic size-structured models (Smith and Addison 2003). Some of the world's lobster fisheries now use recruitment indices to estimate future fishing levels based on settlement strength from long time-series. However, as newly settled *H. gammarus* have rarely been recorded in the wild this method is not achievable (Mercer, Bannister et al. 2001). Regardless of the method followed, for an assessment to be useful it must to some degree simulate reality. As age determination, regional fecundity and size or age at maturity, distribution, movements and catchability rates are often unknown; parameters are often inferred or estimated.

Despite the various methods available, CPUE and catch-size distribution data comprise the basis of most stock monitoring and assessment methods used for European lobster fisheries (Addison 1997). Even with problems of misreporting, catch data via commercial fishing is relatively easy to obtain, whereas defining and measuring fishing effort is problematic. The prevailing view is that CPUE is not necessarily a reliable index of abundance in lobster fisheries, however, some index is required in order to conduct an assessment, and as CPUE is sometimes the only available index it is invariably used (Addison 1997). Fishery-independent surveys have an important role in stock assessment improvement, validating observation from commercial data, provision of management advice, and also providing independently estimated parameters for assessment. The development of fishery-independent methods has long been expected to expand, incorporating technological advances such as remote sensing and computer aided analysis tools (Smith and Addison 2003; Smith and Tremblay 2003).

Three well-known reviews of methods for estimating animal abundances (Seber 1986; Seber 1992; Schwarz and Seber 1999) note that the 'explosion' of papers on estimating population parameters reflects the importance of the subject, the increased computing

power available and the increased statistical sophistication of practitioners. One well-documented fishery-independent abundance index that George Jolly (Jolly 1965) and George Seber (Seber 1965) were pioneers in, is obtained via tagging studies, known as capture-mark-recapture (CMR).

1.5.2 Capture-mark-recapture

Population abundance estimates via CMR models have been widely applied for more than four decades (Jolly 1965; Seber 1965). Estimating probabilities of capture (ρ) and survival or fidelity to the capture area (φ) from observed catch numbers and recaptures allows for the calculation of population abundance in an open population (Dunnington, Wahle *et al.* 2005), with the added benefit of evaluating population gains (recruitment and immigration) and losses (mortality and emigration) (Seber 1965; Lebreton, Burnham *et al.* 1992; Burnham and Anderson 2002). This approach is potentially well-suited to fisheries studies, as fishing methods by their nature capture samples of the available population and direct observations are often impossible. However, CMR can be difficult to conduct on shellfish, due to individuals' mobility and poorly understood behaviour, and in many instances the multi-species nature of the fishery introduces interactions that affect catchability. Despite difficulties, estimates of density via CMR have been applied to several decapod crustaceans: *Cancer irroratus* (Hilborn 1997), *Cancer maenas* (Addison 1997), *Cancer pagurus* (Bell, Eaton *et al.* 2003), *Callinectes sapidus* (Fitz and Wiegert 1992) and *H. americanus* (Dunnington, Wahle *et al.* 2005; Bowlby, Hanson *et al.* 2008). Yet a Jolly-Seber approach has yet to be applied to wild *H. gammarus* (Schmalenbach, Mehrtens *et al.* 2011).

1.5.3 Tracking technology

Conventional means of quantifying animal movements, such as trapping, tagging, and CMR methods rely on repeat observation, which are often few in the marine environment. Alternatively they rely on observations or returns from the public and commercial fishermen; while potentially representing a large collective effort, these data are not certain to provide the spatial or temporal resolution desired and unequal distribution of effort creates bias (Miller 1990). However, technological advances have allowed for the continuous tracking of animals after the initial trapping occasion. Archival or data storage tags store environmental data at set intervals for up

to ten years. However, these require retrieval, which is often difficult when monitoring cryptic benthic animals (Moland, Olsen *et al.* 2011a). Acoustic (and ultrasonic) techniques developed in the 1960's, but not implemented in wildlife studies until much later, use acoustic signals capable of travelling through the marine environment. Unlike radio signals which are quickly absorbed in seawater, acoustics propagate far and at a predictable speed; they can therefore precisely measure distances between a tracked target and receiver stations (hydrophones). Furthermore, if a pulsed signal is detected by three or more fixed (known) location hydrophones, the location of the signal source can be triangulated by time difference of arrival; giving rise to systems now used (Smith, Urquhart *et al.* 1998). For reviews of progress in the technical developments of acoustic telemetry, see; (Baggeroer 1984; Kilfoyle and Baggeroer 2000).

Acoustic tracking eliminates issues of poor visibility, deep waters and low rates of recapture from tagging studies. It allows biologists' access to information otherwise difficult or impossible to obtain. It vastly improves the quantification of movement, migration, distribution, activity patterns and habitat utilisation, within natural habitats and with little interference after initial trapping and tagging. Despite these qualities, its application in crustacean decapod ecology is currently limited (Smith, Collins *et al.* 1998; Smith, Collins *et al.* 2000; Watson, Golet *et al.* 2009; Guerra-Castro, Carmona-Suarez *et al.* 2011). The incremental growth of decapods through ecdysis, consequently means that external tags are lost, usually within the first year of tagging, however, the exoskeleton offers an advantage for attaching external tags without causing injury or mortality (Freire and Gonzalez-Gurriaran 1998). Due to the late uptake of acoustics in marine studies, they often have inappropriate sample size or definition of habitat availability that limits the generality of results and validity of analyses (Pittman and McAlpine 2003). Guerra-Castro and Carmona-Suarez (2011) reviewed the biotelemetry of crustacean decapods, in which the history and limitations in use for crustacean telemetry are discussed (Guerra-Castro, Carmona-Suarez *et al.* 2011). There are several studies on *Homarus* spp, mostly conducted on *H. americanus,* measuring daily movements and the distance of attraction to a baited trap (Watson, Vetrovs *et al.* 1999; Watson, Golet *et al.* 2009; McMahan, Brady *et al.* 2013; Wiig, Moland *et al.* 2013).

Fundamentally, data and knowledge regarding *Homarus gammarus* habitat use and movement remain scarce. Acoustic telemetry studies are beginning to shed light on

such behaviours, while removing some of the complications of fishing effort, catchability, weather and vessel hire, associated with trap based studies.

1.5.4 Marine protected areas

Over the past few decades, MPAs have gained popularity as a fisheries management tool and for marine conservation. They take numerous forms, with different levels of protection. Functioning no-take MPAs are thought to increase density, biomass and average size of species by protecting portions of the fishery from extraction (Sale, Cowen *et al.* 2005). Literature concerned with no-take MPAs is largely derived from work in tropical or sub-tropical waters (Hobday, Punt *et al.* 2005; Sale, Cowen *et al.* 2005; Goni, Quetglas *et al.* 2006; Shears, Grace *et al.* 2006; Goni, Hilborn *et al.* 2010). Halpern (2003) reviewed 89 studies of MPAs, despite data varying in quality, and showed that on average, with the exception of invertebrate biomass and size, biological variables had significantly greater values inside MPAs than outside of them (Halpern 2003). However, the success of an MPA depends upon the expectations and goals for it. It could be argued that to benefit society, no-take MPAs should also export target species adult biomass, referred to as 'spill-over'. Yet the certainty of this is limited by the lack of data regarding *H. gammarus*' connectivity between habitats and locations.

Case studies have shown some benefits of MPAs in Europe (Diaz, Mallol *et al.* 2011; Moland, Olsen *et al.* 2013), increased egg production and spawning biomass within the MPA being thought to in some cases marginally enhance recovery of stocks generally (Hobday, Punt *et al.* 2005). If increased fecundity and egg production is the goal, MPAs clearly have an important role to play, but their direct benefits to the fishery are difficult to detect. Increased concentrations of fishing effort at the edges of MPAs can restrict the level of spill-over from the MPA area, and various studies have noted no direct benefit to surrounding fisheries (Goni, Quetglas *et al.* 2006; Shears, Grace *et al.* 2006; Goni, Hilborn *et al.* 2010). The spatial configuration of marine MPAs therefore should reflect management objectives, if cross-boundary movement of harvestable individuals associated with certain habitats is desired for fisheries purposes, then boundaries should intersect that habitat (Kramer and Chapman 1999; Chapman and

Kramer 2000; Halpern 2003; Freeman, MacDiarmid et al. 2009; Berglund, M. et al. 2012).

Moland *et al.* (2011) investigated space use of *H. gammarus* by ultrasonic tracking within an MPA in Norway. Over a 12 month period, 95% of tagged lobsters (n = 20) remained within the MPA of 1km^2 (Moland, Olsen *et al.* 2011). A second study found distances moved were 15-580m (n = 10) from the site of first capture (Moland, Olsen *et al.* 2011a). Although studies are limited, data suggest that *H. gammarus* can be resident within limited home-ranges, possibly allowing MPAs to afford complete protection by letting boundaries incorporate preferred habitats. However, gaps in knowledge currently preclude implementing them with confidence that they will sustain or enhance surrounding fisheries.

1.5.5 Aquaculture and Enhancement

Conventional management measures maintain stocks by reducing mortality and increasing stock fecundity. With numerous reports raising concerns about the possible long term effects of overfishing of both *Homarus* spp, some managers are aiming towards enhancing the stocks through re-stocking via the release of hatchery-reared juveniles (Addison and Bannister 1994; Van der Meeren 2005; Schmalenbach, Mehrtens *et al.* 2011) or via habitat creation (Jensen, Collins *et al.* 1994; Castro, Cobb *et al.* 2001; Jensen 2002).

Although currently small, lobster aquaculture is a growing sector, driven by an increased worldwide demand for lobster and declines in some parts of *Homarus* spp ranges. *Homarus* are potentially well suited to aquaculture, with a short larval period, willingness to feed on natural or artificial food and rapid growth in warmer waters (Aiken and Waddy 1995; Kristiansen, Drengstig *et al.* 2004). Additionally there are concerns of negative impacts on native stock genetics (Waples 1999; Castro, Cobb *et al.* 2001; Araki and Schmid 2010), despite some of the negative impacts being dismissed, it remains unlikely that aquaculture will replace commercial fishing for lobsters.

Lobster re-seeding or re-stocking via the release of cultured juveniles has continued to receive attention since the 1850's (Addison and Bannister 1994). Enhancement in this manner was comprehensively reviewed by Conan (1986), noting that 'references on

recruitment enhancement are extremely scarce' (Conan 1986). Since Conan's review, new data on the success of releasing micro-tagged juveniles into the wild have become available, and results are discussed in a review by Addison and Bannister (1994). Studies now successfully show hatchery-reared animals recruiting to the fishery to which they were released (Addison and Bannister 1994), but whether they add to the stock or displace it remains unclear. There exist important biological questions on whether re-stocking programmes are likely to provide sustainable benefits to fisheries, with benefits more likely to be observed in areas of low stock levels (Bannister and Addison 1998).

Research has also focused on enhancing the habitat of clawed lobsters by providing refuge in the form of artificial reefs (Scarratt 1968; Briggs and Zawacki 1974; Sheehy 1976; Eggleston, Lipcius *et al.* 1990; Jensen, Collins *et al.* 1994; Castro, Cobb *et al.* 2001; Jensen 2002). Providing additional habitat for settlement and protection may increase overall carrying capacity, growth, reproduction, recruitment and survival if the artificial habitat alleviates limitation by some other resource (Bohnsack and Sutherland 1985). This is most likely if supply of larvae is the limiting factor and/or habitat is not at carrying capacity (Wahle and Steneck 1991; De Lafontaine 1992; Langhamer and Wilhelmsson 2009). Bennett (1980) speculated, that if the cost of construction were ignored, habitat enhancement in areas not suitable for lobsters would be of some value, but in areas of high fishing pressure habitat improvement would probably not improve stock abundance (Cobb and Phillips 1980) as, like hatchery-releases, it is unclear whether artificial reefs enhance or merely redistribute stocks (Jensen, Collins *et al.* 1994; Lindberg 1997).

1.6 Future research and discussion

Homarus spp are amongst the most studied of all marine invertebrates, being model systems for many biological fields (Phillips 2013) and supporting some of the most productive fisheries in the world. European lobster studies have a much longer history than that of American lobster, however the quantity of published literature on *H. americanus* now far exceeds that of *H. gammarus* (Fig. 1.1); it is attributable in part to dramatic increases in catch rates and mass mortality events of *H. americanus* (Steneck and Wilson 2001; Mullen, Russell *et al.* 2004).

Recent *H. gammarus* research largely focuses upon three key topics: genetics (Ulrich, Muller *et al.* 2001; Jørstad, Prodöhl *et al.* 2004; Jørstad, Farestveit *et al.* 2005; Triantafyllidis, Apostolidis *et al.* 2005), disease and parasites (Stebbing, Pond *et al.* 2012; Wootton, Woolmer *et al.* 2012; Davies, Whitten *et al.* 2014), and aquaculture and enhancement (Benavente, Uglem *et al.* 2010; Daniels, Merrifield *et al.* 2013; Drengstig and Bergheim 2013). While these topics are potentially important for UK lobster management, investment in *ex situ* studies without a sound understanding of the *in situ* fishery may not provide sufficient information to ensure the continued productivity, robustness to future pressures, or future enhancement of the stocks.

Despite the accumulated knowledge regarding UK lobster, numerous knowledge gaps remain that potentially prevent the accurate modelling of stock status. The first goal should be improving data and understanding of larval distribution and settlement. In contrast to *H. americanus*, understanding of the relationship between ovigerous females within the catch, larval production, settlement strength and subsequent recruitment to the fishery, is limited. Management regulations should respond to changes in stock recruitment rather than changes to landings, so as to be earlier with their response; further advances in predicting recruitment could enable pre-emptive rather than responsive regulation (Caputi, de Lestang *et al.* 2014; Hintzen, Roel *et al.* 2014).

Secondly, movement, distribution and habitat-utilisation of adult lobsters at various spatial scales should ideally be evaluated in order to understand effects of extraction, protection and environmental change. Historically this has been addressed via commercial catch data and the use of baited traps, however, variations in catchability especially will constrain understanding and evidence. The extent to which spatial and temporal trap catches reflect demographic patterns of abundance and movement is still debated, despite advances in the understanding of the trapping process. Greater certainty and spatial resolution of these behaviours will improve the ability to differentiate between losses due to fishing and losses due to natural mortality, emigration, or being unavailable to capture.

Regionally specific parameters such as maturity, growth increments, spatial extents and connectivity between neighbouring stocks need ideally to be estimated and applied to

regionally specific stock assessments. Alongside this, improvements in the collection of fishery-dependent data should include greater spatial resolution, reporting of undersized individuals and species targeted by the fishermen. This could enable regional biological parameters and commercial catch and effort data to be pooled into biologically appropriate 'unit stocks' for assessment, rather than stocks defined by jurisdictional boundaries.

This literature review also highlights the need for increased use of fishery-independent assessments in conjunction with commercial catch data, and for *in situ* studies to reduce their reliance on baited traps as the sole sampling tool. The extent to which spatial and temporal patterns in trap catches reflect patterns of abundance and movement is still debated (Tremblay 2000; Bell, Addison *et al.* 2001; Tremblay and Smith 2001; Geraldi, Wahle *et al.* 2009).

The exceptionally high landings of *H. americanus* currently being reported are supplying the majority of the global demand for clawed lobster protein. However, as there is little understanding of the sustainability of these catches, they are not certain to continue to meet this demand. Decreases in *H. americanus* landings could lead to increased pressure on *H. gammarus* stocks. If this were the case it is difficult to determine whether current UK management regimes could control increased pressure, without sudden implementation of further regulation and requirements for data. Despite catch rates remaining stable for several decades around the UK, the fishery is not necessarily immune to overexploitation or future stock crash, as has been observed in Norwegian fisheries. If fisheries management were more adaptive in nature it could reduce the risk of future overfishing and stock collapse. Currently there is little scope to predict future UK catches; the first indication of stock collapse would be a sudden significant reduction of commercial catches, at which stage it is very difficult to remedy quickly. Identifying individual UK stocks, monitoring pre-recruit size classes and increasing available data necessary for their management are desirable goals.

1.7 Thesis outline and objectives

The aim of this thesis is to address some of the highlighted knowledge gaps and provide data on behaviour, movement, distribution and abundance of *Homarus*

gammarus off the coast of Northumberland, UK. Findings will act as a basis for the increased understanding and future management of this stock, with potential implications on the wider UK lobster fishery.

Chapter 2 aims to use a Jolly-Seber related CMR approach to provide the first estimate of UK *H. gammarus* density. Fishery-independent trap catch data will be used to estimate short-term parameters of catchability, site fidelity and effective fishing effort of traps over the course of their soak-time.

Chapter 3 investigates the impact of inter-specific and intra-specific interactions on the subsequent catch rates and catchability of target species. This will be achieved via the analysis of a large fishery-independent dataset, and via pre-loading trap studies.

Chapters 4 and 5 aim to elucidate movements and distributions of *Homarus gammarus* in relation to habitat, sex and size. Chapter 4 uses fishery-independent trap catch data and permanent tags to gain recapture data. Chapter 5 uses an acoustic telemetry tracking approach to accurately monitor short-term high-resolution movements, activity patterns and habitat-utilisation.

Chapter 6 provides a synthesis of the key findings from the thesis and addresses limitations and wider implications of the study.

Chapter 2:

Estimating *Homarus gammarus* densities from continuous, short-term capture-mark-recapture catch data

Chapter 2: Estimating *Homarus gammarus* densities from continuous, short-term capture-mark-recapture catch data

2.1 Introduction

Population size estimates via traditional CMR models date back five decades (Jolly 1965; Seber 1965), but were first implemented over a century ago (Petersen 1896; Lincoln 1930). The CMR approach uses a captured sample of animals that are marked and released back into the environment. Subsequent samples of individuals are captured from the same population; these samples will consist of some marked 'recaptures' and some unmarked individuals captured for the first time. Unmarked individuals on each occasion may be marked and released back into the population for subsequent sampling (Burnham, Anderson *et al.* 1987; Cooch and White 2011). Subsequent encounters are a function of two probabilities: the probability of surviving and not emigrating until the next occasion, and, given that the individual is alive and in the sample area, the probability that the individual is re-caught. Population size can then be estimated from as few as two sampling occasions, but usually more occasions are required. The basic probabilistic scheme, common to all Cormack-Jolly-Seber (CJS) type methods involves estimating probabilities of capture (ρ) and survival (φ) from CMR data to calculate the population size, based on subsequent sample catches (Dunnington, Wahle *et al.* 2005).

This approach is potentially well-suited to studies of fisheries resources. Direct observation is often difficult or impossible, particularly when studying mobile, benthic animals that are naturally cryptic in behaviour; furthermore, fishing methods by their nature sample the available population, suiting CMR, although in practice, post-tagging behaviours may require caveats.

Population estimates, particularly those from CMR are difficult to derive for shellfish, due to the potential mobility of the animals, poorly understood behaviour, and the multi-species nature of fisheries introducing inter-specific interactions (*Cancer pagurus* and *H. gammarus*). Estimates of population size via CMR have nevertheless been applied to several decapod crustaceans (Tremblay and Smith 2001), for example *Cancer irroratus* (Hilborn 1997)*, Cancer maenas* (Addison 1997), *C. pagurus* (Bell, Eaton

et al. 2003)*, Callinectes sapidus* (Fitz and Wiegert 1992) and *Homarus americanus* (Cobb, Booth *et al.* 1997; Dunnington, Wahle *et al.* 2005; Bowlby, Hanson *et al.* 2008). Bannister *et al.* (1994) provides provisional estimation of catchability of hatchery-reared lobster, however, CMR studies to calculate ρ, φ and population abundance have not been published for *H. gammarus* to date.

Most CMR (CJS and related) are conducted over long time periods (months-years), where sampling is seen as occurring at discrete intervals, with population dynamic processes occurring between sampling occasions. Each estimate of population therefore gives an estimate at that point in time, allowing for seasonal changes in population to be tracked. However, the use of baited traps over short time periods does not conform to the CJS approach, as the capture process is continuous while the trap is set (soaking). The trapping process is therefore operating alongside short-term population processes such as emigration, immigration, deaths and births. Bell *et al.* (2003) developed a CMR method to estimate densities of *C. pagurus* from short-term trapping, later extended to *H. americanus* (Dunnington, Wahle *et al.* 2005). This method used estimations of continuous logistic parameters that operate alongside the sampling process, rather than discrete probability parameters occurring between them. This allows for instantaneous estimates of population parameters to derive an abundance of crustacean over the study period. Here this method is implemented for European lobster, *H. gammarus*, using an adapted version of the Dunnington *et al.* (2005) model with elements of the Bell *et al.* (2003) model, to take account of the natural decay in fishing effort exerted by traps over the soak period. This decay is due in part to trap saturation and a decrease in the attractiveness of the bait.

The aim of this short-term CMR study was to develop a suitable methodology in order to estimate the catchability, and site fidelity of portions of the population. These estimates coupled with catch data can be used to provide estimates of abundance, density, and composition of European lobster populations independent of fisheries data. The CMR technique will be critically examined to highlight potential sources of error or uncertainty, and challenge the assumptions that are inherent in the method to help provide a credible and suitable method for future assessments.

2.2 Methodology

2.2.1 Study site

Trap-fishing within the region is restricted by the available habitat for target species and potential conflict with other gear types, particularly trawlers. Many fishers use an assortment of trap types, the majority being multi-purpose, side-entry parlour traps, deployed on various ground types at different times of year to target particular species. There are 43 vessels under 12m with registered shellfish permits at the Port of Blyth, although not all registered vessels are active (NIFCA Officer pers comm.). Each registered vessel has the ability to fish up to 800 traps within 6nm of shore, however, most trapping activity off Blyth occurs within the few miles of shore (Turner, Hardy *et al.* 2009).

CMR studies were conducted at a single site 3.2km due East of the Port of Blyth, Northumberland, in 2012 (Fig. 2.1). Surveys were conducted from on-board the 18.9m Research Vessel Princess Royal, (05 Sep 2012 to 10 Oct 2012). The site is composed of a mixture of hard and soft substrate, but predominated by rock and cobble forming two distinct areas of complex habitat, site depth varied from 16.7m to 31.8m. Remote from any significant bathymetric or offshore features, the site is regarded as a typical inshore mixed habitat site.

2.2.2 Data collection

For all scientific trap-fishing, a dedicated fleet of standard, commercial 10mm steel-framed parlour traps were used; measuring 0.68 x 0.46 x 0.38m, with 27mm square mesh and selective grill on the bottom and a single-side 130mm fixed diameter entrance. Escape vents are not required on UK commercial traps and were not desired for this study, as lobsters of all sizes were of interest. Traps were baited with a single frozen flatfish (20-30cm Total Length) per trap, with old bait removed and replaced on each haul occasion. Flatfish, predominantly dab (*Limanda limanda*) and plaice (*Pleuronectes platessa*), were used as bait as they are thought to remain attractive to lobster for longer periods (pers. comm) and are less prone to scavenging by hagfish (Myxinidae).

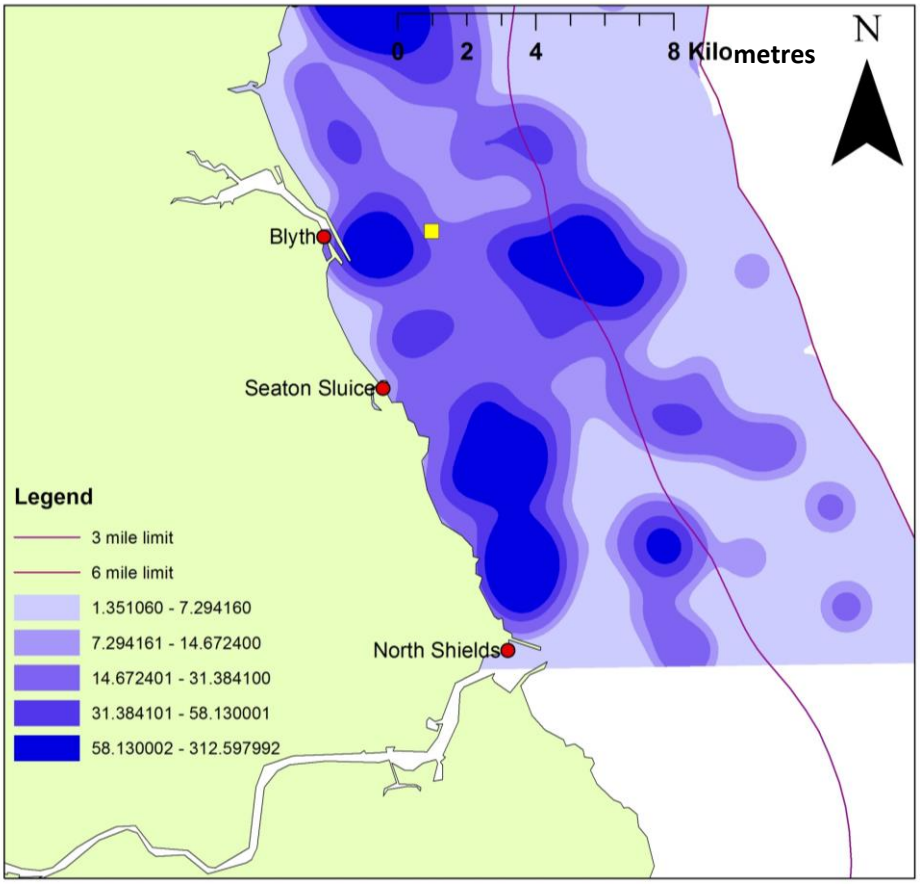
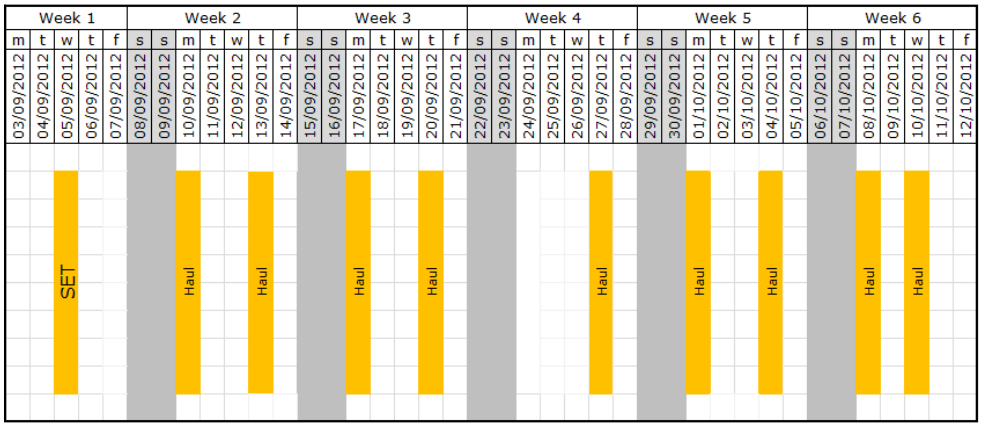


Figure 2.1 Southern most Northumberland coastline; the major fishing ports are highlighted with red circles (●), and the CMR study site highlighted with yellow squares (■). The map is overlaid with lobster landings ($kg^{-km^{\wedge}2}$) (Turner *et al.* 2009).

Traps were arranged in eight identical strings (A-H; West-East) of eight traps, set in a North to South direction, perpendicular to the tidal flow (1-8; North-South). Preliminary studies showed that traditional, commerical spacing's of ca. 18m between traps, caused interactions; therefore spacing was increased to approximately 40m between traps and 100m between strings. To test for interactions between individual traps and strings, the difference in catch rates of total lobsters per trap was tested between outside strings (A and H) and inside strings (B through G), and between the end traps of each string (1 and 8) and inside traps (3 through 6). On setting the strings the vessel was lined up to predetermined string positions with a due North bearing, using the on-board navigation software. Strings were then set by releasing the first weight, once the vessel was at the correct position the string was released at a speed of 3.5 knots. String locations within the array were spatially referenced with GPS and water depths were recorded for each occasion, as equipment can move during shooting, resetting, unfavourable weather, and from interaction with other sea users. However the strings remained within ±10m of the initial location. Although commercial

fishing continued within the area during the study period, there were no commercial traps fished directly within the vicinity of the array. Therefore interactions from other fishing effort inputs were considered to be unimportant.

Table 2.1 Dates of setting and hauling of all strings of traps during the six week study period. Poor weather during the beginning of week four suspended hauling temporarily.



Strings were allowed to soak for five days prior to the first haul occasion, to generate a sample of animals for initial marking. The study consisted of hauling all 64 traps (8 strings of 8 traps) at approximately four day intervals over a five week period, however due to weather restrictions hauling was opportunistic, and soak time was not consistent (Table 2.1). The flexibility of the modelling design allowed for variability in sampling interval to be accommodated during analysis. Of the 64 string-hauls throughout the study period, mean soak time was 3.75 days, minimum 2 days, and maximum 7 days (Table 2.1). To avoid difficulties in the modelling due to strings being at unequal soak times (Bell, Eaton *et al.* 2003), all strings were hauled on each occasion.

Upon hauling of the strings, the catch from each individual trap was removed and stored in separate containers to maintain trap-specific catch information. Biometric data were recorded for every individual *H. gammarus* and *C. pagurus;* including species, carapace length for lobster and width for crab (CL: rear of eye socket to base of the carapace, CW: widest part of the carapace), sex, presence of eggs, general condition and their capture location (site, string and trap number).

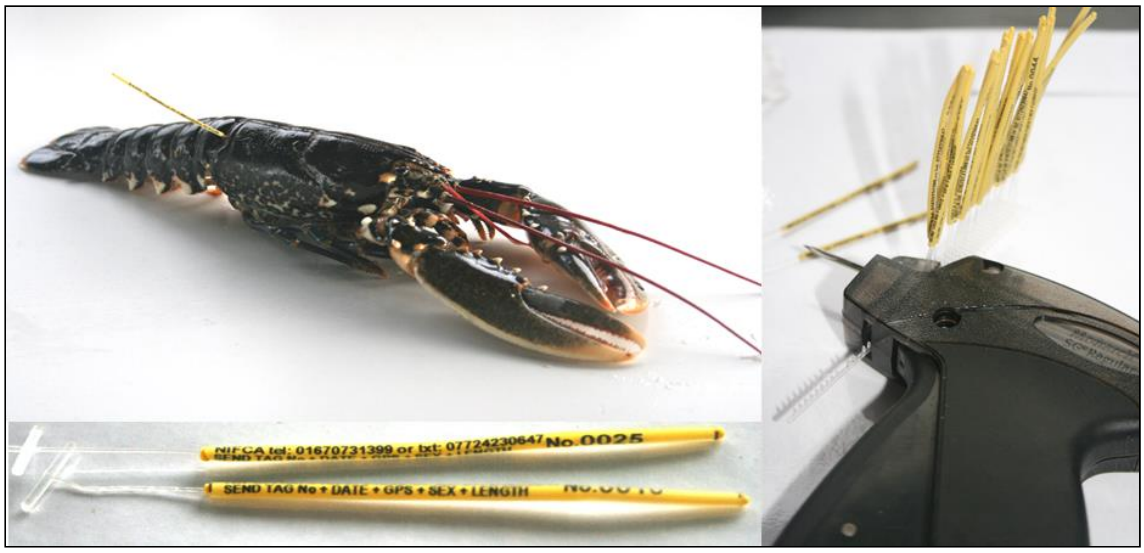


Figure 2.2 Images of lobster with inserted T-bar anchor tag, the tag applicator and loose tags showing the 'T-bar'.

All lobsters were then tagged with a persistent T-bar tag with printed information (TBA1, yellow, 50 × 2mm, Hallprint Pty. Ltd, Holden Hill, South Australia); inserted into the abdominal musculature between the carapace and the first abdominal segment, offset from the centre to avoid the abdominal artery and vital organs (Fig. 2.2). Applied correctly in this position tags remain post-ecdysis, resulting in an individual lobster being identifiable for several seasons. Tests prior to the sampling coupled with previous studies (Smith, Jensen *et al.* 2001; Moland, Olsen *et al.* 2011) show that the T-bar tags are sufficiently durable to enable identification of recaptured animals after periods of up to several years, without appearing to affect survival or behaviour within the first year of tagging. Each tag has a unique four digit identification number, making it possible to construct accurate capture and movement records for each marked lobster (Fig. 2.2). All caught animals were quickly released, unless seriously damaged, in which case they were removed from the experiment. Recaptured animals with an existing T-bar tag, had their unique ID noted and their new string and trap position recorded. Release location was at the approximate location of the trap from which they were captured, by releasing the relevant boxes of animals at the same time as the traps were reset.

2.2.3 Model framework

A general CJS (Cormack 1964; Jolly 1965; Seber 1965) type model framework for CMR data was first defined, in which a cohort of marked lobsters are released, and

subsequent sampling used to recapture the 'survivors' (those that remain within the study area) (See; Appendix III, for RCode provided by M. Bell). Recaptures and newly marked individuals were re-released at approximately the same place and time of capture, and this process was repeated over eight separate fishing occasions. Consequently each marked individual may be captured several times over the course of the study, generating a capture history (CH) where one of three observed states was recorded for each day after first release: **0** not observed; **1** captured and released; **-1** captured and removed from the study. A value of 0 was recorded if no traps were hauled that day or if the tagged lobster was not observed on a haul occasion. A value of -1 was recorded if the lobster was so damaged that it would impact the survival or catchability of the individual, and was then removed from the study site.

The probability of a particular CH occurring was the product of a series of probabilities of the possible fate of the individual over each day following marking and first release (Lebreton, Burnham *et al.* 1992). Given an individual's availability within the capture area during the study ('*Area over which traps exert an influence and the area around traps from which a lobster could potentially enter the area of influence*' (Bell, Eaton *et al.* 2003)), three possible fates could be defined: **(1)** the lobster does not enter a trap, but remains in the capture area; **(2)** the lobster enters a trap and is observed; **(3)** the lobster does not enter a trap and permanently emigrates from the capture area. The probabilities of one of these fates occurring can be described by three parameters describing fishing and population processes between release occasions; probability of capture (p), probability of survival (φ) and fishing effort (f). Given that the study period was short it was assumed that movement processes would dominate over survival processes. Therefore φ is hereafter referred to as site fidelity (not emigrating) (Lebreton, Burnham *et al.* 1992).

For short-term trap fishing, where traps are hauled and immediately reset, the capture process is complex and considered continuous (i.e. capture could occur at any point between one haul and the next). Effectively the model treated an occasion, the hauling and setting of traps, as a single point in time. Calculations within the model outlined here, were therefore conducted on a continuous scale, with capture process parameters cast in continuous terms and population processes described as instantaneous rates operating simultaneously (Dunnington, Wahle *et al.* 2005). To

generate continuous terms the initial probabilistic parameters p and φ (constrained between 0 and 1 to give meaningful probabilities (Lebreton, Burnham *et al.* 1992)) were transformed logistically to continuous parameters of catchability (q) and mortality (μ) respectively. However, due to the assumption that movement processes dominated survival processes, μ is hereafter referred to as rate of loss. Continuous parameters were used for model calculations and the construction of the reduced m-array tables (Table 2.2). Re-casting the parameters from probabilistic to continuous forms, also allowed for easier incorporation of the unequal sampling intervals (Bell, Eaton *et al.* 2003; Dunnington, Wahle *et al.* 2005).

The CMR model required the following key assumptions to be made (Lebreton, Burnham *et al.* 1992): (1) tagged individuals mix freely with the untagged population; (2) tags remain present and are always detected in the catch or the rate of tag-loss is known; (3) capture and tagging does not alter the probability of survival or behaviours that would change the probability of capture, relative to untagged or non-captured individuals; (4) individuals that leave the study area do not return to the study area; and (5) interspecific interactions within and around the trap do not affect capture probability, i.e. effort exerted and probability of capture is equal across all traps and all animals.

Table 2.2 The reduced m-array format of CMR data. R, is the number of lobsters released at occasion *i*, and *m* the number of lobsters recaptured on occasion *j*.

Occasion	**Releases**	**Recaptures**				**Not recaptured**
		j = 2	j = 3	…	J	
i = 1	R_1	$m_{1,2}$	$m_{1,3}$	…	$m_{1,J}$	$R_1 - \sum_{J=2}^{J} m_{1,J}$
i = 2	R_2		$m_{2,3}$	…	$m_{1,J}$	$R_2 - \sum_{J=3}^{J} m_{2,J}$
…	…			…	…	…
I	R_I				$m_{I,J}$	$R_I - \sum_{J=I}^{J} m_{I,J}$

The model (See; Appendix III) was formulated in terms of CMR data summarised in tabular reduced m-array format (Table 2.2). Each row represents recaptures for a

particular release cohort. The release totals (R_i) comprised both newly tagged lobsters and recaptures, and multiple recaptures were pooled with first recaptures from a new release cohort (Burnham, Anderson *et al.* 1987). CHs recorded in a reduced m-array allowed for expected (E) values of each recapture-cell ($m_{i,j}$; Table 2.2) to be calculated. For example, expected value for CH [101] (i.e. released, not observed, and then observed again), for occasions i, j-1, and j respectively, may be calculated as:

$$\boldsymbol{E[m_{i,j}] = R_i \times P(available)_{j-1}^{i} \times P(capture)_{j}^{j-1}} \quad \textbf{[Eq. 2.1]}$$

where $m_{i,j}$ is the number of lobsters that were released on occasion i and recaptured on occasion j; R_i, is the total number of marked lobsters released on occasion i, and the final two terms are probabilities (P) of the two fates leading up to being recaptured on occasion j. $P(available)_{j-1}^{i}$ is the probability of remaining available for capture within the capture area (i.e. not dying or emigrating) from the occasion of release i, up to and including occasion *j-1*, without being captured. $P(available)_{j-1}^{i}$ can be expressed in terms of the parameters of catchability (q) and rate of loss (μ) as:

$$\boldsymbol{P(available)_{j-1}^{i} = exp\left(-\sum_{j-1}^{i}\left(f_{j-1}q_{j-1} + t_{j-1}\mu_{j-1}\right)\right)} \quad \textbf{[Eq. 2.2]}$$

where f_{j-1} is the effective fishing effort over the time between occasion i and occasion j-1, and $q_{j-1}$the catchability on occasion *j-1*. As fishing effort, f, effectively scales q by the time over which traps are set, soak time is not included in this expression ($f_{j-1}q_{j-1}$). The second expression ($t_{j-1}\mu_{j-1}$), includes t_{j-1}, the soak time (t) in days between occasions i and *j-1*, and μ_{j-1}, the rate of loss on occasion *j-1*.

$P(capture)_{j}^{j-1}$ (Eq. 2.1) is the probability of being caught, given the lobster's availability in the capture area, between occasion i and j. This can also be termed the rate of harvest, expressed in terms of continuous parameters as:

$$\boldsymbol{P(capture)_{j}^{j-1} = \left(1 - exp\left(-\left(f_j q_j + t_j \mu_j\right)\right)\right)\frac{f_j q_j}{f_j q_j + t_j \mu_j}} \quad \textbf{[Eq. 2.3]}$$

Equation 2.3 assumes that f, q, and μ occur simultaneously and compete with each other. The last term, $\frac{fq}{fq+t\mu}$ expresses the proportion of losses due to fishing, and the first term expresses the total number of losses. This expression is derived from the

Baranov catch equation, in which the term fq is equivalent to fishing mortality and $t\mu$ is equivalent to natural mortality during the time between occasions (Baranov 1918).

Given the assumption that the fate of each individual lobster is independent, but the identity of parameters between individuals within the same release cohort are the same, the appropriate model for the data is a multinomial one (Lebreton, Burnham *et al.* 1992); this gives the probability of any particular combination of a number of fates for the various cohorts. The kernel of the log-likelihood of parameter θ for the model, $\ln L(\theta)$, can be calculated as:

$$\ln \boldsymbol{L}(\boldsymbol{\theta}) = \sum_{i=1}^{I}\left(\sum_{j=i+1}^{J} \boldsymbol{m_{ij}} \ln \boldsymbol{Pr}\left[\boldsymbol{m_{ij}}\right] + \left(\boldsymbol{R_i} - \sum_{j=i+1}^{J} \boldsymbol{m_{ij}}\right) \ln \boldsymbol{Pr}\left[\boldsymbol{R_i} - \sum_{j=i+1}^{J} \boldsymbol{m_{ij}}\right]\right) \quad \textbf{[Eq. 2.4]}$$

where the probability of the 'recaptured' cell m_{ij}, in the reduced m-array table (Table 2.2), $Pr\left[m_{ij}\right]$, can be summarised using expectations from equation 2.1:

$$\boldsymbol{Pr}\left[\boldsymbol{m_{ij}}\right] = \frac{\boldsymbol{E}\left[\boldsymbol{m_{ij}}\right]}{\boldsymbol{R_i}} \quad \textbf{[Eq. 2.5]}$$

The probability of the 'not recaptured' cell for row i, $Pr\left[R_i - \sum_{j=i+1}^{J} m_{ij}\right]$, the number of lobsters released in cohort i that are never seen again, can be calculated as:

$$\boldsymbol{Pr}\left[\boldsymbol{R_i} - \sum_{j=i+1}^{J} \boldsymbol{m_{ij}}\right] = 1 - \sum_{j=i+1}^{J} \boldsymbol{Pr}\left[\boldsymbol{m_{ij}}\right] \quad \textbf{[Eq. 2.6]}$$

Estimated parameters from the model were scaled by effective fishing effort, creating meaningful constraints between soak times of different length (See; section 2.2.5). To find the values of q and μ that maximise the log-likelihood value, a quasi-Newton algorithm was used (Press, Flannery *et al.* 1989). For the purposes of interpretation, the q and μ parameters were transformed back to scales of probability; leading to parameters of probability of capture per effective effort exerted by traps on occasion j, p_j (not the same as $P(capture)$) and probabilities of site fidelity on each day of the interval leading up to occasion j, φ_j:

$$\boldsymbol{p_j} = 1 - \exp(-\boldsymbol{q_j}) \quad \textbf{[Eq. 2.7]}$$

$$\boldsymbol{\varphi_j} = \exp(-\boldsymbol{\mu_j}) \quad \textbf{[Eq. 2.8]}$$

The variance-covariance matrixes for the logistically transformed parameters were calculated numerically and for derived parameters the delta method was used to obtain approximate standard errors (s.e.) (Press, Flannery *et al.* 1989; Burnham and Anderson 2002; Dunnington, Wahle *et al.* 2005). The goodness-of-fit (GoF) tests, generated in programme MARK use the second part derivative method to generate derivatives numerically (Cooch and White 2011).

Once estimates of parameters μ, q, and f were obtained, the population size (N) could be estimated through the following calculation, allowing for appropriate scaling of catch data per occasion, j:

$$\boldsymbol{N_j = \frac{C_j}{P(capture)_j}} \quad \textbf{[Eq. 2.9]}$$

where $N_j$is the population of lobsters over the entire soak time from which the observed catch at occasion j, C_j, is drawn. The variance covariance matrix was then used to obtain s.e. and confidence intervals (CI) for the population size estimates for each sex over each occasion after the first occasion.

Sexes were treated as two separate groups during this study, males (Group 1) and females (Group 2), this allowed for differences in catchability and rate of loss to be modelled and population estimates between sexes compared. Due to the short time period of the study, each population estimate was essentially a separate estimate of the same population; making it possible to derive a single, mean population estimate for each group. As s.e. could not be aggregated into the mean, the standard deviation of all estimates was used to gain s.e. and 95% CI's of the range of values.

The population estimates was given in terms of abundances within the capture area. To transform these estimates into densities requires some information about the size of the capture area from which the catches were drawn..

To estimate capture area, the trapping area must first be estimated; defined as the area within which the probability of capture of a lobster, during the deployment time of the trap, was greater than 0 (Bell, Addison *et al.* 2001). Trapping area of a single trap was estimated as the area of a circle with radius equal to that of both the area of bait influence (r_b) and average home-range size of a lobster (r_h) (Fig. 2.3). Theoretically this represents the maximum distance a lobster could travel to enter a trap (Watson, Golet

et al. 2009). However, in reality this area is influenced by many factors, such as soak-time, movement and foraging behaviour, habitat type, water movement, temperature and other functions that may vary spatially, temporally and among individual lobsters. It was beyond the scope of this study to determine trapping area from fieldwork. Therefore, an estimate for r_b, from Watson *et al.* (2009), of 11m radius was used. However, r_h from Watson *et al.* (2009) of 30m radius was considered small. *H. americanus* may move about 100-300 m d^{-1} (Krouse 1980; Watson, Vetrovs *et al.* 1999), and further albeit during seasonal migrations, reportedly walking 1-4km^{-day} and covering 30-100km in one season (Dow 1974; Fogarty, Borden *et al.* 1980a; Campbell and Stasko 1985; Campbell and Stasko 1986; Estrella and Morrissey 1997). For European lobster Moland *et al.* (2012) found home-ranges to have 10-250m radius (n=10). Therefore with some reservations related to the country and species differences within the limited evidence available, trapping area radius of a single trap was set at a nominal 100m; this takes into account the uncertain size of the lobster's home-range, but does mean that there is considerable overlap between the trapping areas of individual traps. A minimum convex polygon was drawn around the experimental traps on this basis, covering an area of ca. 0.42km^2 (Fig. 2.4).

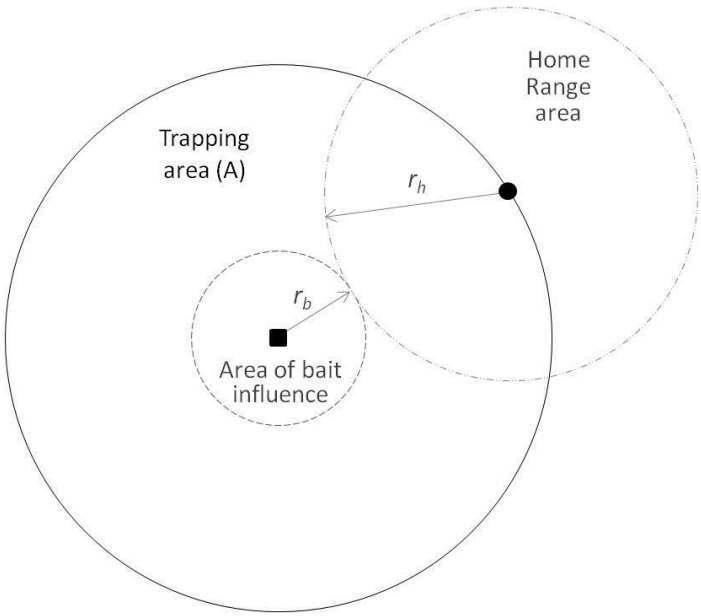


Figure 2.3 Theoretical trapping area (A) of a single trap (black square ■), the home range (radius = r_h) of an individual lobster (black circle ●) and the area of bait influence (radius = r_b)

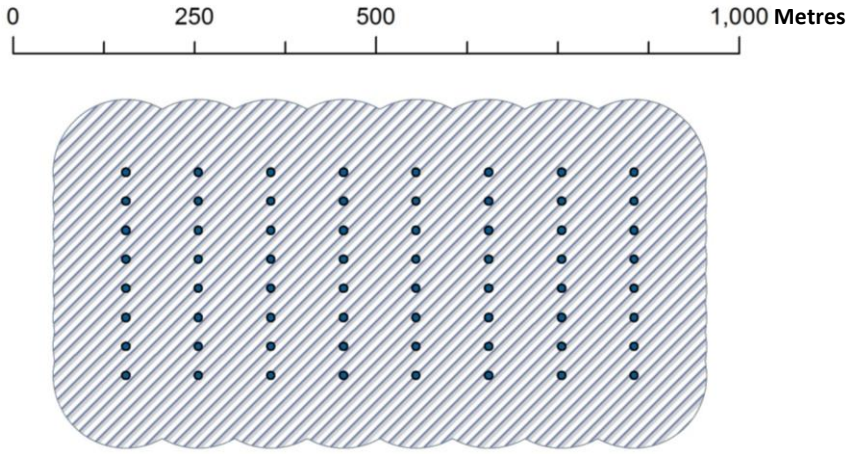


Figure 2.4 Capture area for the study formed from a minimum convex polygon of diameter 100m radius around each trap. The area generated is 416,966m^2.

2.2.4 Model fitting and goodness-of-fit

Twenty-five possible models were defined for the CMR data, constrained to time and sex parameters. From the most complex model ($\mu_{g*t}q_{g*t}$); known as the general or universal model, where parameters q and μ vary independently over time (t) and between groups (g); to the simplest possible model, where parameters μ and q are constant across time and between groups. Also included in the analysis were additive models (Lebreton, Burnham *et al.* 1992), where parameters differed between sexes but had the same pattern over time ($\mu_{t+g}q_{t+g}$).

To select the most parsimonious model (i.e. the simplest plausible model that fits the data with the fewest number of parameters) and therefore the most robust basis for inference about population size, the minimum value of the Akaike Information Criterion (AIC) in its bias-adjusted form, AIC_c was used (Burnham and Anderson 2002). Calculated as:

$$\boldsymbol{AIC_c = -2\,lnL + 2k\left(\frac{n}{n-k-1}\right)} \qquad \textbf{[Eq. 2.10]}$$

Where lnL is the log-likelihood for the whole model [Eq.2.4], k is the number of separately identifiable model parameters and n is the sample size (number of marked individuals). Assuming the most parsimonious model, that with the lowest AIC_c value, has a likelihood of 1, likelihood of other models can be calculated as:

$$\boldsymbol{model\ likelihood} = \boldsymbol{exp}^{\frac{-\Delta \boldsymbol{AIC_c}}{2}} \quad \textbf{[Eq. 2.11]}$$

where, $-\Delta AIC_c/2$, is the negative difference in AIC_c value between the model in question and the most parsimonious model, divided by 2. Burnham and Anderson (2002) suggest that models within 2 AIC units of the most parsimonious model are also supported, and should be considered as alternative models (Burnham and Anderson 2002). If more than one model appears suitable, model averaging is an option. However for simplicity this procedure was not used, since population size estimates were rather insensitive to model choice within the likely set of candidate models.

Once the top model had been selected further GoF tests were conducted in program MARK, to ensure the selected model fitted the data appropriately. Data were entered into MARK in the form of aggregated CH (See; Appendix IV). Firstly, the standard approach of program RELEASE was used to generate 'TEST 2' and 'TEST 3' of the general time-dependent CJS model to the data. TEST 2 tests the failure of the homogeneity assumption that every marked animal present in the population at time i has the same probability of being recaptured (assumptions 1 and 3). TEST 3 tested the assumption that all marked animals alive at i had the same probability of surviving (remaining within the study area) to occasion i+1 (assumption 3).

Because low numbers of captures and few recaptures might have yielded low power for the GoF tests, parametric bootstrapping using programme MARK was also conducted to allow for further testing. Within the bootstrap procedure, the parameter estimates of the model being evaluated were used to generate 1,000 new iterations of recapture data. Parametric bootstrapping was conducted for the general model ($\mu_{g*t}q_{g*t}$), a non-significant result meaning there would be sufficient justification to use this as a starting point for exploring simpler models, provided that those simpler models were nested within the general model. Bootstrapping also tests the dispersion of the data using the observed deviance divided by the mean of the bootstrapped deviances. A value close to 1, would suggest the data is not over dispersed. The observed model deviance and mean bootstrapped deviances, used to establish the likelihood of the observed model output, were also used to work out the dispersion of the data.

2.2.5 Effort modelling

Given unequal soak times between each haul occasion and parameter probabilities defined as instantaneous rates changing between occasions, it was essential to adjust the effective fishing effort applied by the fleet of 64 traps on each day of its soak. Catches are commonly assumed to have asymptotic relationships with soak time, due to trap saturation and declines in attractiveness of bait (Miller 1990; Fogarty and Addison 1997; Lindley, Erickson et al. 2011):

$$\boldsymbol{C_t = C_\infty(1 - e^{-bt})} \quad \textbf{[Eq. 2.12]}$$

Where C_∞ is the asymptotic catch (maximum possible catch +1), C_t the catch for soak time of t, and b the rate at which the increase in catch declines over time. As no independent estimates of b exist for *H. gammarus*, and as there was a positive correlation between C_t and t, catch data from this study were used to infer a value for b. Effort adjustment was also found to be relatively insensitive to choice of C_∞ over a range of realistic values and was therefore assumed to be the maximum catch for a single trap observed over the duration of the experiment + 1, multiplied by the number of traps in a string.

If the effective effort exerted by a string of traps j is set equal to 1 over the first day of the soak time, the effective effort on any subsequent day can be calculated as:

$$\boldsymbol{f_{ij} = f_{i-1,j}e^{-b}} \quad \textbf{[Eq. 2.13]}$$

The following approach was used to determine a value for b:

$$\boldsymbol{ln\left(\frac{1 - C_{tj}}{C_\infty}\right) = -b_t} \quad \textbf{[Eq. 2.14]}$$

where C_{tj} is the catch of string j over time t; this was the catch of individual strings for each occasion. The subsequent estimates of -b_t, were used to plot a curve of b throughout the course of a soak time.

2.3. Results

2.3.1 Catch data

In 2012 a total 597 individual lobsters were caught on nine separate haul occasions at the site. 562 were tagged and released and 77 of these subsequently recaptured, accounting for 13.7% of those tagged. Of the 562 tagged lobsters, 273 were male, and 289 female (M:F = 1:1.06), however, of the 77 recaptures, 57 were male and only 20 female (M:F = 2.85:1). Throughout the study period, 39 ovigerous females were caught, equating to 13.5% of the total number of females observed in the study.

The size distributions of male and female lobster populations were very similar, with average CL of 81.5mm (± 0.41mm$_{s.e.}$) and 82.7mm (± 0.46mm$_{s.e.}$) respectively (Fig. 2.5). The lower quartile was equal between the sexes at 77mm, and the upper quartile differed slightly from 85mm for males to 87mm for females. The overall size frequency distribution of lobsters was unimodal, the single peak in frequency occurring at 80-85mm (Fig. 2.6); the distribution was slightly skewed towards smaller size classes.

Catch rates were found to differ significantly between inside ($\bar{x}_{432}$ = 1.03) and outside ($\bar{x}_{144}$ = 1.59) strings (t-test$_{574}$: $p < 0.001$), however total lobster catches were not significantly different between inside traps and outside traps (t-test$_{574}$: $p = 0.44$).

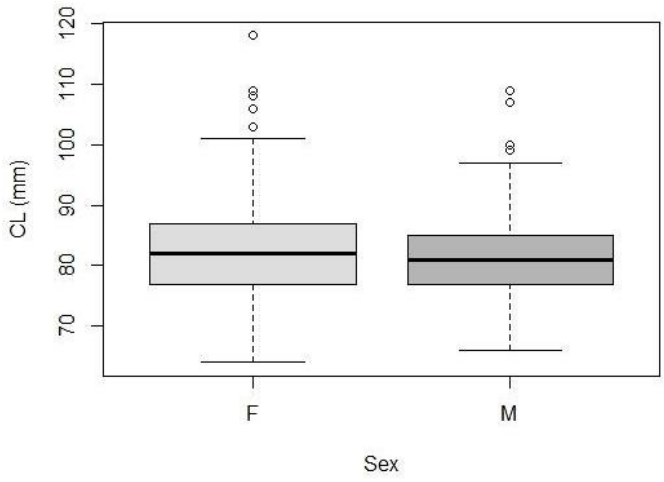


Figure 2.5 Box and whisker plots of the female and male population size distribution, showing mean, UQI, LQI, max, min and outliers.

Assumption 5 stated there was no effect of interspecific interactions on the catchability of tagged and untagged lobsters. Despite lobster and crab catch rates being negatively correlated (y = -0.23; R^2 = 0.90; Fig. 2.7), it is impossible to identify if this is due to agonistic interactions or differences in spatial distributions. However, from knowledge of *H. americanus*, it is assumed that there is no impact of crab presence on catchability, site fidelity or catch frequency of lobster within the study.

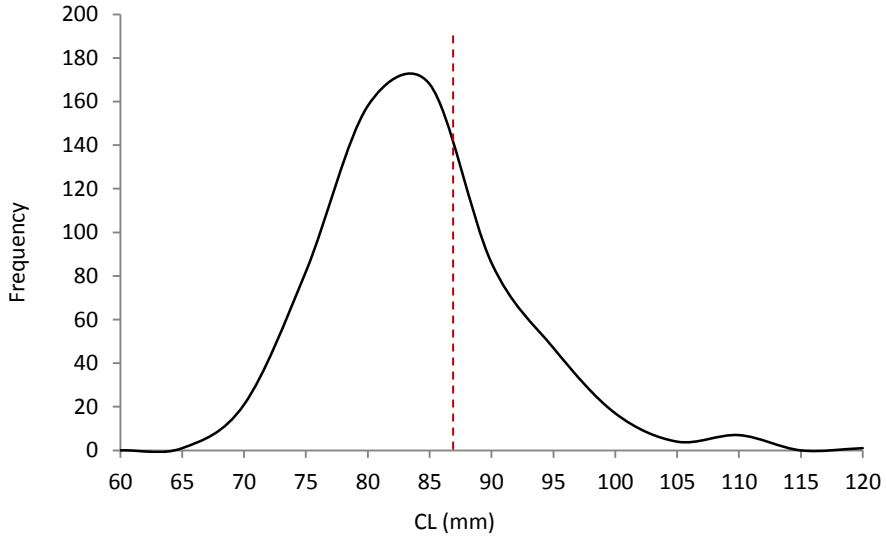


Figure 2.6 Size frequency distribution of observed lobster population during the study period, the red line indicates the MLS of 87mm CL.

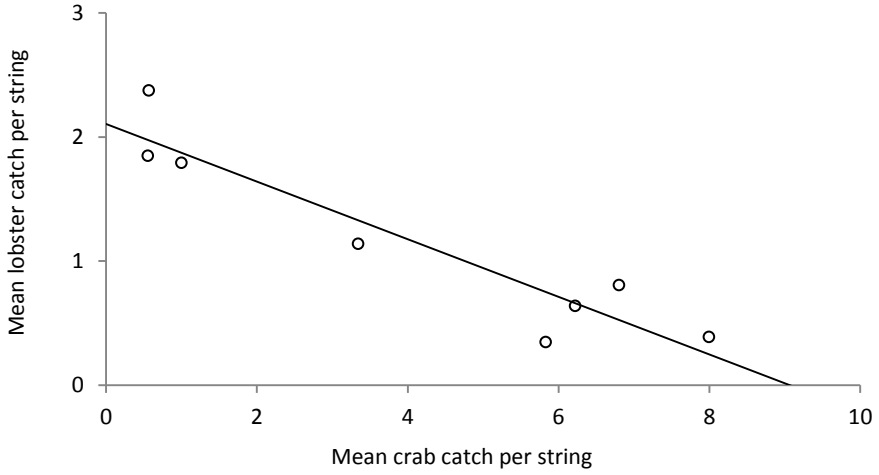


Figure 2.7 Mean catch per string of crab on the x-axis and lobster on the y-axis. Black line represents a linear regression y = -0.2323x + 2.1054; R^2 = 0.8794.

2.3.2 Capture-mark-recapture data and model selection

Rate of recaptures over the study period were relatively low (n = 77), attributable in particular to low numbers of lobsters initially caught. Recapture rates were 21% and 7% for males and females respectively; the lower recapture rate for females could

increase uncertainty of the female population estimates, however pooling the two sexes would remove sex specific observations, therefore analysis with the two separate groups was appropriate.

AIC_c values for the 25 models (Table 2.3), all of which were nested within the most complex model ($\mu_{g*t}q_{g*t}$), indicate that the most parsimonious model was ($\mu_{\cdot}q_g$) (AIC_c = 728.95). According to this model, rate of loss (μ) remained constant throughout the study period and between the two groups ($0.0002^{-day} \pm 0.005_{s.e.}$). Suggesting that fidelity to the capture area was the same for all lobster over the entire study period, and is exceptionally high, with almost complete site fidelity i.e. no population turnover. The model also predicted that catchability (q) remained constant throughout the study period but varied significantly between the groups ($0.0165 \pm 0.002_{s.e.}$ and $0.0059 \pm 0.001_{s.e.}$; male and female respectively), meaning catchability of males was 2.77 times higher than females (Fig. 2.8 *a*).

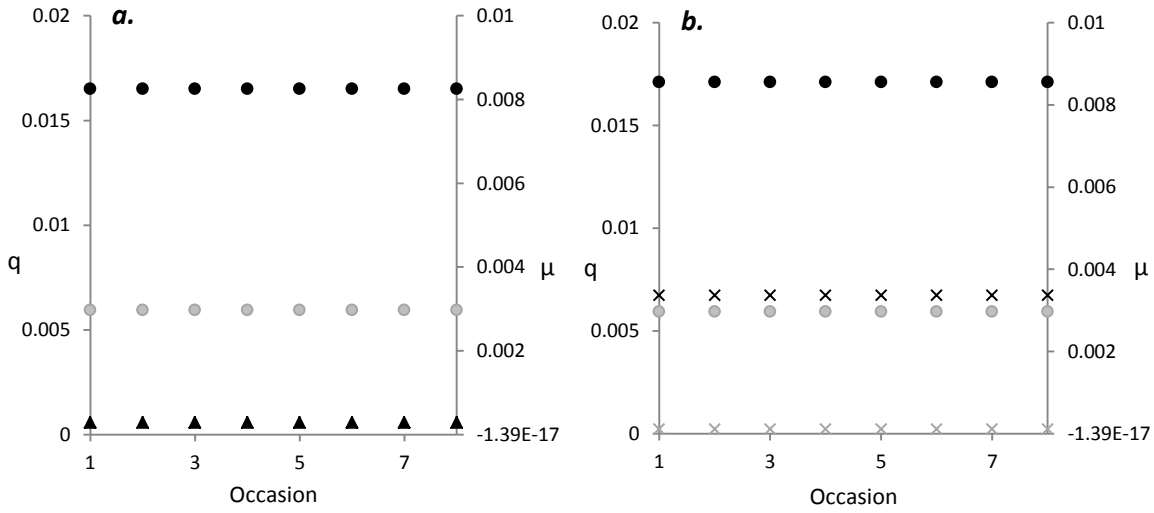


Figure 2.8 Estimated probabilities of male *q* (black circle ●), female *q* (grey circle ●), male μ (black cross ×) Female μ (grey cross ×) and male and female μ (Black triangle ▲), between each occasion of the study period for the two best models ($\mu_{\cdot}q_g$) (***a***) and ($\mu_g q_g$) (***b***).

The model with the next lowest AIC_c value ($\mu_g q_g$) was also considered, because the difference in the AIC_c value with the most parsimonious model was within 2 units (Table 2.3). This second model differs by predicting that rate of loss (μ) also varied between the two groups but remained constant throughout the study period (Fig. 2.8 *b*).

Table 2.3 Model selection statistics ranked from the smallest to the largest AICc (bias-adjusted Akaike Information Criterion). lnL is the log likelihood of the model, NP the number of separately identifiable parameters.

MODEL				ln L	-2 ln L	NP	AIC	AICc	Diff AICc	Likelihood of model
μ	.	q	g	-361.46	722.93	3	728.93	728.95	0.00	1.000
μ	g	q	g	-361.44	722.87	4	730.87	730.91	1.97	0.374
μ	.	q	g+t	-359.22	718.44	10	738.44	738.73	9.78	0.008
μ	g	q	.	-367.13	734.26	3	740.26	740.28	11.33	0.003
μ	g	q	g+t	-359.22	718.44	11	740.44	740.79	11.84	0.003
μ	t	q	g	-360.58	721.15	10	741.15	741.44	12.49	0.002
μ	g+t	q	g	-360.01	720.03	11	742.03	742.38	13.43	0.001
μ	.	q	.	-371.30	742.59	2	746.59	746.60	17.65	0.000
μ	.	q	g*t	-356.80	713.61	17	747.61	748.48	19.54	0.000
μ	g	q	g*t	-356.80	713.61	18	749.61	750.59	21.65	0.000
μ	g+t	q	.	-365.32	730.63	10	750.63	750.92	21.97	0.000
μ	g	q	t	-365.56	731.12	10	751.12	751.40	22.46	0.000
μ	t	q	g+t	-359.02	718.04	17	752.04	752.91	23.97	0.000
μ	g+t	q	g+t	-358.43	716.85	18	752.85	753.83	24.88	0.000
μ	.	q	t	-368.88	737.76	9	755.76	755.99	27.05	0.000
μ	g*t	q	g	-359.53	719.07	18	755.07	756.05	27.11	0.000
μ	t	q	.	-370.32	740.63	9	758.63	758.86	29.91	0.000
μ	g+t	q	t	-363.05	726.10	17	760.10	760.97	32.03	0.000
μ	t	q	g*t	-356.60	713.21	24	761.21	763.01	34.06	0.000
μ	g+t	q	g*t	-356.10	712.21	25	762.21	764.17	35.22	0.000
μ	g*t	q	.	-364.95	729.91	17	763.91	764.78	35.84	0.000
μ	g*t	q	g+t	-357.66	715.31	25	765.31	767.27	38.32	0.000
μ	t	q	t	-368.62	737.24	15	767.24	767.92	38.97	0.000
μ	g*t	q	g*t	-356.04	712.08	30	772.08	774.94	45.99	0.000
μ	g*t	q	t	-362.88	725.75	24	773.75	775.55	46.60	0.000
										1.391

Table 2.4 Blyth, Northumberland, 2012 capture-mark-recapture data presented as a reduced *m-array* for Male (Group 1) and Female (Group 2) lobsters.

Group = 1

Trap		Releases		Recaptures									
haul	First	Re-release	Total	t=2	t=3	t=4	t=5	t=6	t=7	t=8	t=9	Recaptured	Not recaptured
1	59	0	59	3	7	3	4	2	1	1	0	21	38
2	34	3	37		1	3	2	2	2	1	1	12	25
3	28	8	36			2	5	0	1	2	3	13	23
4	26	8	34				1	1	1	3	0	6	28
5	16	12	28					3	0	2	0	5	23
6	51	8	59						0	0	1	1	58
7	34	5	39							4	0	4	35
8	25	13	38								0	0	38
Total	273	57	330	3	8	8	12	8	5	13	5	62	268

Group = 2

Trap		Releases		Recaptures									
haul	First	Re-release	Total	t=2	t=3	t=4	t=5	t=6	t=7	t=8	t=9	Recaptured	Not recaptured
1	50	0	50	1	0	1	1	0	2	0	0	5	45
2	39	1	40		1	0	1	1	1	3	1	8	32
3	24	1	25			1	0	1	0	0	0	2	23
4	30	2	32				1	0	1	1	0	3	29
5	25	3	28					0	0	0	0	0	28
6	61	2	63						1	1	1	3	60
7	28	5	33							1	0	1	32
8	32	6	38								1	1	37
Total	289	20	309	1	1	2	3	2	5	6	3	23	286

2.3.3 Goodness-of-fit

Program RELEASE (run via MARK. See; Appendix IV) was used for testing the fit of the data to the general model, assuming the assumptions previously outlined stand-true. The cumulative results of the general time-dependent CJS model for 'TEST 2' over each occasion and between groups, and 'TEST 3' for both groups are described here. Two assumptions are tested by RELEASE:

(1) Every marked animal present in the population at time (i) has the same probability of recapture (p_i) (assumptions 1 and 3).

(2) Every marked animal in the population immediately after time (i) has the same probability of surviving to time ($i + 1$) (assumption 3).

Both Group1 and Group2 together, had non-significant results for TEST2 ($TEST2_{15}$: p = 0.4931). However, there was a lack of data for some occasions for Group 2 due to very low recaptures; despite this it can be assumed that all animals have equal probability of being recaptured.

The cumulative result for TEST 3 over both groups was non-significant ($TEST3_{16}$: p = 0.4951). There was no evidence over all occasions that φ differed between marked individuals.

From parametric bootstrapping an observed model deviance of 139.97 was attained. Comparing the observed deviance to all the deviances from the simulated data, the observed deviance was reasonably likely. As the probability of a deviance as large as, or greater than the observed value was p = 0.13 (130/1000). Therefore the general model fits the data and is considered suitable to continue to use models nested within the general model for analysis.

The dispersion of the data was also tested; the general model dispersion was, 139.97/116.94 = 1.164, which implies that the data is not over dispersed.

The general model ($\mu_{g*t}q_{g*t}$) and nested within this the most parsimonious model ($\mu_{\cdot}q_{g}$), were considered to sufficiently fit the data, and were an adequate basis for inference about population size at the study site.

2.3.4 Effective effort estimation

Observed catch data show a decline in the rate of increase of catch per day (Fig. 2.9). Possible explanantions for this decline in increase of catch with soak time are, amongst other things, diminished attractiveness of the bait, escapements over time and trap saturation.

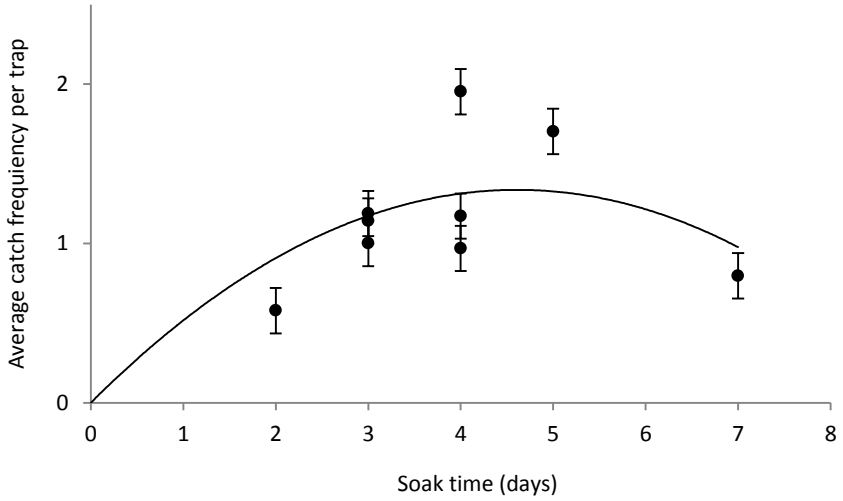


Figure 2.9 The relationship between average catch frequency per trap and soak time, the trend line is polynomial and is forced through the axis, as at 0 soak time catch is 0.

There was insufficient information to quantify C_∞, however as effort adjustment has been shown by Bell *et al.* (2003) to be relatively insensitive to choice of C_∞ over a range of possible values, a value of 72 was used; derived from the highest observed catch of lobster in one single trap (8) +1, multiplied by the number of traps in a string ((8+1)*8 = 72).

Using observed catches of lobster, the value for C_∞ and equation 2.14, *b* was estimated to be 0.146. This estimated value of *b* inserted into equation 2.13, generated effective effort for each soak time (Fig. 2.10). The curve from the subsequent graph of the values from equation 2.13, was used to provide figures of effective effort for the CMR analysis. The first day soak is constrained to an effective effort of 1, as all traps are assumed to have equal effort upon first setting.

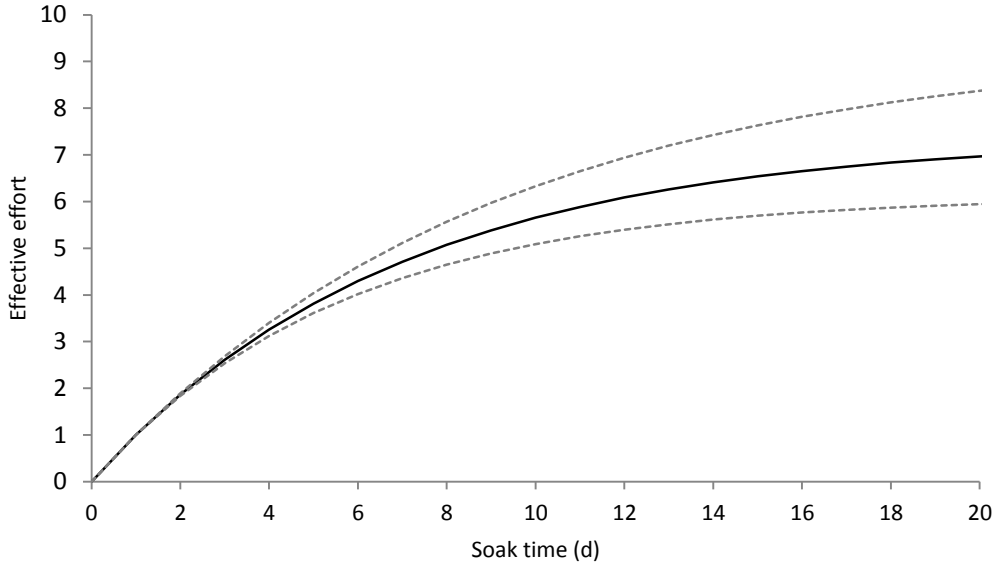


Figure 2.10 Relationship between cumulative effective effort and soak time in days, with 95% confidence intervals for *b*.

2.3.5 Population size and density estimates

Population size estimates for both groups over each occasion were generated by applying the parameter values of μ (rate of loss) and q (catchability), estimated by the top model ($\mu_{\cdot} q_g$), to the catch data for each group on each occasion using equation 2.9 (Fig. 2.11).

CMR population estimates differed significantly between male and female portions of the population (t-test$_8$: p = 0.0002). Female population size estimated as being 2.7 times larger than males (Fig. 2.12). Furthermore the female population estimates had large levels of uncertainty for each occasion. It is evident from figures 2.11 that population estimates are produced by scaling the catch frequency data.

As all strings of traps were used to estimate a single population size for each occasion, it is not possible to compare spatial variability over the site. However, temporal variation was quite large, with the greatest difference occurring between occasion 4 and 5 for both sexes. This coincides with the longest soak time during the study period for occasion 4.

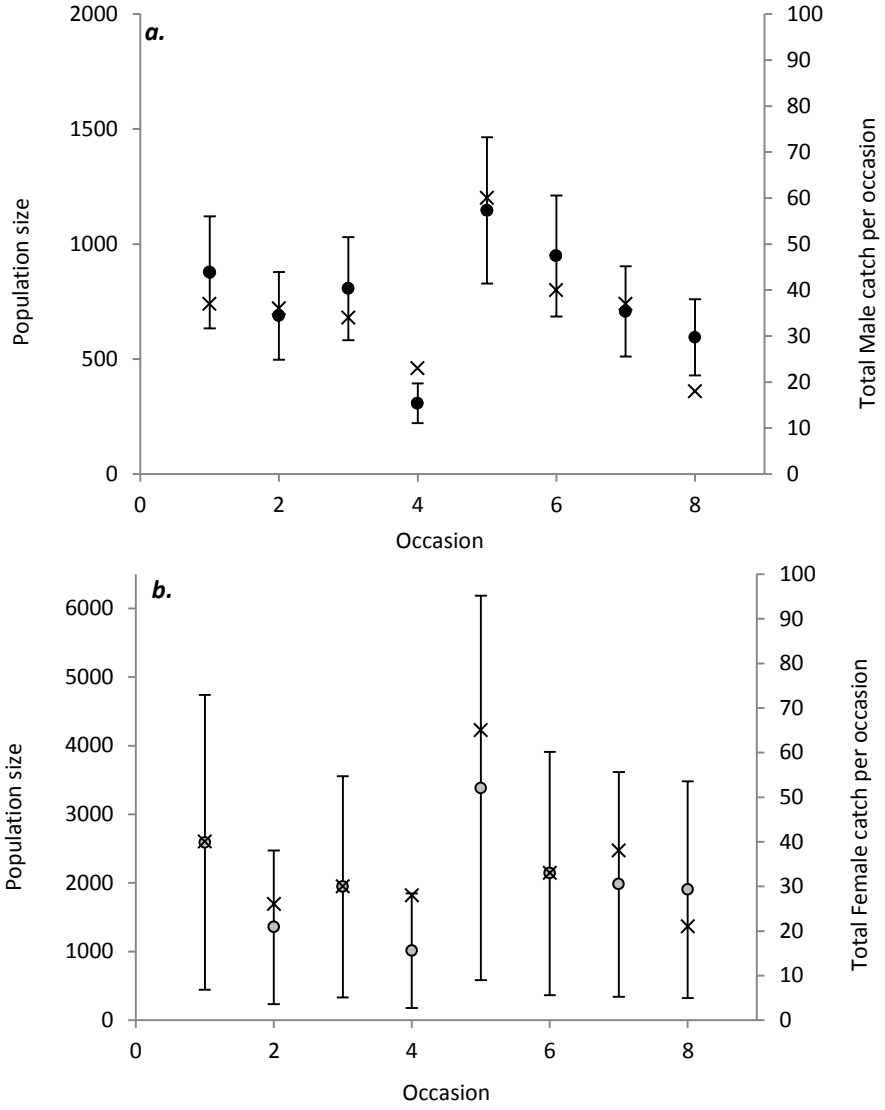


Figure 2.11 Comparison of capture-mark-recapture population estimates for male (black circles •) and female (grey circles •) with error bars (s.e.) and total catch of lobster per occasion (black cross ×) for *a*; male lobster and *b*; female lobsters. There is a three-fold difference in scale for CMR population estimates for male and female.

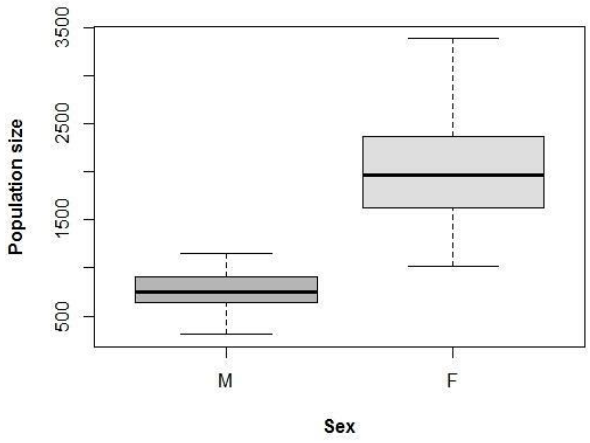


Figure 2.12 Male (dark grey) and Female (light grey) population size estimates, from the model ($\mu.q_g$), showing median, upper and lower quartiles and minimum and maximum estimates.

Due to the short-term nature of the study, each individual estimate for each group is essentially a separate estimation of the same population. Therefore, it is possible to take the mean of all eight estimates for each group of the population. Taking the mean essentially eliminates the noise created by the variability of the catch data, while still allowing each estimate to impact the final figure. The CMR study yielded a final lobster population size estimate of 759 (± 163 95% C.I.) and 2,039 (± 470 95% C.I.) for males and females respectively. Meaning that during the study period approximately 38% of the male population and 14% of the female population were observed.

To maintain the effect of temporal variation in total population estimates, male and female estimates for each occasion were summed individually, and the mean of the eight estimates taken. Estimate of the total lobster population within the study area can therefore be given as 2,798 (± 620 95% C.I.) lobsters.

To convert this population size estimate to a density, a minimum convex polygon of area 0.42km^2 was used for the capture area (Fig. 2.4); which equates to a population density of 6,662 (± 1,475 95% C.I.) lobsters per km^2, equivalent to ca. 1 individual lobster per 150m^2.

2.4 Discussion

2.4.1. Population size estimate

The estimate of ca. 6,660 lobsters per km^2 on a mixed habitat site 3km off the coast of Blyth is the first such estimate of *H. gammarus* population densities in the UK, excluding preliminary studies (Skerritt, Scott *et al.* 2012). The present estimate lies within an expected range when compared with estimates from other studies (Table 2.5) (Eggleston, Elis *et al.* 1999; Dunnington, Wahle *et al.* 2005; Agnalt, Kristiansen *et al.* 2007; Bowlby, Hanson *et al.* 2008). Animals equally distributed at this density would equate to one lobster per 150m^2; an area equivalent to a circle of radius 7m. However, lobster usually cluster their distribution around suitable habitat (Cobb 1971). It should be noted that the site is regularly fished by commercial trap-fishermen, although not during the time of this study, and often has high catches of lobster taken from the area annually (Turner, Hardy *et al.* 2009; Turner, Gray *et al.* 2013).

Table 2.5 Density estimates for *H. gammarus* and *H. americanus* from published literature and grey literature.

Author (Date)	Population Estimate	Location
Skerritt *et al.* (2012)	**2,359** *H. gammarus* per km^2 soft/mixed habitat and **6,163** per km^2 hard habitat	Blyth, UK
Agnalt *et al.* (2009)	**155** *H. gammarus* per km of shoreline	Tysfjord, Norway
Rowe (2002)	**10,000-20,000** *H. americanus* per km^2 and **ca. 2,500** per km^2 soft habitat	Newfoundland, Canada
Dunnington *et al.* (2005)	**65,000** *H. americanus* per km^2	Maine, US

Preliminary studies by Newcastle University using a CMR model framework similar to Bell *et al.* (2003), a necessary approach due to weaknesses in the data, reported density estimates of ca. 2,359 lobster per km^2 on soft/mixed habitat during the winter, and 6,163 lobster per km^2 at the same location to the present study towards the end of the summer (Skerritt, Scott *et al.* 2012). Despite reservations about the accuracy of these density estimates, they provide some corroboration of the estimation in the present study. They also estimated catchbaility of males to be at least twice as high as females.

The only other population estimate for *H. gammarus* available within peer-reviewed literature uses the Petersen estimator, a simple CMR method (Petersen 1896; Seber 1982). Conducted within the 'un-fished' fjords of northern Norway, this study reported a density of only 155 (±76) *H. gammarus* per km of shoreline (Agnalt, Farestveit *et al.* 2009). However, this study suffered from very low capture and recapture rates, increasing the uncertainty of the estimates. Tysfjord, Norway is scarcely comparable to the shallow inshore North Sea of Northumberland, due largely to differences in habitat. Therefore the reported difference in densities is not surprising considering the dichotomy between Norwegian and UK lobster landings. In 2005, at the time of the Agnalt (2009) data, landings of all lobster for Norway were reported as 194 tonnes. UK landings in 2005 were reported as 18,361 tonnes, for a similar gross tonnage (GT) of vessels (eurostat.ec.europa.eu; note landings are only of animals above MLS, while the estimates are for total population).

Bell *et al.* (2003) estimated a density of 2,101 *C. pagurus* per km^2, off the coast of Norfolk, UK. This is relatively low considering the high numbers landed from UK shores. However the majority of those animals were over MLS, so a large portion of the population could have been unaccounted for, (Bell, Eaton *et al.* 2003). The other

notable difference between the present study and Bell *et al.* (2003) is the value cited for area fished, despite deploying a similar number of traps. Bell *et al.* (2003) sampled and area of 2.3km^2, converting a population estimate of 4,800 crabs, to a density of 2,101 per km^2.

Population estimates for *H. americanus* are more numerous, and often report much higher densities. Rowe (2002) found 10,000-20,000 lobsters per km^2, falling to 2,500 per km^2 on less complex substrates (Newfoundland, Canada). Dunnington *et al.* (2005) estimated 65,000 per km^2 at their summer peak using CMR (Maine, US). While, Bowlby (2008) found as few as 450-500 per km^2 (Northumberland Strait, Canada (Bowlby, Hanson *et al.* 2008)), however, the use of otter trawls to gain catch data in this study brings in to question the accuracy of the density cited (Roddick and Miller 1992; Harris and Andrews 2005). Higher densities of *H. americanus* are expected, compared to *H. gammarus*, due in part to the reported increase in catches over the past few decades (Steneck and Wilson 2001), and is evidence that very high densities can be supported in hard and complex inshore habitats.

Despite there being only one previous attempt of estimating *H. gammarus* density via CMR (Agnalt, Farestveit *et al.* 2009), they are perhaps more suited than *H. americanus*. Recorded migrations and high dispersal rates of *H. americanus* (Smith, Collins *et al.* 1998; Frusher and Hoenig 2003; Moland, Olsen *et al.* 2011; Moland, Olsen *et al.* 2011a) could increase population turnover and possibly increase the likelihood of overestimating population size. Density estimates for any mobile crustacean species are spatially highly variable and further CMR studies would need to be conducted throughout the Northumberland district, and the rest of the UK, to augment findings in this study.

The proportion of the estimated total population that was observed in the catch was 36%, 14% and 21% for male, female and total population respectively. This compares favorably with Dunnington *et al.* (2005), who observed approximately 18% of the estimated population; the pool of catchable lobsters available to trapping being much smaller than the number of lobsters in the area. Dunnington *et al.* (2005) confirmed this via diver-based counts at the site. Visual census was not possible in the present study. Of the observed population in the present study, 75% were below the MLS of 87mm CL. As smaller lobsters are often observed much less frequently than larger

lobsters, this could indicate that portions of the population are not always available to trapping. Population estimates were derived using observed catches of animals available for capture. Lobsters undergoing ecdysis or near to releasing eggs may not be captured, as would be the case for all lobsters <50mm and >150mm CL, due to exclusion from the traps (Addison and Bannister 1994; Barnhardt, Kelley *et al.* 1998; Watson, Golet *et al.* 2009). The models in this study are developed only for sex as a factor, models could have been extended further to include additional factors (i.e. size; >MLS/<MLS). Due to low catches of large lobster in this study, it was not feasible to split the catch into size groups.

While it is impossible to draw general conclusions about the lobster population from a single site, short-term trapping study, some differences between the sex's abundance and catchability characteristics were predicted by the model. The significantly female biased sex ratio within the total population estimate (M:F = 1:2.7) is largely due to the differences in catchability estimated by the model (q = 0.016 and 0.006; male and female respectively). Despite almost equal sex ratio in the observed and tagged catch, only 7% of females, compared to 21% of males were observed again. This would imply that the pool of female lobsters from which the observed catch was drawn is larger than that of the male lobsters.

Although UK lobster sex ratios have been reported to be skewed in favour of females (Thomas 1955), this is not reflected in trap catch data. Commercial trap catches in Northumberland in 2012 show a 50:50 sex ratio; however landings are skewed significantly in favour of males (NIFCA data). The reasons are not clear, and could be due to numerous influences, including differences in behaviour, increased protection for females from management regulations or seasonal periods of low female catchability. Typically lobsters in the UK breed through the summer (Pawson 1995), with ovigerous females appearing during September and onwards (Debuse, Addison *et al.* 1999; Debuse, Addison *et al.* 2003). The increased proportion of the female population not available for capture could be due to seasonal female behaviour. Females carrying eggs, finding or being guarded by males, or becoming more defensive of refuge during reproduction and moulting are less likely to enter a baited trap, particularly in areas of higher lobster densities (Steneck 2006). Male lobsters might therefore have higher rates of mobility than females, allowing for greater foraging

potential, to interact with more females and with more baited traps. A study of *H. gammarus* found that on average home range area was largest in males, followed by ovigerous females and non-ovigerous females (Moland, Olsen *et al.* 2011). Behavioural differences between male and females have led to decreased females catchability, which in turn biases the female population estimate upwards. However, no conclusion can be drawn about the effect of season on sex ratio, without further studies during the non-breeding season, or a simulation study being ran to work out what this difference in catchability means.

It is difficult to determine whether variability in population estimates is a true reflection of a highly changeable local population. Due to the short-term nature of the study, and that *H. gammarus* are generally regarded as resident to an area (Moland, Olsen *et al.* 2011; Moland, Olsen *et al.* 2011a), site fidelity was almost 100% per day. It is likely that the variation in population estimates is a product of deficiencies of the model to take account of highly variable catch rates, rather than the observation of a changeable local population. Unequal soak time has led to some of that variability in catch (Fig. 2.9). Fewer numbers of new lobsters entering and increased escapements, are thought to lead to uncharacteristic trap catches (Jury, Howell *et al.* 2001). Therefore, over long soak times the observed catch is not the number of lobster that have entered the trap, but the number of lobster present at the time of hauling. Both low numbers of lobster caught on occasion 4 and the large cumulative effective effort over the extended soak have artificially reduced the population estimates for that period. Variability of catch haunts much of shellfish research, as the catch of a trap is influenced by many, largely unpredictable, factors (Fogarty and Addison 1997; Ziegler, Frusher *et al.* 2003).

Catch rates were found to differ significantly between inside and outside strings (t-test: $Total_{574}$ $p = 3.74E^{-06}$), with outside strings slightly higher, however total lobster catches were not significantly different between inside traps and outside traps (t-test: $Total_{574}$ $p = 0.44$). Therefore the difference trap catches was not due to trap interactions (Bell, Addison *et al.* 2001), more likely due to differences in habitat, depth or other environmental variables. However, as all strings of traps were combined to estimate a single cumulative population size for each occasion, it is not possible to

compare spatial variability over the site. This offers the advantage of minimising the effect of small-scale habitat variation on the population size estimates.

Population estimates for the top two models were found to be very similar, so estimates are not sensitive to model choice. Instead they are largely scaled by the catch, which introduces most variation. Understanding micro-scale population changes, and triggers for these changes in catch would aid the modelling of population processes.

2.4.2 Assumptions and uncertainties

The accuracy of CMR estimates depends largely on how well the key assumptions have been satisfied. The GoF tests show that two of these assumptions were sufficiently met; the other assumptions are difficult to test for. The impact of tag loss is considered to be minimal in this study. Despite some tag loss being observed, this was often from previous year's studies; short-term tag loss was assumed negligible. From observations during the study, tag loss was estimated to be less than 1%, over a period of 2-12 months. Tag-induced mortality was not observed, due to fast turnaround of lobsters and minimal time on deck, any mortality occurring once returned to sea, although unlikely, would be impossible to observe. *Ex-situ* tank studies in which a cohort of tagged lobsters was kept under observation for three months found no mortality. Therefore tag-induced mortality was not considered to impact the results of this study. Interspecific interactions in and around baited traps were not considered to impact this study despite lobster and crab catch rates being inversely proportional (Fig. 2.7). This inverse relationship could be due to either, inhibitive interactions, a product of the underlying habitat or another influence. Intraspecific interactions are also likely to impact the catch rate of smaller, subordinate lobsters. However, as little research exists on the impact of these interactions in the UK (Addison 1995), for the purpose of this analysis it was assumed that interactions had no impact on population estimates, but likely added to the variation in catch.

Four key uncertainties were identified within the methodology:

(1) Estimates of q (catchability) and μ (rate of loss): It is difficult to assess how closely the model outputs for q and μ reflect reality. The model fits the data efficiently,

despite CI for μ being high. There is no method to test how close model estimates of parameters match reality, hence the need for a model to simulate the data. The model can be refined or parameters added, but more complex models will not necessarily imitate reality any better, and this uncertainty is an inherent part of any modelling exercise. However, as only the two top models explained the data sufficiently, and as these two models did not produce significantly dissimilar population estimates (population estimates were robust to model selection), selected outcomes are robust to uncertainty about the model selection process.

(2) Value of *b* (rate at which the increase in catch declines over time): Quantifying the decline in effective fishing effort over time is one of the weaker aspects of these analyses, but is fundamental for its application. Bell *et al.* (2003) found the method used here gave results equivalent to those from more extensive methodologies. Inferences about this relationship can only be weak, as the 'real' value of *b* is impacted by numerous factors, which will vary spatially and temporally, and between individuals. Generating a unique value of *b* for each study, from real catch data, is considered more suitable than finding a generic value. The estimate here, derived from catch data, is supported by strong experimental and literature evidence that catch rate per day is asymptotic or parabolic with soak time, the parabolic fit being and adopted here for the purpose of estimation of population size.

(3) Small sample size and low recapture rates: Low catch rates are a common problem of European lobster fisheries. Increasing the number of fishing occasions at each site to increase the proportion of population tagged might increase the number of subsequent recaptures, and therefore the accuracy of the estimates. Increasing the number of traps within the study area could increase recapture rates. However, adding more traps increases the likelihood of trap interaction, and makes the process of setting and hauling much more problematic.

(4) Estimate of capture area: Accurate estimation of the capture area is essential in determining density from the population estimate. As size-, sex-, site- and season-specific movement rates are largely unknown for *H. gammarus*, it is impossible to accurately estimate capture area. The area of bait influence will vary between sites due to hydrodynamics, as lobster locate bait by odour, and bottom complexity influences the hydrodynamics of bait plumes (Beier and Noss 1998; Castro, Cobb *et al.*

2001). Additional data is essential on the movement, home-range, and habitat use of European lobsters in their natural environment. If this information were available, it could be possible to construct more accurate capture areas using habitat maps to determine natural habitat boundaries, and constraining the capture area within these limits for example.

However, it is unlikely that the catch is drawn from a much greater area than the estimate reported. Given the low population turnover, and as no trap interaction was observed between catches of individual traps, this was deemed to be a suitable area for the purpose of this study. Density estimation is very sensitive to the choice of capture area; if the capture area for a single trap was set at 55m diameter, density would be estimated at 9,329 lobsters per km^2, while at 150m diameter capture area, the density would be 5,032 per km^2. If the same area is used for capture area, year to year, then changes in population can still be elucidated, assuming capture area doesn't fluctuate.

2.4.3 Sampling design

The sampling survey was designed so that it could be easily replicable, without the need for specialist equipment, or technical understanding. The most important requirement for the method outlined in this study is complete sampling of all strings during each haul occasion. This is a weakness of the model, rather than the sampling technique. Ideally complete sampling would be coupled with equal soak time between all occasions; this would eliminate the need for estimating effective effort, thus reducing the number of parameters in the model. However, equal soak times are scarcely achievable due to the nature of working at sea.

There is scope to increase the likelihood of recaptures and to minimise the potential saturation effect of traps, by hauling the traps more regularly. This is probably necessary as two to three days are considered to be a suitable soak time for lobster fishing, and shows the least variation in catch and effort (Fig. 2.9 and 2.10). Increasing the length of the study time to increase number of haul occasions could help to increase recaptures. Conducting seasonal surveys to discover if the higher female abundance is observed all year round, or an artefact of sampling during or near to breeding season, would be beneficial.

Ideally it would be good to have a comparable method to validate the CMR estimates, working from different data but within the same small area, i.e. visual dive transects or drop down camera, however, this is often unfeasible within the North Sea and the cryptic nature of lobsters makes it difficult. While this technique is considered to be robust, and insightful, raising numerous questions about European lobster for the first time, it is unlikely to be used by fisheries management due to the complexity of attaining suitable data for analysis.

2.4.4 Model framework

The approach outlined within this study implements the CMR model in continuous terms with instantaneous parameters, similar to studies such as Dunnington *et al.* (2005) and Frusher and Hoenig (2003). The model framework presented, is thought to be more than suitable for this study and an improvement upon previous methods. It is variation in catch and our understanding of the behaviour of lobsters that is holding back the technique. It could be improved, by having an additional parameter that could take into account the presence of crab or the effect of conspecifics within the catch, as this likely decreases the effective fishing effort of the trap or possibly inhibits lobster from entering.

2.5 Conclusion

This study used an adapted CJS style CMR model framework to analyse catch and recapture data, in order to provide estimates of sex composition and the first UK estimates of lobster density. While it was acknowledged that population estimates from CMR have sources of error, they at least provide a credible method for studying capture, recapture, and site fidelity rates, and at best they provide a useful tool for assessing population size of lobsters within small areas. There is scope to use this process to create maps of distribution of abundance throughout the district, or for monitoring impacts of increased fishing, protection measures, or offshore structures on the population size within the immediate vicinity.

A study by Steneck and Wilson (2001) conducted several years of surveys over numerous sites, to discover both hotspots; with high densities of >1 lobster per m^2, and cold spots (Steneck and Wilson 2001). It found highly segregated populations with adults, and juveniles unequally distributed. This kind of study would be very important

particularly in view of MPA and future protection of the lobster within the UK, and could extend the present study.

The method is considered accurate, and the modelling robust, based on the outcomes stated in comparison to other studies that have directly compared the CMR output to either dive surveys, or drop down camera (Melville-Smith 1988; Tuck, Chapman *et al.* 1997; Dunnington, Wahle *et al.* 2005) .

Results from this study raise important questions about European lobster populations, and the observed dichotomy between catchability of the sexes that will hopefully provoke further work, and further highlight our lack of understanding. There could be hidden portions of the male population not entering traps. It is even more important as management measures are based on the observed landings. This could be missing important population dynamics due to the threefold difference in catchability between the sexes.

This study has been essential in working out what additional information on behaviour, movement, distribution, and sources of catch variability, needs to be known in order to effectively assess, and therefore manage lobster populations. The question about female male population size is interesting, as most catch data shows a close to 1:1 ratio, but this may not be the case, and management needs to be aware of any sex skews. This study also demonstrates that given the correct sampling design, CMR studies that incorporate several hauling occasions within a small area, have the potential to give discrete estimates of population size, catchability coefficients and rate of loss, which are all important parameters for assessing fish stocks. However, replication is required to corroborate findings.

Chapter 3:

Inter- and intra-specific interactions affecting the *Homarus gammarus* catch in a mixed coastal fishery

Chapter 3: Inter- and intra-specific interactions affecting the *Homarus gammarus* catch in a mixed coastal fishery

3.1 Introduction

Continued sustainability of commercial crustacean shellfish relies among other things on monitoring the state of stocks using catch and effort (CPUE) data, and carrying out stock assessments that estimate mortality, yield per recruit, egg per recruit and recruitment. To achieve this, local and species-specific information about catch, fishing effort, and growth are required. Comprehensive information of good quality is scarce, particularly for UK *Homarus gammarus* fisheries which typically are modelled using size-based length cohort analyses (Smith and Addison 2003). The catch-effort and size distribution data tend to be derived from landings of baited traps, the effectiveness of which is influenced by many behavioural, environmental and ecological factors, including the catchability of target species.

Catchability may be determined by four key factors: seasonal and diurnal patterns of activity, the ability of an individual to detect the bait, its ability to locate the trap, and its willingness to enter the trap. Each process is influenced by complex interactions between biological, physiological, behavioural and environmental factors (Elner 1980; Krouse 1989; Miller 1990; Fogarty and Addison 1997; Montgomery 2005). All baited traps regardless of design or configuration selectively sample both target and non-target populations; although some of this selectivity is intentional (e.g. escape vents, entrance diameter), much of it is not. This chapter aims to investigate the influence of inter- and intra-specific behavioural interactions in and around a baited trap on an animal's willingness to enter it.

In the North East of England, fishermen targeting shellfish with static baited traps rely upon four main commercial species: European lobster (*H. gammarus*), brown crab (*Cancer pagurus*), nephrops (*Nephrops norvegicus*) and to a lesser extent velvet swimming crab (*Necora puber*). Overlaps between these species' spatial distributions (Bennett and Brown 1983; Smith, Jensen *et al.* 2001) and their attraction to the same bait, make it difficult to target one species exclusively; the fishery is therefore multi-

species. Interactions between *H. gammarus* and *C. pagurus* are most likely to occur due to the high degree of overlap of areas from which they are caught and the design of trap that targets them. Some local fishers suggest that lobster and velvet crab will inhibit the entry of brown crab and smaller lobster into the trap (pers. comm). In areas of high brown crab densities some fishermen will leave undersized lobster within a trap to deter entry of the less valuable brown crab (pers. comm); however, this inhibitory effect has rarely been quantified. Previous studies suggest that one of the main factors limiting the catch of both *H. gammarus* and *H. americanus* is the interaction between individuals both inside and outside baited traps (Richards, Cobb *et al.* 1983; Addison 1995; Jury, Howell *et al.* 2001). Laboratory and some field studies, mostly in the US with *H. americanus*, have shown that both inter- and intra-specific interactions occur (Bennett 1974; Richards, Cobb *et al.* 1983; Miller and Addison 1995; Jury, Howell *et al.* 2001; Williams, Floyd *et al.* 2006; League-Pike and Shulman 2009; Rossong, Quijon *et al.* 2011), causing reduced subsequent entry and trap saturation (Miller 1979; Karnofsky and Price 1989; Fogarty and Addison 1997).

Interactions may occur because of both proximate and ultimate causes, such as competition for limited resources such as food or shelter, or increased survival (Bennett and Brown 1979). Due to the generally solitary and cryptic nature of lobsters, when they do interact and compete, agonistic behaviours are sometimes displayed (Rossong, Williams *et al.* 2006). If lobsters are equally matched the agonism may escalate to physical contact such as antennae whips, claw locking and pushing (Karnofsky, Atema *et al.* 1989). In many crustacea relative size is the foremost factor that affects which individual ‘wins’ in any encounter (Caldwell and Dingle 1979; Hyatt 1983); other factors may include moult stage (Tamm and Cobb 1978), or general condition (O'Neill and Cobb 1979). As lobsters grow and develop defence mechanisms, their tendency to spend more time foraging and less time sheltering increases, as is the case for other decapod crustacea such as the hermit crab *Pagurus bernhardus* (Ramsay, Kaiser *et al.* 1997); larger lobsters may be less inhibited in entering traps, unless their entry is restricted by the diameter of the entrance.

Most studies of lobster interactions with conspecifics, heterospecifics or the trap itself, are limited to laboratories, semi-natural mesocosms (Krouse 1989; Miller 1990; Miller and Addison 1995; Addison and Bell 1997; Fogarty and Addison 1997; Debuse, Addison et al. 1999; Rossong, Williams et al. 2006) and *in situ* diver observations (Auster 1985; Karnofsky, Atema *et al.* 1989; Miller 1989; Miller 1995). Although laboratory studies have effectively demonstrated how interactions can cause a reduction in catchability (Miller and Addison 1995; Williams, Floyd *et al.* 2006; League-Pike and Shulman 2009), the extent to which normal behaviour is exhibited in such studies is uncertain (Jury, Howell *et al.* 2001; League-Pike and Shulman 2009). Diver observations are also useful but tend to be expensive, require favourable conditions and are temporally and spatially limited. The small number of published *in situ* trap studies (Richards, Cobb *et al.* 1983) suggest one of the main factors limiting catch of *H. americanus* is the interaction between conspecifics inside and outside of the trap. Some studies have concluded that therefore CPUE is not necessarily a good indicator of density (Addison 1995; Addison 1997; Fogarty and Addison 1997). Cobb (1995) stated that "*more research is needed on factors affecting trap encounter and entry before traps can be truly effective for measuring abundance*". This research has not been forthcoming within the UK.

Interactions have received little attention outside North America and Canada (Addison 1995) and are often not included in stock assessments, which usually rely on fisheries-dependent catch data in the form of CPUE from multi-species fisheries. Ignoring additional species caught and the resulting changes in catchability may lead to inaccurate stock assessments with implications for managing the fishery as a whole (Addison 1995).

This study aimed to use both fishery-independent commercial fishing techniques and pre-loaded trap studies to quantify the effect of animal interactions on the catch of baited parlour traps. The objectives were to determine whether trap efficiency is affected by the presence of individuals of three key shellfish species in the traps and to elucidate if the first species entering a trap influences the subsequent number of animals caught and catch composition of that trap. The relationship between lobster

and crab catch numbers were explored using a large fishery-independent trap-catch dataset. Where interactions occur, potential effects of sex, size, species and habitat are explored. Implications for management and interpretation of catch data are discussed.

3.2 Methodology

3.2.1 Study sites

The study was conducted off Blyth, Northumberland (Table 3.1; Fig. 3.1). Trap fishing within the region largely targets two species, *H. gammarus* and *C. pagurus*; recorded UK commercial catches in 2010 were 2,700 and 26,600 tonnes respectively, representing approximately £26.6 and £35.2 million (MMO 2010). *N. puber* catches do not exceed 1,000 tonnes in England, but the species has long contributed to inshore trap catches. Fishers target different species depending on availability and market opportunity, deploying gear on various ground types at different times of year.

Interaction behaviour studies using pre-loaded traps were conducted *in situ* between 2011 and 2013 at two sites approximately 2km and 2.5km due East of Blyth (BL and BL4; Fig. 3.1). Catch data from several fishery-independent trap surveys between 2010 and 2012 were also analysed (BL1-BL4, SS and MB; Fig. 3.1). During 2011 and 2012 fieldwork was conducted from the 21m NIFCA patrol vessel *St Oswald* (28 Nov 2011 to 15 Dec 2011 and 14 Nov 2012 to 30 Nov 2012). In 2013 fieldwork was conducted from the 18.9m Newcastle University research vessel *Princess Royal* (15 Feb 2013 to 07 Mar 2013). Study sites have a mixture of hard and soft substrate, rock and cobble forming distinct areas of complex habitat among more homogeneous patches of sand and mud; site depths varied from 16m to 42m (Table 3.1). A variety of habitat types were targeted to ensure all species would be present in sufficient numbers.

Table 3.1 Site information: approximate centre of the site, average depth and habitat type.

Site	Approximate location	Mean depth (m) ±s.e.	Mean hardness ±s.e.	Sediment
BL	55° 7.37 N; -01° 27.42 W	24.67 ±0.06	34.14 ±0.27	Hard
SS	55° 5.75 N; -01° 26.76 W	18.00 ±0.04	16.39 ±0.20	Soft
MB	55° 4.28 N; -01° 25.22 W	18.20 ±0.04	23.79 ±0.18	Hard
BL1	55° 8.12 N; -01° 23.16 W	41.20 ±0.02	15.04 ±0.09	Soft
BL2	55° 6.85 N; -01° 23.51 W	34.45 ±0.03	18.73 ±0.12	Mixed
BL3	55° 4.89 N; -01° 21.73 W	38.11 ±0.02	34.44 ±0.16	Hard
BL4	55° 7.53 N; -01° 27.15 W	25.47 ±0.05	36.67 ±0.50	Hard

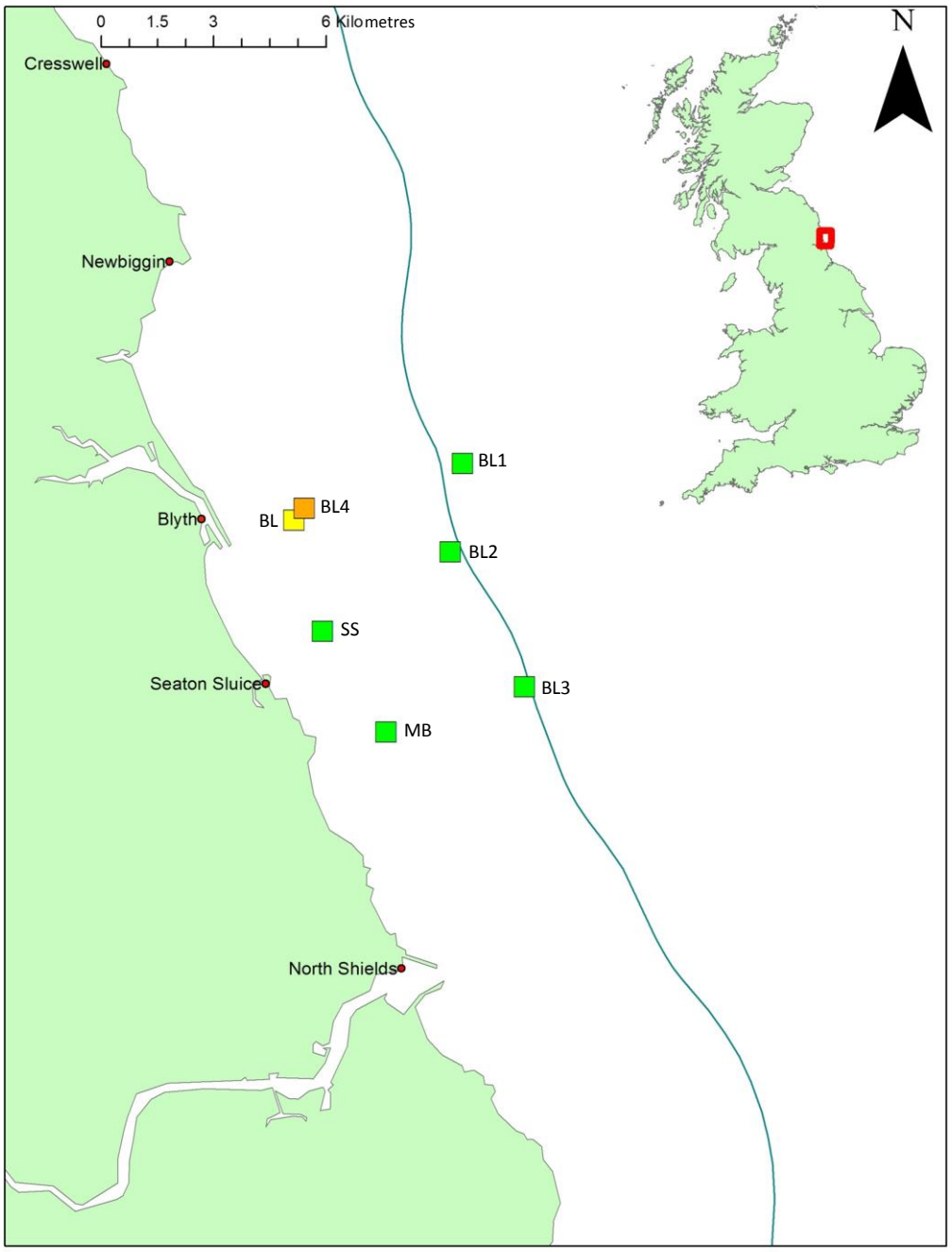


Figure 3.1 Northumberland coastline; the major fishing ports are highlighted with red circles (●), and the *in situ* study sites are highlighted with a yellow square for the 2011-2012 sites (■), and the orange site is the 2013 interaction study (■) all other trap catch data has come from the green sites (■).

Substrate hardness data were collected continuously using the vessel's on-board mapping and navigation software, Olex 8.0. This allowed for ground discrimination and relative change in bottom hardness to be assessed by reporting backscatter values from the vessel's single-beam echo-sounder as a ratio of sent and received acoustic

energy via a proprietary algorithmic treatment of the sonogram. This translates to a linear scale from 1 (i.e. low reflection due to soft habitat) to 100 (i.e. 0dB energy lost due to hard habitat) however, values above 60 are uncommon. As readings can be impacted by environmental conditions, only strong readings are reported by the software. Olex cannot use backscatter to assess bottom roughness (unlike e.g. RoxAnn), and only provides a value as a proxy for substrate hardness. Previous studies have shown there is little difference in broad scale substrate classification of Olex and multi-beam sonar systems (Elvenes, Dolan *et al.* 2013). Hardness for each site was calculated by taking the mean Olex hardness value from verified points within the trap array, standard error of the mean was also calculated to give an indication of the variation (Table 3.1).

3.2.2 Data collection

A fleet of 64 commercial, 10mm steel-framed, parlour traps, measuring approximately 0.68 x 0.46 x 0.38m, with 130mm fixed diameter single-side entrance, 27mm square mesh and selective grill on the bottom was used throughout. Escape vents are not required on UK commercial traps, and were not desired for this study, as animals of all sizes were recorded. Traps were baited with a single, frozen flatfish per trap (20-30cm total length), with old bait removed and replaced on every haul occasion. Flatfish, predominantly dab (*Limanda limanda*) and plaice (*Pleuronectes platessa*) were used as they are thought to remain attractive for longer periods, and are less prone to scavenging by hagfish (Myxinidae). Traps were arranged in strings of eight, set North to South, perpendicular to the tidal flow, with approximately 40m between traps. Although commercial fishing continued within the area during the study period, no commercial traps were fished directly within the study site; consideration of interactions with commercial traps was therefore not required.

The majority of the data came from *in situ* trap studies at BL and BL4, where the parlour of traps randomly selected from a string, were loaded with a known animal, and then placed back in the sea. Subsequent catch was then recorded. All other trap data were from fishery-independent trap surveys, where the same fleet of traps was fished and all catches recorded.

For the 2011-2012 pre-loaded interaction study, each trap was randomly allocated to one of four treatments: lobster, brown crab, velvet crab, or empty (control). It was assumed that all traps would attract an equal number of animals to approach them; therefore any difference in catch could be attributed to interactions with the pre-loaded animal. The number of treatments varied from three (lobster, brown crab and control) in 2011, to four (including velvet crab) in 2012 to two (lobster and control) in 2013. Pre-loaded animals had morphometric measurements taken, including CL (CW for crabs), claw propodite length (PL) (Fig. 3.2) and reproductive state, sex and any observable damage. Animals were then marked with a small cable tie around their carpus, without impairing movement, to distinguish them from subsequent catches, and placed in the parlour of the trap to minimise escapement. Escaped velvet crabs and lobsters were observed, and the catch data from these traps were not used.

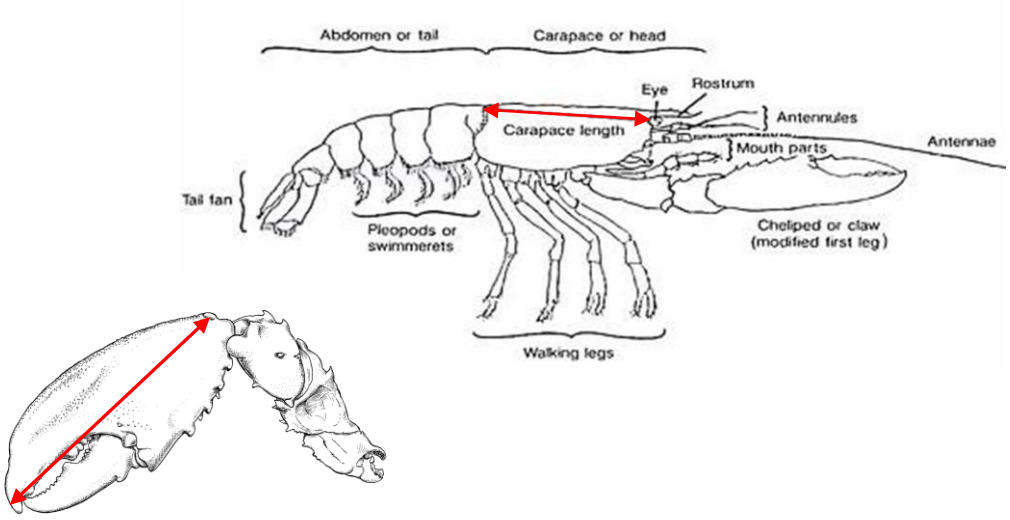


Figure 3.2 Illustration of a lobster crusher claw, and the whole lobster morphology. The red lines indicate the crushing claw propodite measurement (left) and the carapace length (above) from rear of the eye socket to end of the carapace. (Ref: www.nationallobsterhatchery.co.uk).

During pre-loaded interaction studies, traps were hauled at approximately four day intervals, however due to weather restrictions, hauling was opportunistic and soak-times varied between 2 and 9 days over the three years. There were 45, 85, and 281 successful trap-hauls in 2011, 2012, and 2013 respectively. Upon hauling, the catch from each individual trap was removed and stored in separate containers, biometric data were recorded for every individual crustacean caught including species, CL for lobster, CW for crab, claw PL, sex, presence of eggs, general condition, and their

capture location (string and trap number). All caught animals were immediately released once processed, unless seriously damaged or required for pre-loading.

Traps were re-baited, and pre-loaded with another randomly allocated treatment. If pre-loaded animals were in good condition, they were reused, if the health and general condition of animals had deteriorated or they had been used for two successive hauls they were replaced by newly caught animals. Replacing the pre-loaded animals also allowed for a more complete representation of the range of sizes found in the population, and an equal number of males and females. The initial pre-load animals were caught by setting the experimental traps three days before the start of the study, and using the subsequent catch on the first day. Replacements were taken from each successive catch as and when needed.

For fishery-independent trap surveys, traps were arranged in eight identical strings of eight traps, the strings set approximately 100m apart. All 64 traps were hauled at approximately four day intervals, however due to weather restrictions soak time was not consistent ($\bar{x}_{263}$ = 4.15 ± 0.12$_{s.e.}$; range = 1 – 15 days). Upon hauling, the catch from each individual trap was removed and stored in separate containers to maintain trap-specific catch information. Data were recorded for every individual animal including species, CL for lobster, CW for crab, sex, presence of eggs, general condition, and their capture location (site, string and trap number). There were 690, 888, and 575 successful trap-hauls that caught animals in 2010, 2011, and 2012 respectively.

3.2.3 Statistical analysis

All statistical analysis was conducted in R 2.15.3, using the '*stats*' package for statistical tests, and '*Rcmdr*' for some graphics. The Chi Squared test for goodness-of-fit was used to determine if species proportion varied between the various pre-load treatments and subsequently Wilcoxon rank tests were used to determine individual sources of significance. Following testing for normality and homogeneity of variance, data were identified as non-normally distributed. Linear regressions were conducted to test for association between pre-load and subsequently caught animals' biometric data, such as PL and CL. Chi squared tests for goodness-of-fit were used to determine

whether lobsters of the same sex were more deterred from entry more than lobsters of the opposite sex.

Fishery-independent trap survey data were non-normal count data, thus required a Poisson or negative binomial approximation regression to explore relationships between lobster and crab catches in the same trap. All data were first pooled regardless of the site or year: trap surveys were conducted over three years; 2010 (Trap-hauls; n = 621), 2011 (n = 1,093) and 2012 (n = 552). Traps were set over seven sites (Fig. 3.1; Table 3.1) BL (n = 205), BL1 (n = 301), BL2 (n = 290), BL3 (n = 223), BL4 (n = 831), MB (n = 169), and SS (n = 247). Because catch rates of lobster and crab differed considerably between sites, it was appropriate to include site as a factor within the model, producing a separate slope for each site. To obtain a single model including substrate hardness at each site, mean site hardness values (Table 3.1) were included within the negative binomial generalised linear model (GLM) as a continuous coefficient. Mean site hardness was determined by exporting raw data from Olex into ArcMap 10.1, the raw data points containing both a hardness value (0-100) and a depth value (z); mean hardness and mean depth were gained from all data points within a 20m radius of all traps within each site. Year could not be included in the analysis, as not all sites were surveyed each year, causing site and year to be confounded. To determine if same sex lobster pairings occurred more often than opposite sex lobster pairings, all trap catches with exactly two lobsters and no crabs were analysed, tested against expected sex parings based on the overall sex ratio during the entire study period.

3.3 Results

3.3.1 Fishery-independent trap survey data

Crab catches ranged from 0 to 62 per trap ($\bar{x}_{2266}$ = 6.27 ± 0.13$_{s.e.}$), while lobster catches ranged from 0 to 8 per trap ($\bar{x}_{2266}$ = 0.55 ± 0.02$_{s.e.}$). Pooled together regardless of site or year, the data were non-normal and over dispersed, due to large variations in the catch rates of crab at different sites. A negative binomial general linear model was used to account for this.

Because catch rates of both lobster and crab differed considerably among sites, site was included as a factor within the model, producing a separate slope for each site. All sites except BL were found to be significantly different from MB (Table 3.2; Fig. 3.3). The negative binomial general linear model (Crab ~ Lobster + Site [factor]) described the data from all sites except BL.

Table 3.2 Results of fitted GLM: estimated coefficients values, relative error, Z value and significance. Residual deviance: 2479.2 on 2258 degrees of freedom. AIC: 10998

	Estimate	Error	Z-value	P-value
Intercept	0.91	0.09	10.40	< 0.001
Lobster	-0.70	0.03	-23.70	< 0.001
SS	1.79	0.10	18.36	< 0.001
BL	-0.21	0.11	-1.85	0.06
BL1	1.23	0.10	12.75	< 0.001
BL2	0.63	0.10	6.38	< 0.001
BL3	0.36	0.10	3.52	< 0.001
BL4	0.95	0.09	10.66	< 0.001

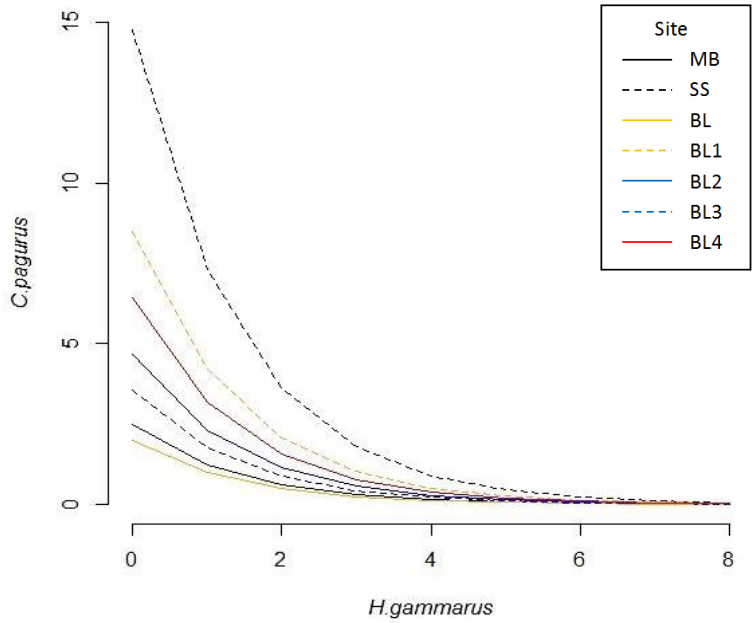


Figure 3.3 Plot of lobster and crab catch frequencies within the same trap, with fitted negative binomial GLM for each site.

A second model including mean site substrate hardness (Table 3.1) as a continuous coefficient (GLM2: Crab ~ Lobster + Hardness) instead of site fitted the data better (Table 3.3; Fig. 3.4). The modelled number of lobster per trap also varied with mean substrate hardness.

Table 3.3 Results of the fitted GLM2: estimated coefficients, relative error, Z value and significance. Residual deviance: 2506.2 on 2263 degrees of freedom. AIC: 11631.

	Estimate	Error	Z-value	P-value
Intercept	2.56	0.06	42.26	< 0.001
Lobster	-0.74	0.03	-23.78	< 0.001
Hardness	-0.03	0.002	-11.67	< 0.001

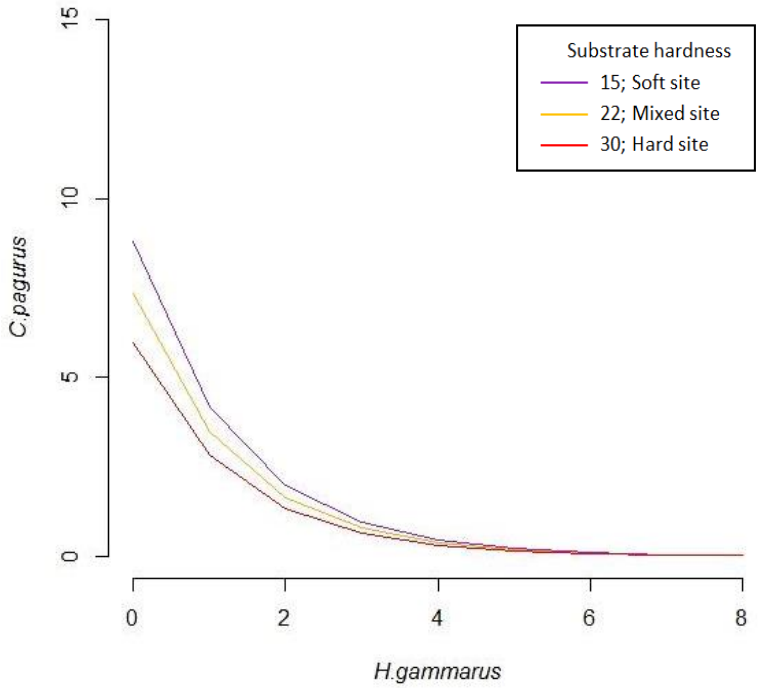


Figure 3.4 Plot of fitted negative binomial GLM2 with hardness as a covariate; model predications for various substrate hardness values, representing a soft, mixed and hard site.

Table 3.4 Showing the ratio and numbers of female and male lobsters caught in each year of sampling.

Year	Female	Male	Ratio F:M	Total
2010	300	286	51:49	586
2011	111	89	55:45	200
2012	185	163	53:47	348
Total	596	538	53:47	1134

Table 3.5 Observed and expected distributions of the sex of 175 pairs of lobsters caught in pairs throughout all study periods. (Overall sex ratio over this period was 0.526:0.474; F:M (See Table 3.7.). $\chi^2 = 25.73$; df = 2; $p < 0.05$.

Pair	Observed	Expected
2 males	34	55
1 female 1 male	88	58
2 females	53	61

Trap catches with exactly two lobsters and no crabs were tested against expected sex parings based on the overall sex ratio during the entire study period (Table 3.4). Chi-squared goodness-of-fit showed observed sex pairings were significantly different from the expected distribution ($\chi^2 = 25.73$, $p < 0.05$). Mixed sex pairings were much more likely than expected ($\chi^2 = 15.5$, $p < 0.05$). While male-male pairings were less likely to occur than expected ($\chi^2 = 8.01$, $p < 0.05$). Female-female pairings were the only non-significant pairings ($\chi^2 = 1.05$, $p = 0.31$) (Table 3.5).

3.3.2 Pre-loaded trap catch data (2011 – 2012)

In 2011 and 2012 there were 130 successful trap-hauls with four pre-loaded treatments: lobster (n = 33), brown crab (n = 40), velvet crab (n = 15) and control (n = 42). Mean catch rates of the three target species varied among treatments (Fig. 3.5 *a-d*). Chi squared (χ^2) tests showed significant differences between observed and expected ratios of lobster, brown crab and velvet crab in the traps from the four different treatments ($\chi^2 = 33.26$; $p < 0.001$) (Table 3.6). Treatments had significant effects on proportions of the three target species caught, the greatest deviation from expected catches relating to crab and lobster in the lobster treatment (Table 3.6).

When traps were pre-loaded with a single lobster the subsequent number of *C. pagurus* caught per trap was significantly lower ($\bar{x}_{33} = 0.21 \pm 0.10_{s.e.}$) than in control traps ($\bar{x}_{42} = 3.90 \pm 0.72_{s.e.}$) (Wilcoxon-test$_{73}$: $V = 261.5$; $p < 0.001$). The number of *N. puber* caught per trap in the presence of pre-loaded lobster ($\bar{x}_{33} = 0.18 \pm 0.08_{s.e.}$) also differed from control traps ($\bar{x}_{42} = 1.10 \pm 0.21_{s.e.}$) (Wilcoxon-test$_{73}$: $V = 227$; $p < 0.001$). Despite the mean catch of lobster per trap being lowest in the lobster treatment ($\bar{x}_{33} = 0.42 \pm 0.12_{s.e.}$) there was no significant difference in lobster catches among treatments. These data show the only treatment to have a significant influence on subsequent catch of any species was when traps were pre-loaded with a single lobster. To increase replication of trap-hauls, the study focused on the lobster and control treatments (Section 3.3.3).

The CL and PL of pre-loaded lobsters were positively correlated with the mean CL and PL of lobsters subsequently caught in the same traps (Figs. 3.6 and 3.7, respectively)

(CL; $R^2 = 0.305$, $p < 0.05$. PL; $R^2 = 0.623$, $p < 0.01$). There was scope to fit a model to predict the size of subsequently caught lobster from size of pre-loaded lobster, however the data were limited and greater replication was needed.

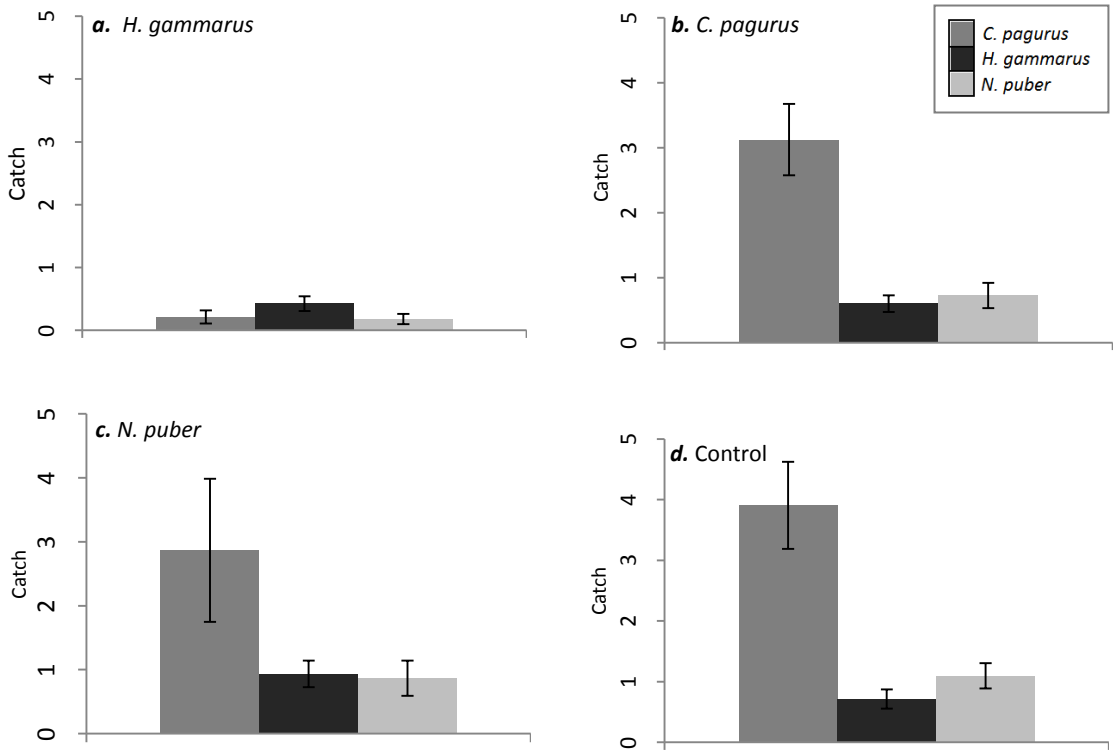


Figure 3.5 Mean (±s.e.) number per trap by species (see key, top right) for 2011 and 2012 data combined in the four pre-load treatments: a. *H. gammarus* (n = 33), b. *C. pagurus* (n = 40), c. *N. puber* (n = 15), and d. control (n = 42).

Table 3.6 Observed and expected distributions of total catch for each species, for all four treatment types. $\chi^2 = 33.26$; df = 6; $p < 0.001$.

Observed	**Control**	**Lobster**	**Crab**	**Velvet**	**Total**
Lobster	30	14	24	14	44
Crab	164	7	125	43	171
Velvet	46	6	29	13	52
Total	240	27	178	70	267
Expected					
Lobster	40	4	29	12	44
Crab	154	17	114	45	171
Velvet	47	5	35	14	52

The relationships between CW and PL of pre-loaded *C. pagurus* and mean CW and PL of *C. pagurus* subsequently caught within the same trap (Fig. 3.8) were not significant (CW: $R^2 = -0.03816$, $p = 0.9317$; PL: $R^2 = -0.0829$, $p = 0.9461$). Replications were insufficient for detailed analysis of pre-loaded animal size effects on catch.

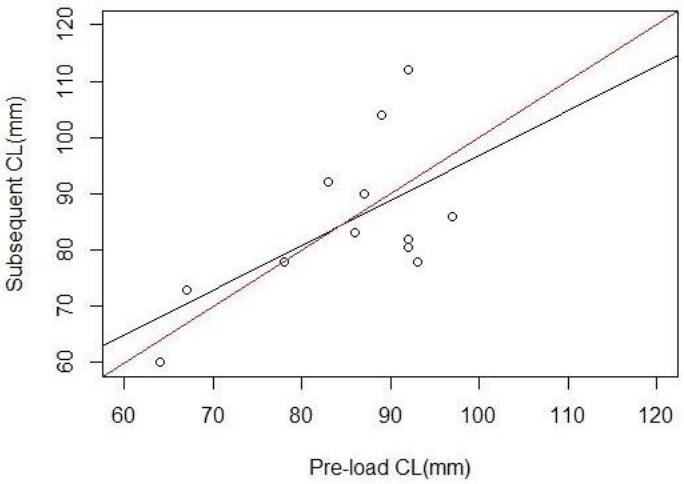


Figure 3.6 Plot of CL of the pre-loaded lobster against the mean CL of subsequently caught lobsters for lobster treatment, for 2011 and 2012. Red line shows y = x; black line represents a linear regression $y = 0.798x + 17.067$; $R^2 = 0.305$; $p = 0.03651$.

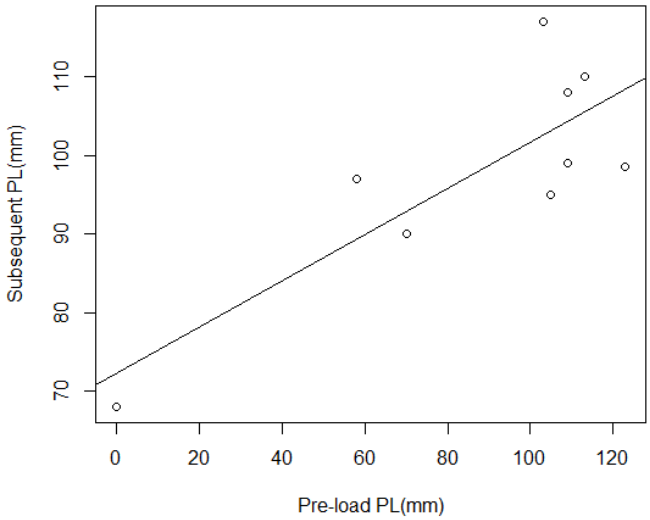


Figure 3.7 Plot of PL of the pre-loaded lobster against the mean PL of subsequently caught lobsters within the lobster treatment, for 2011 and 2012. The black line represents a linear regression $y = 0.294x + 72.207$; $R^2 = 0.623$, $p = 0.006966$.

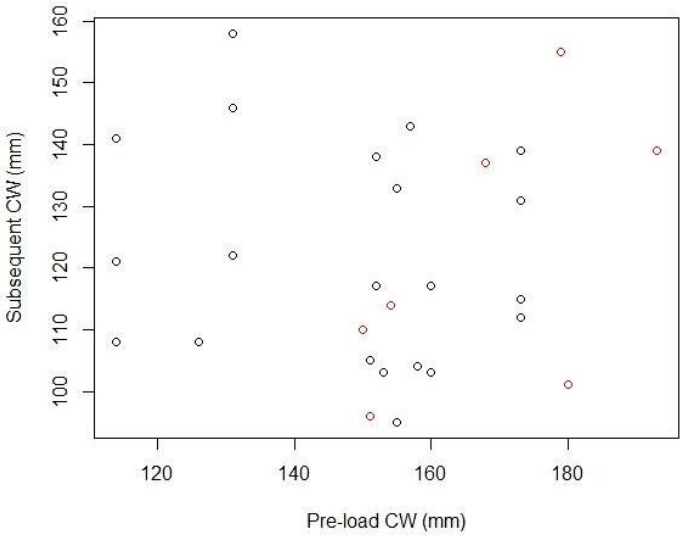


Figure 3.8 Plot of CW of pre-loaded crab against the mean CW of subsequently caught crabs for brown crab treatment, for 2011 and 2012. Female pre-loads are highlighted in red (o), males in black (o).

3.3.3 Pre-loaded trap-catch data (2013)

During 2013 there were 281 successful trap-hauls with two treatments: lobster (n = 166; 84 male, 82 female) and control (n = 115). CL of pre-loaded individuals was distributed as closely to that of the natural population as possible; ranging from 68 to 98mm (Fig. 3.9; $\bar{x}_{166}$ = 79mm ± $0.5_{s.e.}$). PL ranged from 69mm to 116mm ($\bar{x}_{166}$ = 95mm ± $0.64_{s.e.}$); and showed strong positive correlation with CL (Male R^2 = 0.198, $p < 0.001$, female R^2 = 0.539, $p < 0.001$), however, due to individuals re-growing lost claws outliers were observed (Fig. 3.10).

There was a significant difference in total catches of all species from all traps among the six haul occasions (Kruskal-$Wallis_5$: χ^2 = 12.12; $p < 0.05$), much of the difference attributable to a decrease in mean catch on occasion 4 (Figs. 3.11 and 3.12). When data from occasion 4 are omitted, the difference was not significant (Kruskal-$Wallis_4$: χ^2 = 9.26; p = 0.06). No significant difference was detected in total catches among strings (Kruskal-$Wallis_5$: χ^2 = 8.31; p = 0.14); data from all strings were therefore pooled to assess interactions.

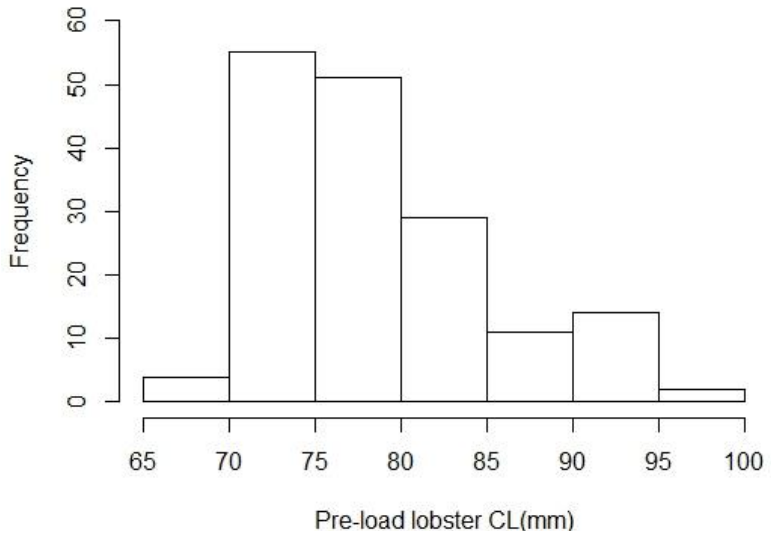


Figure 3.9 Size distribution of pre-loaded lobsters, 2013 (n = 166).

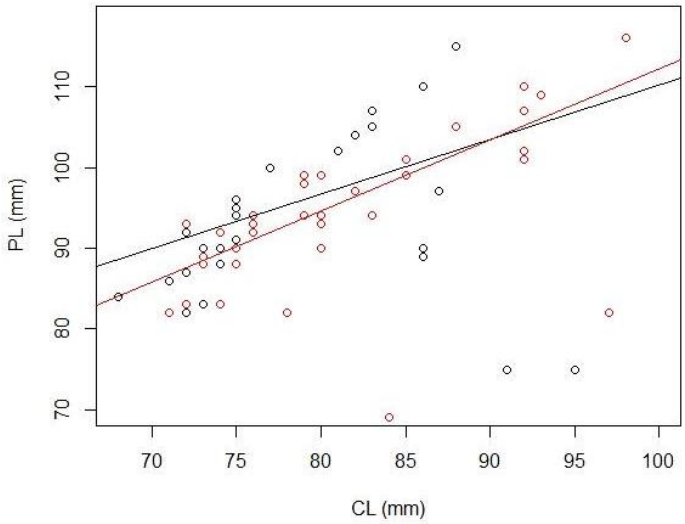


Figure 3.10 Plot of 2013 lobster CL against PL (n = 166), for females (o), and males (o). The black line represents a linear regression for male lobster, $y = 0.674x + 42.736$, $R^2 = 0.1985$, $p = 1.289e\text{-}05$. The red line a linear regression for female lobsters, $y = 0.883x + 23.943$, $R^2 = 0.5391$, $p = 2.547e\text{-}15$.

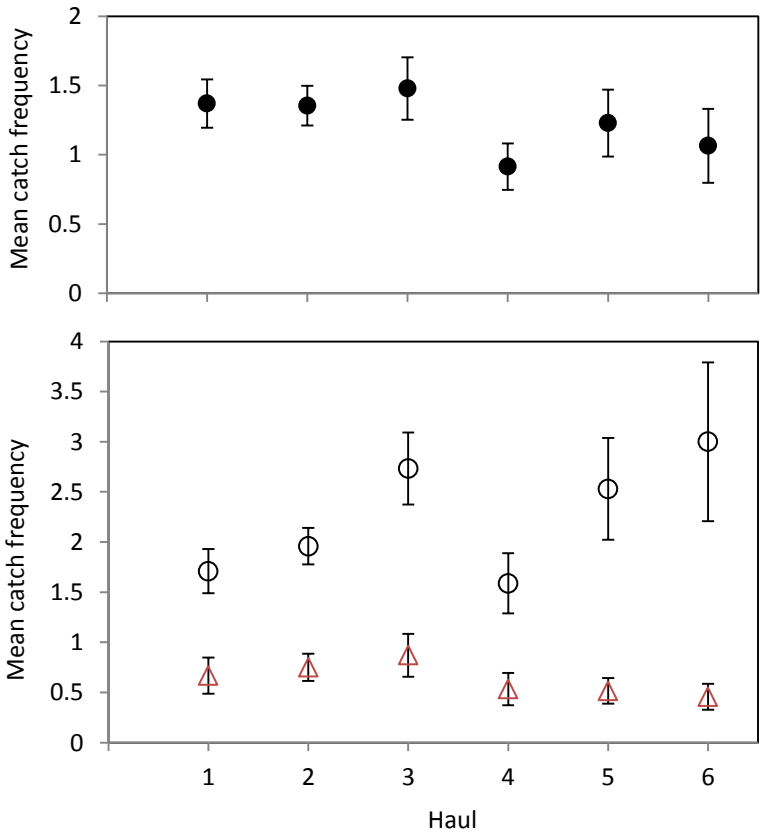


Figure 3.11 Plots of mean catch frequency (± SE) of all species, per trap for all traps (●), control traps (o) and treatment traps (Δ) by haul occasion.

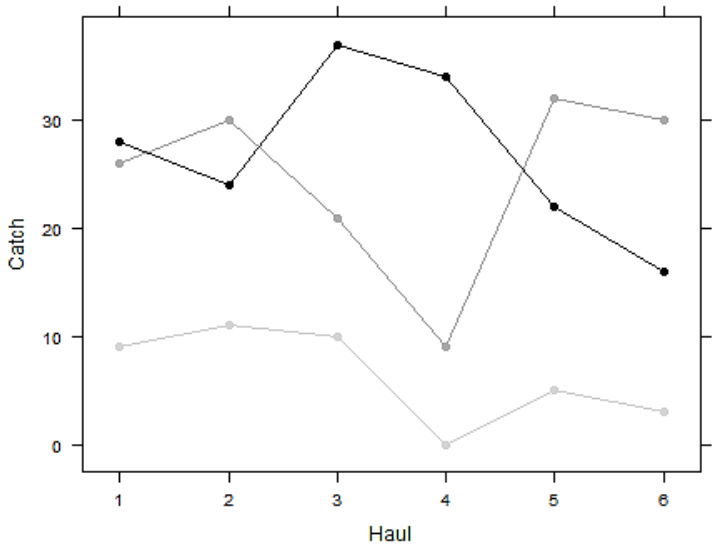


Figure 3.12 Plot of total catch frequency per haul occasion for each species; *H. gammarus* (●); *C. pagurus* (●); *N. puber* (●); grouped by haul occasion (1-6).

Average catches per trap of *H. gammarus*, *C. pagurus* and *N. puber* (Fig. 3.12) showed significant differences between observed and expected numbers in both treatment and control traps (Table 3.7, $\chi^2 = 65.44$; $p < 0.001$). Total catch of all species differed between control and treatment traps (Wilcoxon-test: W = 15364.5; $p < 0.001$), with traps pre-loaded with a single lobster ($\bar{x}_{166} = 0.62 \pm 0.07_{s.e.}$) catching on average one third the numbers of animals as control traps ($\bar{x}_{115} = 2.12 \pm 0.15_{s.e.}$).

Table 3.7 Observed and expected distributions of catch frequency for both control and treatment traps. $\chi^2 = 65.44$; df = 2; $p < 0.001$.

Observed	**Lobster**	**Crab**	**Velvet**	**Total**
Control	79	133	32	244
Treatment	82	15	6	103
Total	161	148	38	347
Expected				
Control	113	104	27	244
Treatment	48	44	11	103

The catches of lobster were not significantly different between control and treatment traps (Wilcoxon-test: $W = 10910$; $p = 0.99$), despite the mean catch per trap being lower in the treatment traps ($\bar{x}_{115} = 0.49 \pm 0.06_{s.e.}$) compared to the control traps ($\bar{x}_{166} = 0.69 \pm 0.08_{s.e.}$).

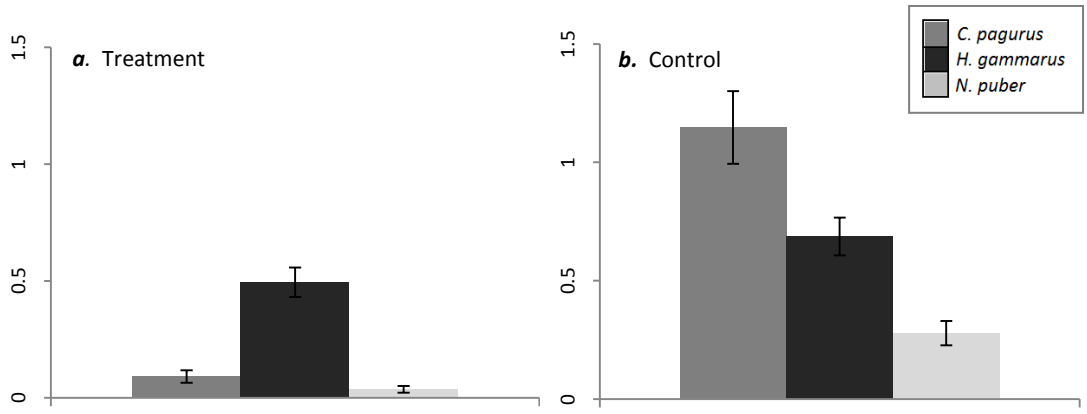


Figure 3.13 Average catch frequency by species; *C. pagurus*, *Homarus gammarus* and *N. puber* (see key top right) for 2013 data from both the treatment (*a*) and control traps (*b*). Error bars represent one standard error above and below the mean.

With a single lobster present within the parlour of a baited trap the mean subsequent catch of *C. pagurus* per trap was significantly lower ($\bar{x}_{166}$ = 0.09 ± 0.03$_{s.e.}$) than in control traps ($\bar{x}_{115}$ = 1.15 ± 0.15$_{s.e.}$) (Wilcoxon-test: W = 13897.5; p < 0.001). The proportion of *C. pagurus* in the total catch was 54% in control traps and 14% in treatment traps. The mean CW of *C. pagurus* was not significantly different between control ($\bar{X}_{143}$ = 136.68mm ± 2.59$_{s.e.}$) and treatment traps ($\bar{x}_{20}$ = 144.60mm ± 8.64$_{s.e.}$) (t-test$_{161}$: t = 0.213; p = 0.832), but catch frequencies of *N. puber* were lower in the treatment traps ($\bar{x}_{115}$ = 0.03 ± 0.04$_{s.e.}$) than control traps ($\bar{x}_{166}$ = 0.27 ± 0.02$_{s.e.}$) (Wilcoxon-test$_{73}$: W = 11376; p < 0.001).

Although more *C. pagurus* were caught in the presence of female ($\bar{x}_{82}$ = 0.12 ± 0.05$_{s.e.}$) than male lobsters ($\bar{x}_{84}$ = 0.06 ± 0.03$_{s.e.}$), this difference was not significant (Wilcoxon-test: W = 3347.5; p = 0.49). There was also no difference in the average catch of all species following pre-loading between female and male lobsters (Wilcoxon-test: W = 3274; p = 0.54), or in the total subsequent catch of lobster between male and female pre-loaded lobsters (Wilcoxon-test: W = 3438; p = 0.98).

The observed ratios of male and female in total catch was not significantly different from the expected distribution (Table 3.8, χ^2 = 1.642; p = 0.439), although the sex ratio of subsequently caught lobsters was different for traps pre-loaded with a single male lobster.

Table 3.8 Showing the number and ratio of female and male lobsters that entered the three different treatments of traps.

Treatment	Female	Male	Ratio (F:M)
Female pre-load	23	19	55:45
Male pre-load	27	13	67:33
Control	45	34	57:43

Neither PL or CL of pre-loaded lobster were significantly correlated with the mean PL or CL of subsequently caught lobster from the same trap (Figs. 3.14 and 3.15) (PL: R^2 = -0.008, p = 0.451, CL: R^2 = -0.013, p = 0.598). GLMs showed neither sex, pre-load PL or pre-load CL were significant predictors of the subsequent lobsters, PL or CL.

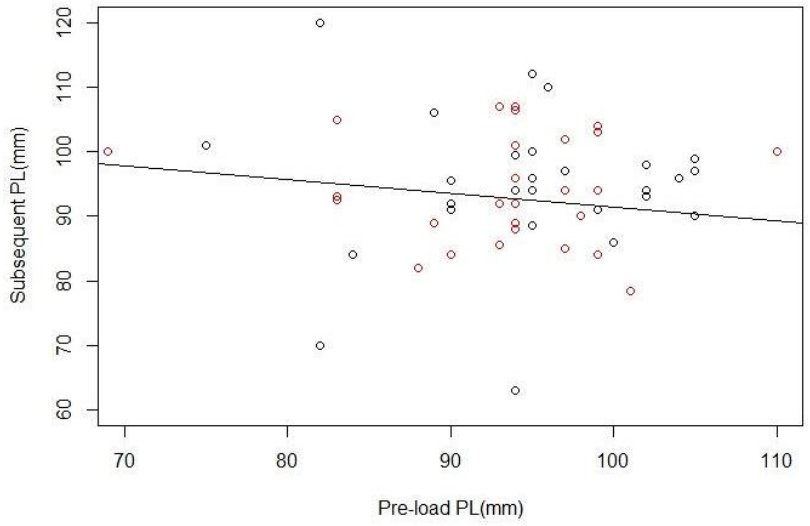


Figure 3.14 Plot of pre-load lobster propodite length (mm) against the average propodite length (mm) of subsequently caught lobster. Sex of the preloaded individuals are highlighted by males in black and females in red. Fitted regression is y = 112.9459 - 0.2155x; R^2 = -0.008, p = 0.451.

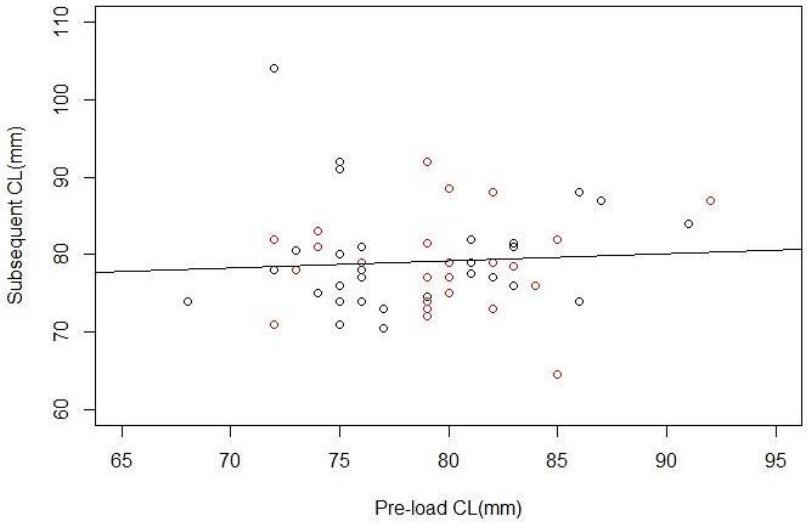


Figure 3.15 Plot of pre-load lobster CL (mm) against the average CL (mm) of subsequently caught lobster in the same trap. Male preloaded individuals are in black and females are highlighted in red. Fitted regression is y = 0.095x + 71.575; R^2 = -0.013, p = 0.598.

The number of lobsters caught (including pre-loads) within an individual trap was negatively correlated with the number of crabs caught within the same trap (Fig. 3.16). The average number of crabs caught fell significantly with the presence of a lobster ($\bar{x}_{37}$ = 2.65 ± 0.3$_{s.e.}$; ≥ 1 lobster: $\bar{x}_{223}$ = 0.22 ± 0.04$_{s.e.}$), and no crabs were caught when four or more lobsters were present in a trap. Due to the nature of count data, a Poisson estimated GLM was used to plot this relationship (Fig. 3.16), and described the data sufficiently (Table 3.9) (y = 0.9269 - 1.9899x).

Table 3.9 Results of fitted GLM: estimated coefficients values, relative error, Z value and significance. Residual deviance: 235.28 on 258 degrees of freedom.

	Estimate	**Error**	***t*-value**	**P-value**
Intercept	0.927	0.164	5.638	< 0.001
Lobster	-1.99	0.254	-7.850	< 0.001

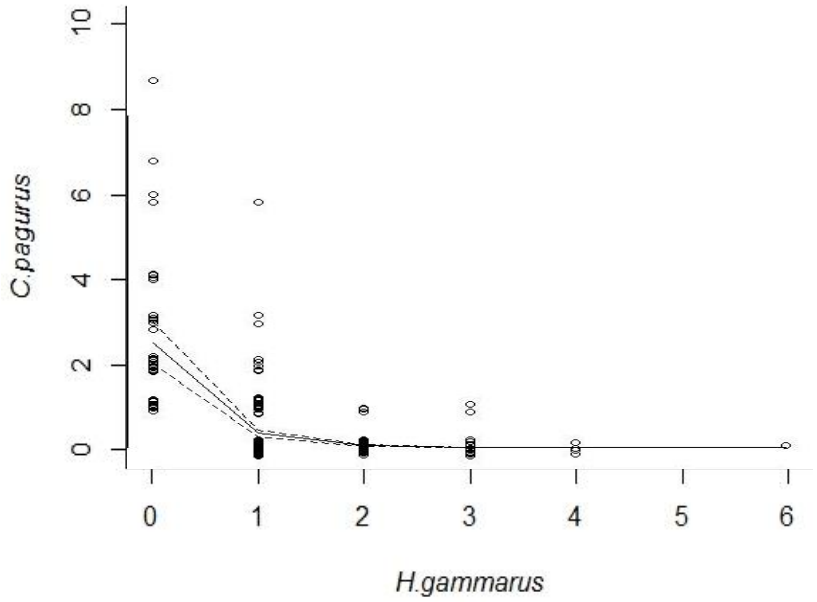


Figure 3.16 Plot of numbers of crabs against numbers of lobsters in an individual trap, for 2013 data (n = 260). Crab data has a jitter function added so that multiple points can be observed. Fitted Poisson GLM; y = 0.9269 - 1.9899x. Dashed error lines show 95% confidence intervals.

3.4 Discussion

The presence of lobster within a trap had a significant effect on both number and species composition of subsequent catches, significantly lowering numbers of *C. pagurus* and *N. puber*. This relationship was also observed in the fishery-independent catch data; a strong negative correlation between *H. gammarus* and *C. pagurus* catch

numbers; significantly impacted by site hardness, softer grounds having higher crab catches. No significant impacts were observed on catch numbers of *H. gammarus* in any treatment.

Total mean animal catch abundances were significantly reduced by lobster pre-load treatment; there was an approximate four-fold reduction per trap. Catch compositions during 2011-2012 were also significantly altered. Catches comprising of 87%, 80% and 86% crab species in the *C. pagurus*, *N. puber* and control trap treatments, respectively, declined to a mean of 48% crab species in the lobster treatment.

There was no correlation between sex or size of pre-loads with subsequent catch number or size of subsequent animals entering the trap. There was however, a significantly lower number of observed male-male lobster pairings from the fishery-independent catch data, compared to expected number of pairings.

3.4.1 Intra-specific interactions

The present study found that one *H. gammarus* within the parlour of a trap did not have a significant effect on subsequent catch rate of conspecifics. In contrast, an earlier UK study, in Bridlington Bay, indicated one *H. gammarus* to significantly reduce catches of conspecifics (Addison 1995). In the US, despite low replication, three and eight *H. americanus* significantly lowered catch rates of conspecifics (Richards, Cobb *et al.* 1983). These differences in findings could be due, in part, to disparities in local lobster catch rates. Addison *et al.* (1995) reported catches of one or more lobster more likely than none, and mean number of lobster caught per trap was more than twice that of both historical fishery-dependent data used in the study and data in the present study, 67% of traps in the present study caught no lobster. *H. americanus* are caught in greater numbers than *H. gammarus* (Miller 1994), eight per trap being regarded as “natural” by Richards *et al.* (1983). In the present study, eight lobsters in a trap was observed once in 2,266 traps analysed. Low lobster abundances have previously been shown to increase catchability (Tremblay and Smith 2001), (Ziegler, Frusher et al. 2003). If the inhibitory effect of a single lobster on catches is small and

catchability is high at low catch rates, differences between control catches and pre-load lobster catches may be less significant.

CL and PL of pre-load lobster had no effect on the number, CL or PL of subsequently caught lobster. Possibly due to restricted size range, the effect of other variables such as plasma protein levels and exoskeleton calcium concentration may be significant (Vye, Cobb *et al.* 1997), and could be tested in further work. Intra-specific lobster interactions may also be unobserved, due to escapements prior to hauling; underwater observations of *H. americanus* have shown larger lobster defend the bait and prevent smaller ones from entering (Jury, Howell *et al.* 2001). In the present study lobsters were placed within the parlour of the trap to minimise escapement, but as Jury *et al.* (2001) showed, it is often lobsters within the kitchen (first compartment of trap, with bait inside) that show dominance over the food source. Lobster within the parlour that cannot access the bait may be less likely to inhibit smaller lobster from entering (Huntingford, Taylor *et al.* 1995). However, the placement of the pre-load is not thought to have affected overall catch rates compared with previous UK interaction studies; other pre-loading studies also placed lobsters within the parlour (Richards, Cobb *et al.* 1983; Addison 1995).

Sex of pre-loads did not have a significant effect on the sex of subsequent lobsters (Addison 1995), despite fewer male-male pairings being observed than expected. However, observed fisheries-independent sex pairings differed significantly from expected (Table 3.7); lobsters were less likely to be caught with a lobster of the same sex, while mixed-sex pairings were much more likely to occur than expected, possibly due to either competition of same sexes, or sexual attraction of opposite sexes. This has also been observed elsewhere (Karavanich and Atema 1998; Bushmann and Atema 2000; Hunt, Breuker *et al.* 2009). Placement of the pre-loaded animal within the parlour may allow interaction between the sexes to be observed as these occur largely due to pheromone release. Whereas size-related interactions are less likely to be observed, as these occur due to physical interaction, so was not possible in the present study until the approaching lobster entered the trap. Intra-specific interactions will affect catchability and catch rates, however, the relationships are evidently complex

and individual sex- or size- interactions must be assessed for each trap study using the data.

3.4.2 Inter-specific interactions

Lobster catch rates did not differ between treatments, indicating that lobster catchability is not significantly impacted by the presence of a single crab. However, a single lobster significantly inhibited the catchability of *C. pagurus* and *N. puber*. This has previously been observed in the UK (Addison 1995), and *H. americanus* discourages entry of *Cancer borealis* and *Cancer irroratus* (Richards, Cobb *et al.* 1983). Inhibitory effects of *H. americanus* on crab catchability have been attributed the inverse relationship between lobster and crab catches in other US studies (Stasko 1975; Krouse 1978; Fogarty and Borden 1980), and could be the cause of the inverse relationship seen here (Figs. 3.3 and 3.4). While large lobsters may prey on small crab, suggesting the inhibitory effect may be predator-avoidance, this is unlikely for the majority of the crabs in this study, due to the relatively large mean CW of *C. pagurus* ($\bar{x}_{151}$ = 136mm) and *N. puber* ($\bar{x}_{38}$ = 72mm). It is likely that crabs were avoiding lobster due to lobsters' dominance during aggressive interactions.

Neither *C. pagurus* nor *N. puber* significantly affected the catchability of any of the three target species, despite the aggressive nature of *N. puber* (Smith, Huntingford *et al.* 1994; Thorpe, Huntingford *et al.* 1994). Previous laboratory work has shown lobster inhibit the entry of crabs, while crab catchability remains constant at different loading densities of conspecifics (Miller and Addison 1995). No correlation was found between CW or PL of pre-loaded *C. pagurus* and subsequent *C. pagurus* CW or PL. *C. pagurus* do not aggressively defend bait or space against smaller conspecifics, but form feeding groups around bait (pers. obs.). They stay with the same prey for up to several hours, feeding in the presence of conspecifics (Lawton and Hughes 1985; Lawton 1989). In contrast, *H. gammarus* and *H. americanus* tend to either aggressively defend bait (Jury, Howell *et al.* 2001), take bait back to shelter before consuming (Lawton 1987; Spanier, McKenzie *et al.* 1998), or bury bait for later retrieval (Wickins, Roberts *et al.* 1996); they are also known to predate on immature conspecifics (Olst, Carlberg *et al.* 1975; Wahle 2003). Lobsters tend to be solitary, whereas crabs can be found at relatively

high densities, so the presence of conspecifics is not a deterrent to crab foraging (Williams, Floyd *et al.* 2006). This dichotomy in feeding behaviours has been observed when *Carcinus* spp and *H. americanus* compete for the same food source; the crabs were often first to arrive at the food, and spent more time with the food, but were outcompeted by large lobsters (Rossong, Williams *et al.* 2006; Williams, Floyd *et al.* 2006; Williams, MacSween *et al.* 2009; Rossong, Quijon *et al.* 2011). Understanding feeding behaviours and their influence on catchability will increase the ability to include the effects in trap-based assessments.

Homarus gammarus and *C. pagurus* fishery-independent catches were strongly negatively correlated with each other (Fig. 3.4), however, the cause of this relationship cannot be determined from these data alone. It is likely that both inhibitory interactions and spatial distribution disparity between the two species affect catches. The presence of high crab numbers in a trap will diminish the bait, and saturate the trap, making it less attractive to lobster; agonistic interactions are not thought to affect lobster catchability, even at the high crab densities present on soft sediment sites. While it is clear that species proportions change with habitat, it is unclear if this is driven by changes in abundance or catchability, a key limitation of trap-based data analysis.

3.4.3 Methodological improvements

In the study, animals were pre-loaded into the parlour of the trap and such placement may impair interactions with animals approaching or entering the trap. Pre-loads within the kitchen of the trap may feed directly upon bait, more readily defend the bait, and/or physically block or prevent subsequent animals from entering the trap. The scope for frequency and strength of interactions to differ between pre-loaded animals within the parlour and kitchen is unknown. Comparing pre-loads positioned within each compartment would permit the quantification of interaction when lobsters are in control of the bait, compared to placements within the parlour. This would permit elimination of control of the bait as the determinant to inhibiting trap entry, particularly between intraspecific lobster interactions. Recording the position of the subsequent entries within the trap (e.g. Richards *et al.* 1983), may also improve

understanding of animal behaviours within traps. The inclusion of underwater television would also improve understanding of unobserved interactions. Otherwise the catch data merely pertain to animals caught at the time of hauling, rather than animals that have entered the trap or interacted during soak (Jury, Howell *et al.* 2001).

One additional caveat concerns the fishery-independent trap survey data used. These need to be analysed with care for two main reasons. Firstly, there are potentially confounding effects of site. Sites were significantly different in location, depth, habitat type, year studied and therefore local abundances of lobster and crab. Secondly, the data were markedly zero-inflated; a potentially contributing factor was that the catch method masks the history of animal-trap interactions; lobster can escape traps very easily. A null result on hauling the trap does not mean that no animals entered the trap. Empty traps observed over rocky grounds could have had lobster in them throughout the soak period, preventing the entry of crab spp, but upon hauling the trap appears to have been empty throughout the entire period. Another problem is determining which animal enters the trap first. A trap catch of 30 crabs and 1 lobster does not necessarily mean that crabs are willing to enter the trap with a lobster. However, the large amount of replication, and reliability of trap data recordings justifies its inclusion; this is the type of data used for analysis of stocks, from fisheries data. Better understanding of site and abundance impacts, could be obtained in future studies increasing the number of preloaded lobster and number of study sites.

It was assumed that all traps would attract an equal number of animals to approach them; therefore any difference in catch could be attributed to interactions with the pre-loaded animal. In reality this assumption is unlikely to hold, as trap efficiency changes both spatially and temporally, however, high replication is likely to avoid this impacting results.

3.4.4 Future implications of the study

These findings have important consequences for local stock assessments. CPUE for example could be a poor proxy for abundance in this mixed fishery without taking into consideration relationships between lobster and crab in the catches. CPUE is

therefore not necessarily linearly related to abundance, as is ideally assumed. Species catches cannot be examined in isolation; a decline in catch of crabs one month may be explicable by an increase in lobster the same month, rather than being interpreted as a reduction in the crab abundance. Overall, the interactions found here will affect the monitoring of crab abundance much more severely than lobster abundance.

Behavioural interactions between lobsters and other animals clearly play an important role in determining rate of entry, exit, and ultimately catch of a trap. The probability that a lobster enters a trap and remains to be caught, is a complex process dependent upon numerous factors (Ennis 1973; McLeese 1973; Miller 1978; Miller 1978; Miller 1979; Miller 1983; Richards, Cobb *et al.* 1983; Krouse 1989; Miller 1989; Smith and Jamieson 1989; Miller 1990; Miller and Addison 1995; Tremblay 2000). This study demonstrates that the presence of a single lobster in a trap can reduce CPUE of *C. pagurus* by a factor of 12.8 and *N. puber* by a factor of 9. This helps to explain some of the inverse relationship observed between lobster and crab catches (Fig. 3.4). *C. pagurus* may not be any less abundant on rocky or mixed habitat than on soft sediment sites, but their catchability is heavily reduced if traps are occupied by lobster. Care must be taken when analysing baited trap catch data from such a mixed fishery. All animals within the trap must be recorded, to allow the user to determine if inhibitory effects are altering the trap catch rates.

3.5 Conclusion

Individual lobsters did not have a significant impact on the subsequent catch or size of other lobster off Blyth, however, male-male pairings were significantly less likely to occur than expected. Interaction between lobster and crabs is a complex process, it is clear that lobsters inhibit both *C. pagurus* and *N. puber* from entering baited traps; this could lead to conventional CPUE approaches under-estimating the abundance of crab spp.

Different results have been described from areas where lobster populations are believed to be higher; suggesting that catchability may not be constant with density. One lobster may be the most common number observed in a trap regardless of density

(Addison 1995). This could have important consequences when using catch data for monitoring and assessment (Bannister and Addison 1998); as behavioural interactions may turn an aggregated distribution of lobsters on the seabed into a random or even distribution of trap catch (Addison and Bell 1997). Therefore, only using CPUE from baited traps is not necessarily a good indicator of the crustacean density (Addison 1995; Addison and Bell 1997; Fogarty and Addison 1997).

Chapter 4:

Investigating movement and spatial distribution of *Homarus gammarus* using mark-recapture and fishery-independent trap survey methods

Chapter 4: Investigating movement and spatial distribution of *Homarus gammarus* using mark-recapture and fishery-independent trap survey methods

4.1 Introduction

European lobsters, *Homarus gammarus*, are large, mobile crustaceans with an economically important fishery; yet there are few published studies on their movement, *in situ* behaviour or habitat utilisation. Such information is potentially very useful for understanding density dependent population dynamics and therefore determining seasonal patterns of distribution, potential connectivity of stocks, and the relationship between fishing effort, catchability and catch rates; all of which are necessary for stock monitoring and management (Bannister 1986; Milinski and Parker 1991; Fogarty 1995; Lawton and Lavalli 1995; Addison and Bannister 1998). Including enhancement schemes and marine protected areas (MPA) (Bannister, Addison *et al.* 1994; Perry, Walters *et al.* 1999; Smith, Collins *et al.* 2000).

Water temperature is known to influence crustacean behaviour and large-scale distributions (Factor 1995; Koeller 1999; Fogarty, Incze *et al.* 2007) due to temperature tolerance limitations and females limited capacity to thermoregulate during egg development (Hutchison and Maness 1979; Magnuson, Crowder *et al.* 1979; Ennis 1984; Kivivuori 1994; Crossin, Al-Ayoub *et al.* 1998). Temperature also dictates activity levels and catchability (Drinkwater, Harding *et al.* 1996; Smith, Collins *et al.* 1998; Koeller 1999; Smith, Collins *et al.* 1999; Comeau and Savoie 2002; Schmalenbach and Buchholz 2013), affecting observed catch rates, but this relationship is complex. On a finer scale habitat type, quality and location are likely determinants of animal movement, distribution, and abundance (Wahle and Steneck 1991; Tremblay and Smith 2001; Tews, Brose *et al.* 2004; Selgrath, Hovel *et al.* 2007; Geraldi, Wahle *et al.* 2009). The provision of shelter-providing refuge, available mates and suitable prey items, will cause local changes in lobster density (Howard 1980; Smith, Jensen *et al.* 2001).

Movements of *Homarus americanus* are well documented over much of its range (Cooper and Uzmann 1980; Krouse 1980; Campbell and Stasko 1985; Campbell 1986; Campbell and Stasko 1986). Offshore movements of over 100km have been recorded (Cooper and Uzmann 1971) and there is evidence of inshore migrations of mature lobsters (Fogarty, Borden *et al.* 1980a; Munro and Therriault 1983; Ennis 1984; Campbell and Stasko 1985). However, most recapture distances are less than 15km (Krouse 1981; Campbell and Mohn 1982; Ennis 1984). *H. gammarus* is generally regarded as sedentary, remaining within small areas for long periods (Bannister, Addison *et al.* 1994; Jørstad, Prodöhl *et al.* 2004). Seasonal migrations have not been clearly defined (Cooper and Uzmann 1980). A lack of published data on *H. gammarus* limits understanding (Smith, Jensen *et al.* 2001). Previous CMR studies are limited over most of its range, use hatchery-reared lobsters (Latrouite, Léglise *et al.* 1981; Bannister, Addison *et al.* 1994) or have the primary goal of estimating mortality or growth rates. However, they offer insights into the potential mobility of *H. gammarus*; most recaptures (95%) occur within 3km of release with no pattern in direction or between sexes, and only small proportions have been observed to travel up to 15km in a season (Thomas 1954; Simpson 1961; Jensen, Collins *et al.* 1994; Smith, Collins *et al.* 1999; Smith, Jensen *et al.* 2001). With the exception of a few studies (Smith, Collins *et al.* 1999; Smith, Collins *et al.* 2000; Smith, Jensen *et al.* 2001; Moland, Olsen *et al.* 2011), understanding of *H. gammarus*' spatial distribution is exclusively based on fishery-dependent landings data, or inferred from behavioural studies of *H. americanus*.

This chapter presents data of fishery-independent trap catches and on the movement of tagged lobsters released at known locations off the coast of Northumberland via commercial and scientific fishing recaptures. The objectives are to determine the distribution of trap catch frequency and lobster size and sex data, analysed by substrate hardness, depth and distance to reef of trap-location, and a model developed to predict these catches based on these variables solely. Secondly to determine distances moved and the mean direction of any long-distance movements, by sex and size, and movements of lobster released from the capture site are compared with those released away from the original capture site.

4.2 Methodology

4.2.1 Study sites

Between 2011 and 2012 fishery-independent trap data were collected from 4 sites within 9km of the port of Blyth, Northumberland (Fig. 4.2). During 2011 surveys were conducted from on-board the 21m NIFCA fisheries patrol vessel *St Oswald* (04 Oct 2011 to 15 Dec 2011). In 2012 the survey was conducted from Newcastle University's 18.9m Research Vessel *Princess Royal* (05 Sep 2012 to 10 Oct 2012). Sites were composed of a mixture of hard and soft substrate forming distinct patches. Site depth varied from 14.2m to 43.3m; mean site depths are shown in table 4.2.

Between 2011 and 2012, 1,483 individual lobsters were tagged and released on multiple occasions at 4 sites and along 11 transects (Fig. 4.2). Tagging occasions were opportunistic, conducted during fishery-independent trap surveys and the NIFCA 'v-notching programme' in 2012. As a conservation measure, the NIFCA v-notches and releases approximately 1,000 ovigerous lobsters per year throughout their district. This involves the removal of a section of the uropod, adjacent to the telson (DeAngelis, Cooper *et al.* 2010) (Fig. 4.1) and legally protects the animal from landing via the NIFCA Byelaw 6, '*Protection of 'V' Notched Lobsters*' (NIFCA 2013).

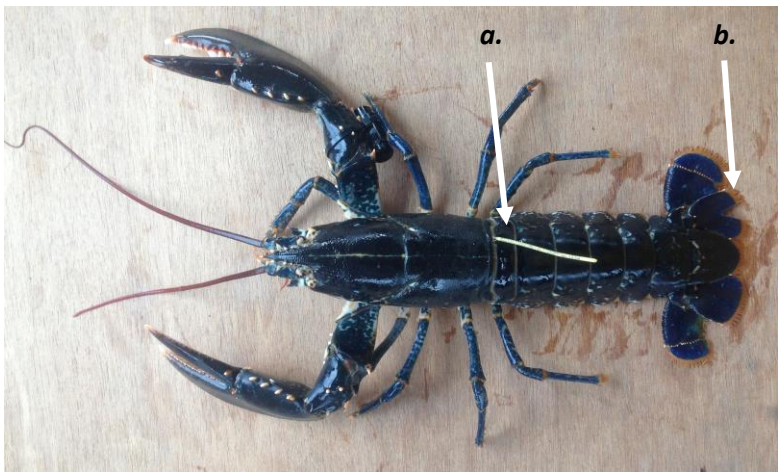


Figure 4.1 Image of a tagged lobster; ***a.*** yellow T-bar tag located off-centre within the dorsal musculature; ***b.*** V-notch mark on the right-side uropod.

Release sites for lobsters were determined as either the location of capture during fishery-independent trap surveys (BL1, BL2, BL3 and BL4), or randomly assigned to transects during the v-notching survey release (V1B1 to V3B4) (Tables 4.1 and 4.2). Substrate hardness data were collected continuously using both vessels' on-board Olex 8.2 mapping and navigation software. This provides a relative assessment of change in substrate hardness by reporting backscatter values from the vessel's single-beam echo-sounder as a ratio of sent and received acoustic energy via a proprietary algorithmic treatment of the sonogram. This translates into a linear scale from 1 (i.e. low reflection) to 100 (i.e. 0dB energy lost). As acoustic returns are impacted by environmental conditions, only strong readings are used by the software. Olex does not use backscatter to assess bottom roughness, and only provides data as a proxy for habitat hardness. Previous studies reveal that there is little difference in broad scale habitat classifications derived using Olex or multi-beam acoustic systems (Elvenes, Dolan *et al.* 2013); Olex is a cost-effective approach to habitat discrimination for the purpose of this study. Hardness for each site, transect and trap location was calculated by taking the mean Olex hardness value within the trap array and within 40m diameter of each geo-referenced trap location (Table 4.1 and 4.2), a raster of hardness was created via the Kriging interpolation tool in ArcMap 10.1; using a Gaussian distribution semi-variogram model, with variable search radius that included 10 points, and fixed output cell size of 5m, equivalent to the resolution of the Olex raw data.

Table 4.1 V-notch transect information; date, approximate start and finish location, mean depth, hardness.

Transect	Date	Approximate start	Approximate finish	Mean depth (m) ± s.e	Mean hardness ± s.e
V1B1	03/08/2012	55° 16.27 N; -01° 28.62 W	55° 16.95 N; -01° 28.91 W	34.73 ±0.05	34.93 ±0.90
V1B2	03/08/2012	55° 17.97 N; -01° 28.97 W	55° 17.79 N; -01° 29.30 W	34.94 ±0.04	41.62 ±0.74
V2B1	13/08/2012	55° 36.54 N; -01° 37.94 W	55° 37.17 N; -01° 37.25 W	23.60 ±0.30	23.32 ±0.59
V2B2	13/08/2012	55° 29.81 N; -01° 27.30 W	55° 29.20 N; -01° 26.82 W	29.76 ±0.54	52.08 ±0.47
V2B3	13/08/2012	55° 12.39 N; -01° 28.45 W	55° 11.90 N; -01° 28.43 W	29.81 ±0.16	29.19 ±1.05
V2B4	13/08/2012	55° 11.90 N; -01° 28.43 W	55° 11.01 N; -01° 28.52 W	24.52 ±0.32	42.44 ±0.64
V2B5	13/08/2012	55° 20.42 N; -01° 30.92 W	55° 19.28 N; -01° 30.95 W	29.03 ±0.15	37.07 ±0.91
V3B1	24/08/2012	55° 14.20 N; -01° 29.66 W	55° 15.09 N; -01° 30.69 W	17.56 ±0.32	35.49 ±0.79
V3B2	24/08/2012	55° 25.09 N; -01° 33.54 W	55° 23.34 N; -01° 33.87 W	6.95 ±0.06	19.82 ±0.36
V3B3	24/08/2012	55° 05.14 N; -01° 26.57 W	55° 04.38 N; -01° 25.63 W	16.24 ±0.05	20.59 ±0.26
V3B4	24/08/2012	55° 04.38 N; -01° 25.63 W	55° 03.73 N; -01° 24.92 W	15.53 ±0.09	21.95 ±0.41

Table 4.2 Site information; year fished, approximate location of the centre of the site, mean depth, hardness.

Site	Years	Approximate location	Mean depth (m) ±s.e	Mean hardness ±s.e	Substrate
BL1	2011	55° 8.12 N; -01° 23.16 W	41.20 ±0.02	15.04 ±0.09	Soft
BL2	2011	55° 6.85 N; -01° 23.51 W	34.45 ±0.03	18.73 ±0.12	Mixed
BL3	2011	55° 4.89 N; -01° 21.73 W	38.11 ±0.02	34.44 ±0.16	Hard
BL4	2011, 2012	55° 7.53 N; -01° 27.15 W	25.47 ±0.05	36.67 ±0.50	Hard

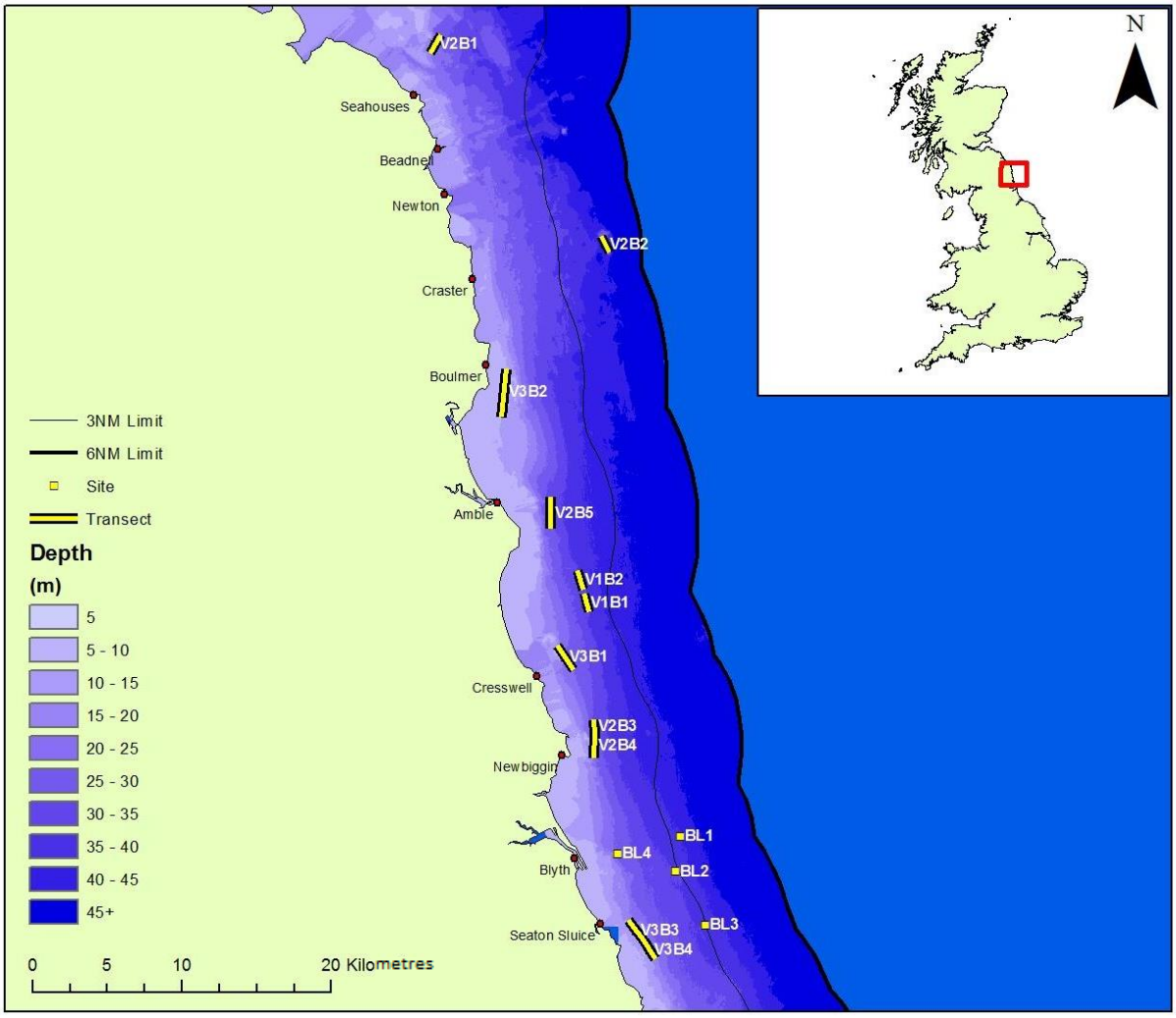


Figure 4.2 Diagram of locations of fishing port, study site and v-notch transect during 2010 – 2012. Approximate depth up to the 6 nautical mile district limit, as recorded by the on-board Olex software.

4.2.2 Data collection

The study comprised two distinct methods of data collection: trap catch data from a series of fishery-independent geo-referenced trap surveys, and movement data collected via the recapture of tagged animals from both scientific and commercial fishing.

4.2.2.1 Fishery-independent trap data

A fleet of 64 standard commercial, 10mm steel-framed, parlour traps, measuring approximately 0.68 x 0.46 x 0.38m, with a 130mm fixed diameter single side entrance, 27mm square mesh and selective grill on the bottom were used throughout the study. Traps were baited with a single frozen flatfish 20-30cm total length, primarily dab (*Limanda limanda*) or plaice (*Pleuronectes platessa*). Old bait was removed and replaced on every haul occasion.

Traps were arranged in eight identical strings of eight traps, spaced with approximately 100m between strings and 40m between traps. Upon each setting of traps, the vessel was lined up to predetermined string positions using the on-board navigation software, with a due North bearing. String locations within the array were spatially referenced with GPS and water depths were recorded. During hauling, the catch from each individual trap was removed and stored in a separate container to maintain trap-specific catch information. Biometric data were recorded for every individual animal. This included species, CL for lobster and CW for crab, sex, presence of eggs, general condition, and their capture location (site, string and trap number). All lobsters were tagged with a persistent T-bar tag (TBA1, yellow, 50 × 2mm, Hallprint Pty. Ltd, Holden Hill, South Australia), resulting in an individual lobster remaining identifiable (see; p.34). Tests prior to sampling, coupled with previous studies, show T-bar tags to be sufficiently durable to enable identification of recaptured animals after periods of up to several years, without appearing to affect survival or behaviour (Smith, Jensen *et al.* 2001; Moland, Olsen *et al.* 2011). Each tag displays printed information including a unique four digit identification number, making it possible to construct accurate capture and movement records for each marked lobster and details for reporting recaptures. All caught animals were released from the location of capture within 30 minutes of landing. Recaptured animals with an existing T-bar tag, had their unique ID noted and their new capture location recorded.

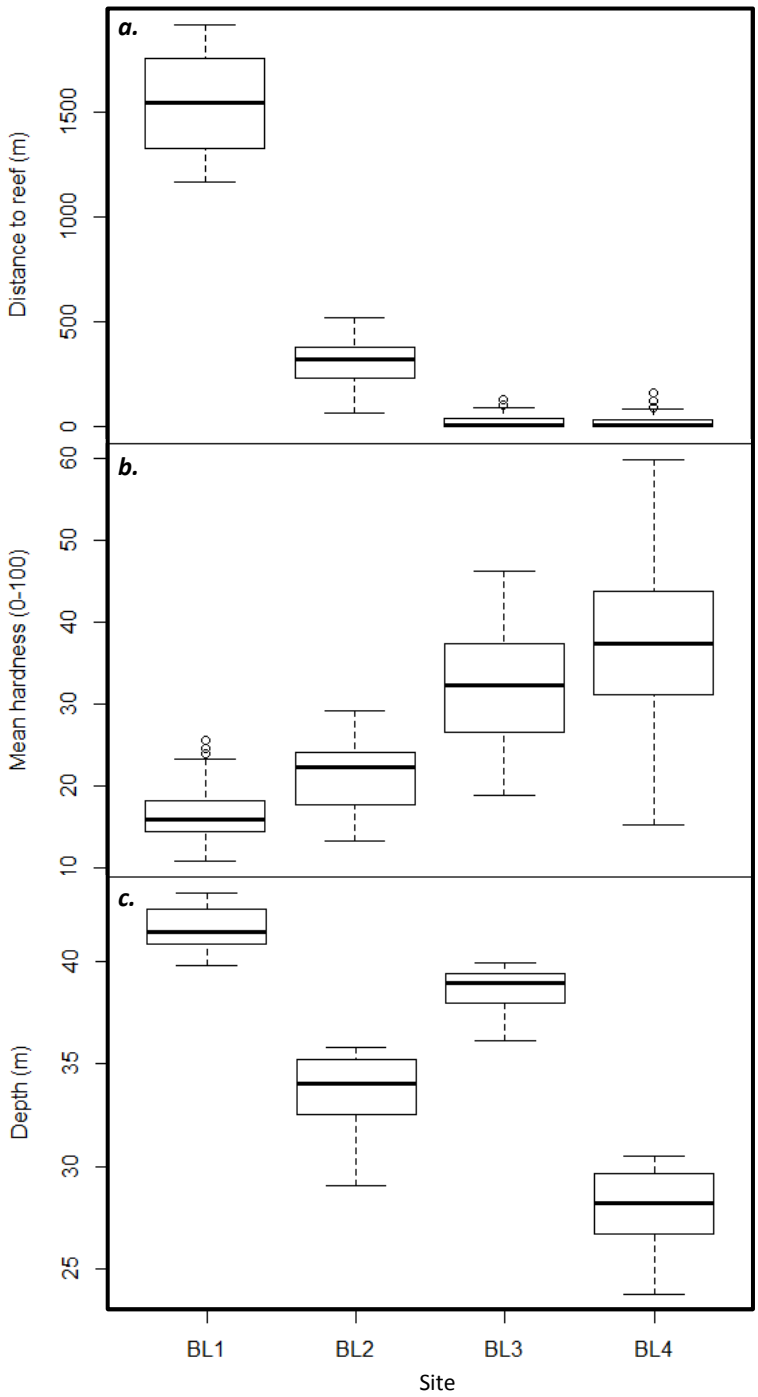


Figure 4.3 a. b. c. Boxplots of (a) distance to reef (m), (b) mean substrate hardness, and (c) depth (m) of each site sampled (n = 1,792).

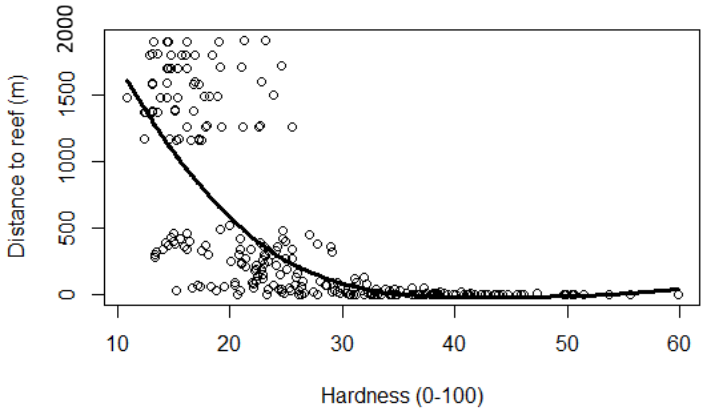


Figure 4.4 Hardness plotted against distance to reef, with a non-parametric Gaussian smoother, span 0.75.

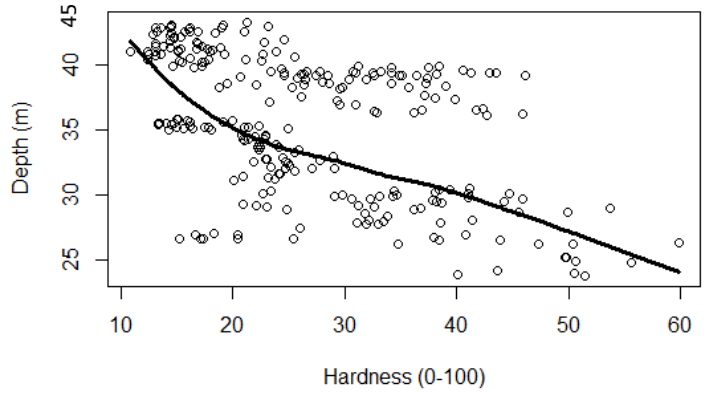


Figure 4.5 Hardness plotted against depth, with a non-parametric Gaussian smoother, span 0.75.

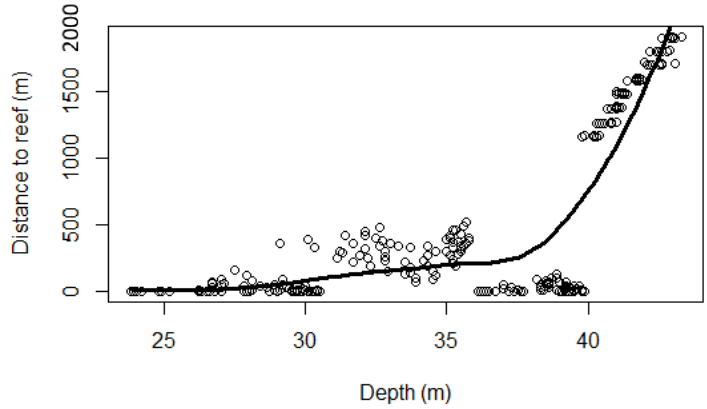


Figure 4.6 Depth plotted against distance to reef, with a non-parametric Gaussian smoother, span 0.75.

Over the course of the study period, 1,792 traps were hauled from the 4 sites (BL1 320; BL2 320; BL3 256; BL4 896) encompassing a range of depths and substrate hardness values (Fig. 4.3 a-c). BL1 was far from any reef, with very low mean hardness and great depth. Depth and hardness data of trap locations were gained via verified Olex data

points, using a Gaussian regression method of interpolation. Mean hardness for individual traps was gained taking the mean value for the substrate in a circle of radius 20m from the fixed trap location. Hard, reef habitat was assigned a value of 35 or greater from the Olex data. Distance to reef was calculated from the shortest straight line distance of each trap location to the nearest recorded hardness value > 35. BL4 was also somewhat different from other sites in the degree of habitat fragmentation, and the wide range of patches, causing an increase in habitat-edges within the site. Then environmental variables showed different relationships between them (Fig. 4.4 to 4.6); there was some degree of interaction and collinearity between the three variables, particularly distance to reef with both hardness and depth.

4.2.2.2 Capture-mark-recapture

Lobsters were collected for tagging during both fishery-independent trap surveys (n = 772; F 407; M 365) and the NIFCA 'v-notching programme' (n = 711; F 693; M 18). Lobsters from the v-notching programme, mostly ovigerous females (n = 679), were purchased by the NIFCA officers from wholesalers Berwick Shellfish Company, Blyth Fish Ltd. and Moir Seafoods Ltd. Once collected the lobsters were taken to the NIFCA patrol vessel, St. Oswald, and transferred to a continuous flow seawater holding tank prior to release at a designated transect. Lobsters were released on 3 occasions along 11 transects. Transect start and end locations and times were recorded via Olex.

Size, sex and reproductive state were recorded for every *H. gammarus*, then individuals were tagged with a persistent T-bar tag (See; p.34) and the unique identifying number recorded, prior to their release along predetermined transects (Fig. 4.3). Releasing lobsters by hand from the surface immediately after tagging and in tag number sequence allowed more accurate release locations to be recorded. All shellfish permit holders were then incentivised with a financial reward, to return recapture information, including date, location, sex and CL of recapture. Recaptures were reported to the NIFCA (a common practice amongst active fishermen) or via text message to a mobile phone number indicated on the T-bar tags. Recaptures recorded prior to the start of April 2014 are reported here.

Table 4.3 Site information; date fished, number of lobster released, number of females and males, and mean CL of releases.

Site	Date	Number released	F	M	Mean CL (mm) ±s.e.
BL1	04/10/2011 – 16/10/2011	10	4	6	79.4 ± 2.65
BL2	31/10/2011 – 27/11/2011	43	24	19	86.14 ± 2.04
BL3	08/11/2011 – 20/11/2011	12	4	8	86.17 ± 2.22
BL4	28/11/2011 – 10/12/2012	707	375	332	81.65 ± 0.30
V1B1	03/08/2012	34	34	0	96.68 ± 1.29
V1B2	03/08/2012	34	34	0	91.65 ± 0.73
V2B1	13/08/2012	50	46	4	97.52 ± 1.44
V2B2	13/08/2012	39	38	1	94.69 ± 0.94
V2B3	13/08/2012	50	47	3	95.18 ± 1.17
V2B4	13/08/2012	50	46	4	97.92 ± 1.10
V2B5	13/08/2012	65	59	6	95.29 ± 0.86
V3B1	24/08/2012	100	100	0	93.2 ± 0.52
V3B2	24/08/2012	99	99	0	96.24 ± 0.98
V3B3	24/08/2012	98	98	0	93.67 ± 0.67
V3B4	24/08/2012	92	92	0	92.53 ± 0.49

4.2.3 Statistical analysis

The fishery-independent trap survey variables were first tested for normality and homogeneity of variance. Confounding influences and interactions between variables and between sites were then identified using interaction plots and boxplots. Distance to reef was non-normally distributed, therefore a non-parametric test was used for exploratory analysis and data square root transformed for visualisation; parametric tests were used for the other variables. Prior to implementing models of relationships among catch per trap and environmental and biometric variables, variables were first tested for collinearity via the '*corvif*' function within the '*HighStatLib.R'* package. Estimated variance inflation factor (VIF) values indicated that biometric variables caused most collinearity, and were subsequently excluded from analysis (Dormann, Elith *et al.* 2013). Plots of model simulated values for each regression parameter showed further correlation between parameters; standardising the remaining covariates removed this, but there may be non-linear relationships too (Zuur, Ieno et al. 2010; Dormann, Elith et al. 2013).

As response data were counts, a Poisson or negative binomial distribution was required, but, as the range of the response variable was small (0-6), major over-dispersion was not expected and it was deemed suitable to apply a Poisson approximation (Zuur, Saveliev *et al.* 2012). Further models included a mixed effect of

'*site*', as the trap data were nested within sites. A model for an individual site over a single year was implemented to reduce temporal and site effects. Analysis was conducted using R 2.15.3, and packages '*BRugs'*, '*R2OpenBUGS',* '*R2WinBUGS'*, '*reshape'*, '*lme4'*, '*coda'*, '*coefplot2'* and '*pscl'* (Sturtz, Ligges *et al.* 2005; Zuur, Saveliev *et al.* 2012). The prior distribution used for all models was Poisson, the burn-in rate was initially fixed at 5,000 and the number of draws for the posterior 10,000 using 3 chains. Model selection was conducted using the Deviance information criterion (DIC) (Spiegelhalter, Best *et al.* 2002) and Akaike information criterion (AIC) (Akaike 1974) values for Bayesian models (WinBUGS) and regression models, respectively. However as DIC and AIC cannot be directly compared, and as there are criticisms of the use of DIC for mixed models (Celeux, Forbes *et al.* 2006; Plummer 2008), model selection was somewhat subjective. Model validation was conducted using graphical plots of the Pearson residuals against each covariate, qq-plots, and plots of the draws of the posterior distribution for each parameter and mixing of the chains was assessed (Zuur, Saveliev *et al.* 2012). Relationships between lobster biometric data and environmental parameters of trapping locations were explored using linear regression.

Movements of individual lobsters were represented as the shortest straight line distance between release location and last recapture occasion. Where land intersected the line (n = 1) vectors were directed around headlands. The incidence of movement direction was calculated as the direct bearing between position of release to last recapture position, recorded as degrees, with 0^{o} due north. The azimuth (mean angle), circular correlation and its significance, and the measure of angle dispersion (*r*), which ranges from 0 (uniform dispersion) to 1 (complete concentration in one direction) were calculated within ArcMap 10.1 and R 2.15.3 packages '*CircStats'* and '*circular*' (Mardia and Jupp 2009). Distribution of direction data were non-unimodal, and therefore directions were grouped into 30^{o} directional bins prior to analysis (Fisher 1993; Fisher 1995). The Watson's U^2 test was used to test if the distribution of directions was significantly different from a uniform distribution around the compass. Distance moved and 'time at liberty' were non-normally distributed, so were normalised via a log-transform. Recaptures were divided into a series of groups for some analyses; method of collection (v-notch or independent survey), short-term or

long term (≤ 30 days or > 30 days at liberty) and as either over or under MLS (≥ 87mm or < 87mm CL).

4.3 Results

4.3.1 Fishery-independent trap data

From 04 Oct 2011 to 10 Oct 2012 there were 1,792 successful trap hauls catching 865 lobsters (F 439; M 426) in 489 trap hauls and CL ranged from 61 to 119 mm CL ($\bar{x}_{865}$ = 81.94 ± 0.29mm) (Table 4.4).

Table 4.4 Mean (±s.e.) of distance to reef, square root distance to reef, depth, hardness directly under trap location and hardness in surrounding 40m Ø; for all trap locations grouped by observed lobster catch per trap.

Catch Frequency	No of hauls	distance to reef (m)	$\sqrt{}$ distance to reef	depth (m)	hardness	$\bar{x}$ hardness (40m Ø)
0	1,303	446.12 ± 17.65	14.73 ± 0.42	34.72 ± 0.15	27.42 ± 0.28	27.42 ± 0.29
1	270	86.22 ± 15.63	7.64 ± 0.47	29.08 ± 0.22	33.82 ± 0.62	34.79 ± 0.71
2	121	63.07 ± 17.60	6.50 ± 0.59	27.69 ± 0.26	34.58 ± 0.99	34.74 ± 1.14
3	57	30.37 ± 6.76	3.51 ± 0.56	26.85 ± 0.24	36.34 ± 1.55	36.01 ± 1.72
4	27	14.78 ± 4.93	2.09 ± 0.62	26.19 ± 0.32	38.98 ± 2.23	38.83 ± 2.54
5	10	0.5 ± 0.32	0.31 ± 0.20	25.68 ± 0.38	44.73 ± 1.98	43.50 ± 1.59
6	4	0	0	25.18 ± 0.52	50.93 ± 1.20	45.86 ± 3.60

Lobster catch per trap was negatively correlated with distance to reef (Fig. 4.7). There was a significant difference between the median distance to reef of all lobster catch numbers greater than 0 (Kruskal-Wallis$_5$: χ^2 = 17.8236; p < 0.005). Tukey HSD post-hoc analysis shows the greatest difference was between catches of 5 and 6 lobsters and those of 1 and 2; the highest frequencies only occurred directly on reef. Hardness was positively correlated with lobster catches, but there was wide variation in hardness at low frequencies, showing that small numbers of lobster were caught over a range of hardness' (Fig. 4.8).There was a significant difference between the mean hardness value for each lobster catch number (ANOVA$_{5and483}$: F = 5.19; p < 0.001), and post-hoc analysis showed the difference was between catches of 5 and 6 and those of 1, 2 and 3. Few lobsters were caught in depths over 30m (Fig. 4.8). There was a significant difference with mean depth and each catch number (ANOVA$_{5and483}$: F = 10.81; p < 0.001), the difference being between catches of 1, and catches of 2, 3, 4, and 5 (Fig. 4.9). Lobster catches were spatially heterogeneous however the environmental variables that might help explain them were related to each other (Figs. 4.3 to 4.6).

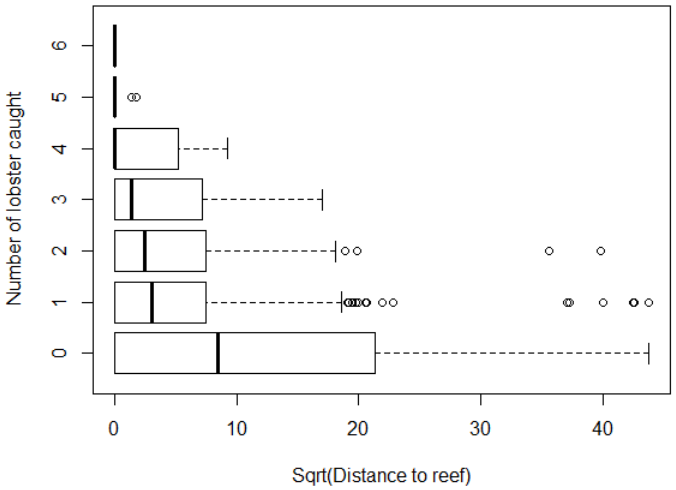


Figure 4.7 Square root transform of the distance to reef, of traps with corresponding lobster catch frequencies (n = 1,792).

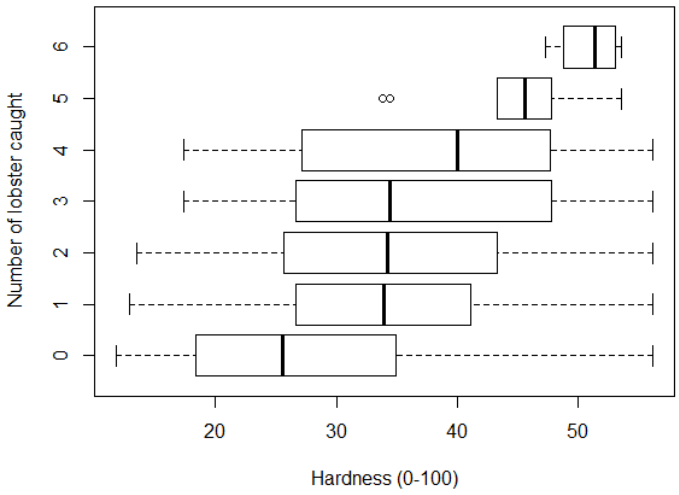


Figure 4.8 Hardness of substrate underneath traps plotted against corresponding lobster catch frequencies (n = 1,792).

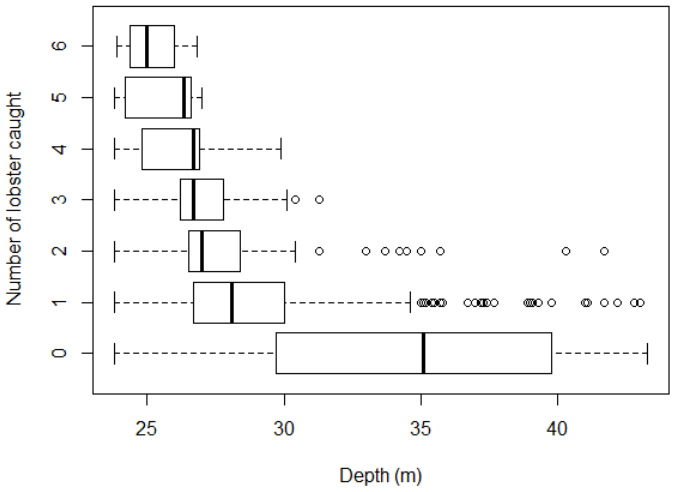


Figure 4.9 Depth from which traps were drawn with corresponding lobster catch frequencies (n = 1,792).

The frequnecy of zero catch observations (empty traps) was considerably higher than those of traps with 1 or more lobsters (Fig. 4.10); indication that the data are zero inflated. Meaning models used for analysis should be based on a distribution that allows for frequent zero-valued observations, and include a random event containing excess zero-count data in unit time.

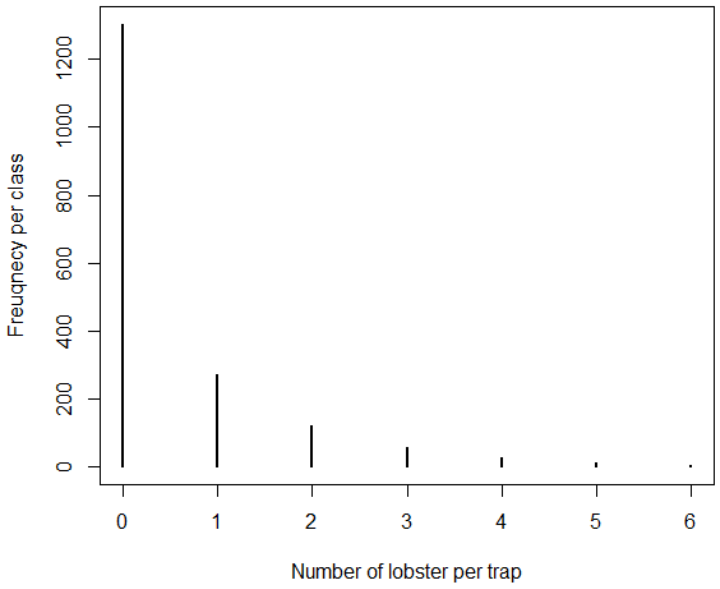


Figure 4.10 Frequencies of the specific numbers of lobster caught per trap; 1303 were empty, 270 caught 1, 121 caught 2, 57 caught 3, 27 caught 4, 10 caught 5 and 4 caught 6 (n = 1,792).

When a zero-inflated Poisson generalised linear mixed model (ZIP GLMM) was run, this would not converge, therefore, various models for the whole dataset (all years, all sites) and a zero-inflated model of a single site and single year were run. As over-dispersion was not observed, all models were restricted to Poisson approximation.

The three models on the total dataset used both standard regression and Bayesian analyses (WinBUGS) (Table 4.5). None of the models were significantly over-dispersed, and all were therefore candidate models; however, as AIC and DIC cannot be directly compared, and as literature states difficulties in relying on DIC for model selection (Celeux, Forbes *et al.* 2006). In a quasi-arbitrary manner, two models, the ZIP GLM and GLMM WinBUGS models were selected (Burnham and Anderson 2002; Johnson and Omland 2004). Especially as estimated parameter regressions showed little difference between the models (Fig. 4.11).

Table 4.5 Model selection statistics ranked from the smallest to the largest AIC/DIC. Number of parameters (NP)/ measure of model complexity (pD), and the model deviance.

Model	AIC/DIC	NP/pD	Deviance
ZIP GLM	2652.00	4	2492.77
GLM	2691.90	3	2517.70
GLMM	2693.88	4	2683.88
GLMM WinBUGS	2689.00	5.7	2681.83
GLM WinBUGS	2692.00	3.9	2687.88
ZIP GLM WinBUGS	2875.00	560.4	3215.66

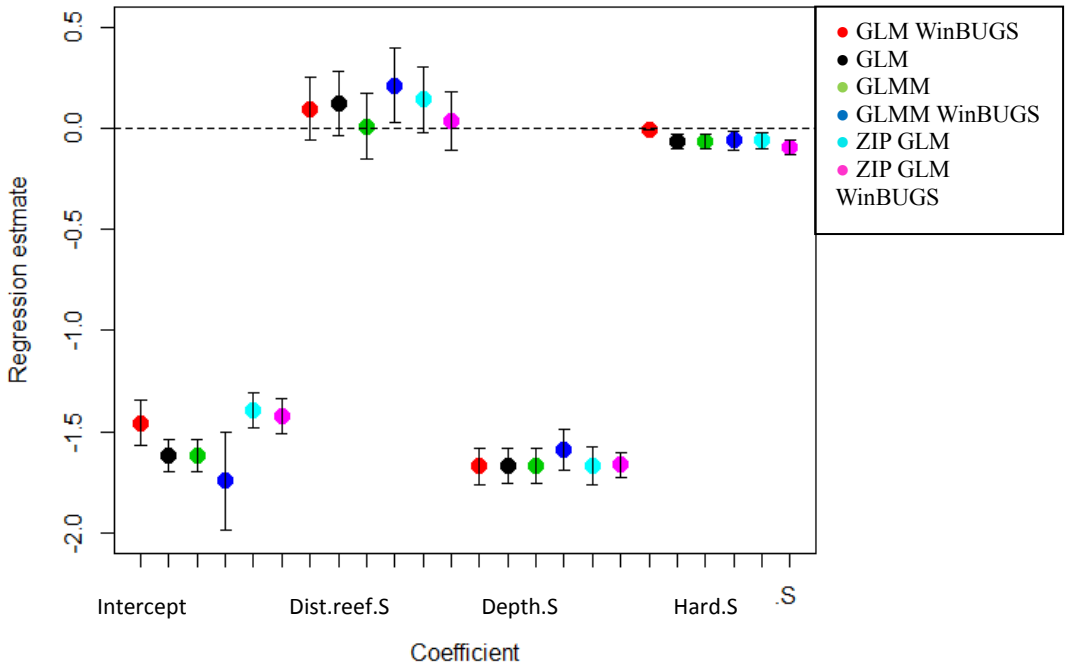


Figure 4.11 Plot of the results from all the Poisson models successfully run using all catch data, it shows mean estimate for each coefficient and their associated standard deviation.

All models produced similar results for the explanatory variables regardless of the type of model (Fig. 4.11), however, only intercept and depth were significant. Depth was negatively correlated with numbers of lobsters per trap. The ZIP GLM model estimated the value of the intercept in the logistic function to be -1.39 (-1.42 in ZIP GLM WinBUGS); therefore, the probability of a 'false' zero was approximately 0.19 (Zuur, Ieno *et al.* 2009; Zuur, Saveliev *et al.* 2012). This equates to a 20% probability that an observation of an empty trap was a 'false' zero, where lobsters were present on the sea bed but went unobserved by the trap (Austin and Meyers 1996). ANOVA between models with and without mixed site effect showed that models with a mixed effect

explained the data more appropriately ($ANOVA_{5and6}$: L-ratio: 77.00; $p < 0.0001$). The GLMM WinBUGS model found the mixed effect of site to be small, but significant.

A zero-inflated Poisson regression model of the effect of environmental variables on the numbers of lobster caught tested for a single site (BL4) over a single year (2012) removed the need for a mixed effect of site, and also reduced the level of collinearity and interaction between variables (Dormann, Elith *et al.* 2013). This model found a significant negative correlation between depth and numbers of lobster per trap (Table 4.6). All pairwise environmental variable interaction effects were significant, but interactions among three variables were not; meaning that the effect of one variable depended upon the value of the other variables independently. The predicted intercept of false zeroes was significant, meaning that the data are zero inflated. The ZIP was a significant improvement over the standard Poisson regression model (Vuong test: $p < 0.001$).

Table 4.6 Results of fitted Zero-inflated GLM: estimated coefficient values, relative error, Z value and significance; for the coefficients, intercept, variable interactions, and intercept for the zero inflation logistic portion of the model. Log-likelihood: -1314 on 9 d.f.

	Estimate	**Error**	**Z-value**	**P-value**
Intercept	-2.00	0.25	-8.14	< 0.001
Dist.reef.S	-0.74	0.45	-1.65	0.099
Depth.S	-1.32	0.23	-5.74	< 0.001
xHard.S	-0.57	0.33	-1.75	0.081
Dist.reef.S:Depth.S	0.83	0.34	2.45	< 0.05
Dist.reef.S:xHard.S	-1.37	0.63	-2.17	< 0.05
Depth.S:xHard.S	0.75	0.30	2.51	< 0.05
Dist.reef.S:Depth.S:xHard.S	0.81	0.42	1.91	0.056
Intercept	-1.43	0.20	-7.15	< 0.001

Relationships between minimum, maximum and mean size of lobster caught in each trap and environmental variables were explored. Minimum size of lobster caught was positively correlated with depth (Fig. 4.12; $LM_{1and747}$: $F = 195.8$, $p < 0.001$). No correlations were found between size of lobster and any other environmental variable. Mean size of lobsters varied among sites ($ANOVA_3$: $F = 3.148$, $p < 0.05$), however, post-hoc analysis was not significant, possibly due to the increased sensitivity of ANOVA tests compared with post-hoc analysis techniques.

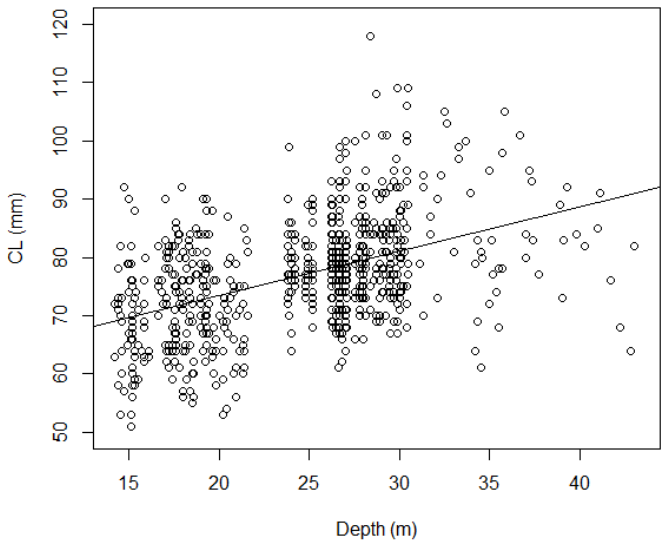


Figure 4.12 Plot showing the relationship between minimum lobster carapace lengths (mm) from each trap against depth at which they were caught. Black line represents a linear regression $y = 0.76x + 58.288$; $R^2 = 0.2066$; $p < 0.001$.

No significant differences were observed between caught female and male lobsters with environmental variables of trapping locations. Distances from reefs were very similar between the two sexes (Wilcoxon: $W = 105984$; $p = 0.228$), as too were depth (t-test$_{937}$: $t = 0.2649$; $p = 0.7911$), and hardnesses (t-test$_{939}$: $t = 0.9195$; $p = 0.358$).

4.3.2 Movements via capture-mark-recapture

Between October 2011 and October 2012 1,484 individual lobsters (CL 61 to 131mm; $\bar{x}_{1,483}$ = 88.08 ± 0.27mm) tagged off the coast of Northumberland (1,100 F and 383 M) were released and 138 individuals recaptured (71 F and 67 M) (Figs. 4.13 and 4.14). Nineteen of these were caught on a third occasion (8F; 11M); and 3 were caught on four separate occasions (1F; 2M). Recapture rates of lobsters tagged via v-notching and trap-survey were 7.03 and 11.40%, respectively. Intervals between release and recapture ranged from 2 to 555 days, with a median of 175 days ($\bar{x}_{138}$ = 72.72 ± 9.64 days). Distances covered ranged from 0 to 76km, however > 90% were less than 3.4km ($\bar{x}_{138}$ = 1.65 ± 0.59km). One outlying individual that moved 76km was removed from analysis. Seven lobsters had moulted between recaptures with a recorded mean growth increment of 9mm (± 1.53) observed.

Lobsters released during v-notching were recaptured significantly further from their release location ($\bar{x}_{36}$ = 5.56 ± 2.11km) than lobsters released during fishery-

independent surveys ($\bar{x}_{102}$= 0.27 ± 0.05km) ($ANOVA_{1and136}$: F = 17.46; p < 0.001). However, number of days at liberty was significantly different between the two methods ($ANOVA_{1and136}$: F = 78.2; p < 0.001). There was also a significant difference in distance travelled by tagged between those lobster below MLS (87mm) ($\bar{x}_{77}$= 0.27 ± 0.05km), and those greater than or equal to MLS ($\bar{x}_{61}$= 3.38 ± 1.29km) ($ANOVA_{1and136}$: F = 7.21; p < 0.01). However, mean distance moved per day was equal between groups ($\bar{x}_{77}$= 38.46 ± 21.69m^{-day}; $\bar{x}_{61}$= 38.11 ± 8.17m^{-day}; < MLS and ≥ MLS respectively). Distance moved by recaptures grouped by 'time at liberty' was significantly different between those at liberty for ≤30 days ($\bar{x}_{91}$= 0.34 ± 0.08km), and those at liberty for >30 days ($\bar{x}_{47}$= 4.18 ± 1.65km) ($ANOVA_{1and136}$: F = 10.17; p < 0.01) (Table 4.7). There was no significant difference between distance moved between the sexes within groups (v-notch: $ANOVA_{1and34}$: F = 0.426; p = 0.518. Survey: $ANOVA_{1and100}$: F = 0.165; p = 0.686).

Distance moved was very variable but was positively correlated with both 'time at liberty' ($LM_{1and136}$: R^2 = 0.0989; F = 16.04; p < 0.001; Fig. 4.15), and CL ($LM_{1and136}$: R^2 = 0.0297; F = 5.197; p < 0.05; Fig. 4.16). There was also a positive correlation between CL and depth of the final recapture location, larger lobsters being likely to be caught in deeper waters ($LM_{1and136}$: R^2 = 0.0569; F = 9.262; p < 0.005).

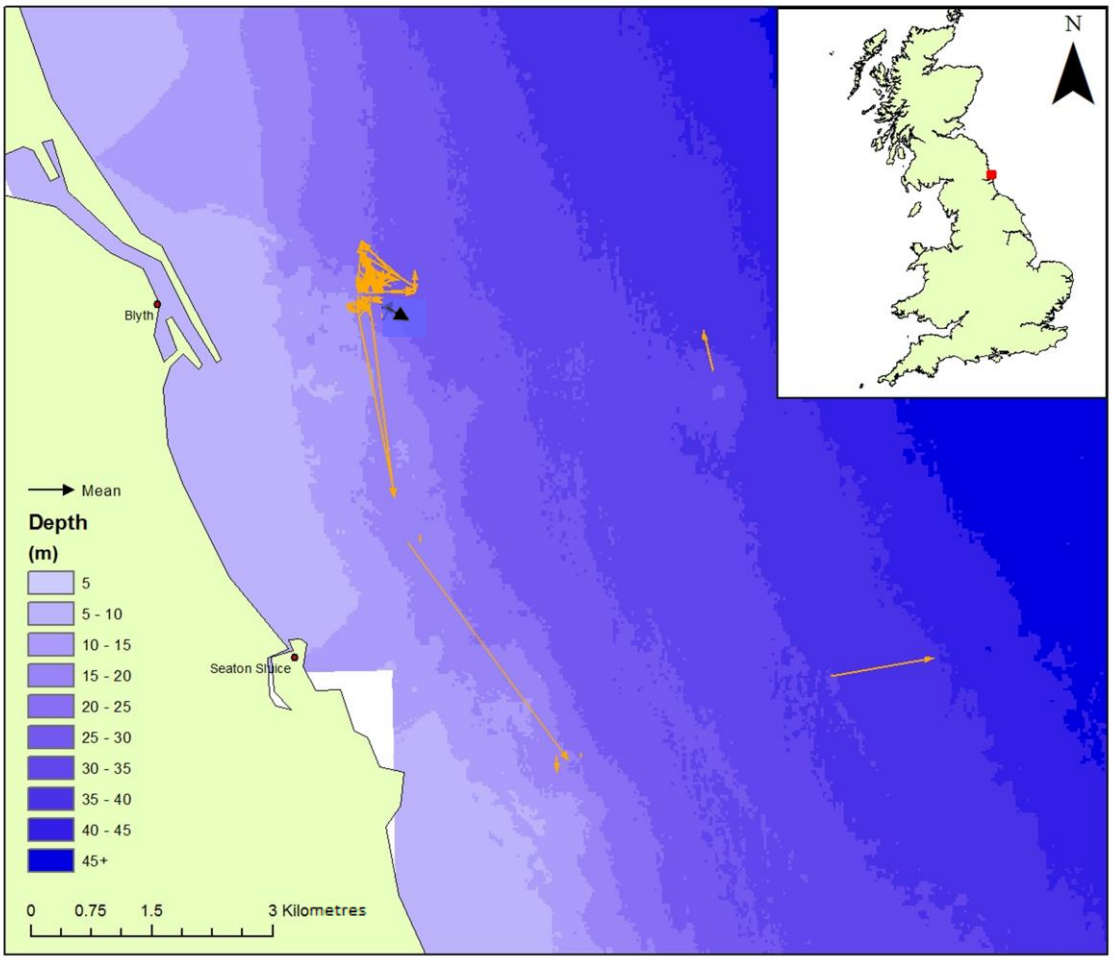


Figure 4.13 Movements of recaptured lobsters from the fishery-independent trap survey (n = 102): mean direction, distance and location in black.

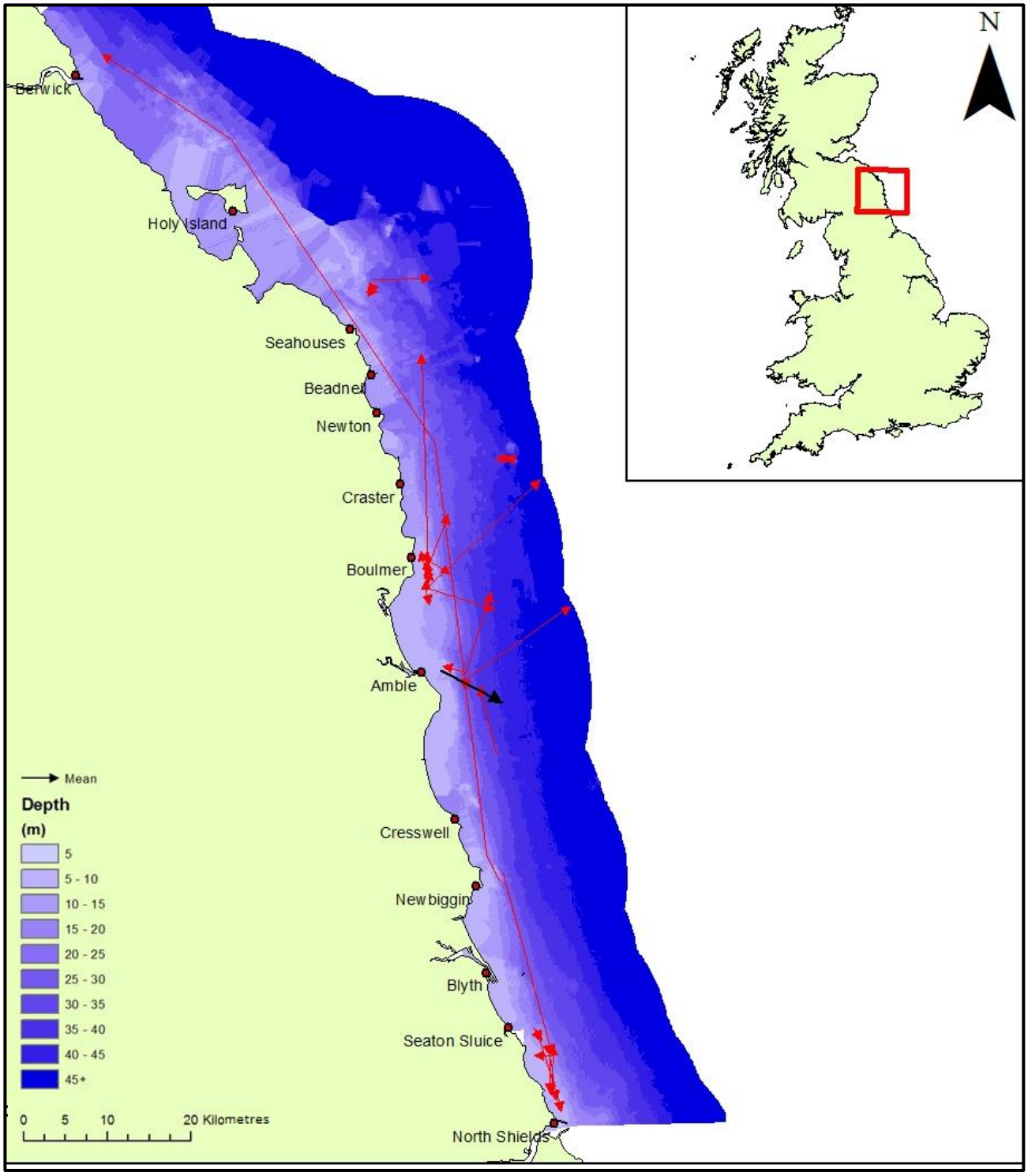


Figure 4.14 Movement of recaptured lobsters from the v-notching programme (n = 36): mean direction, distance and location in black.

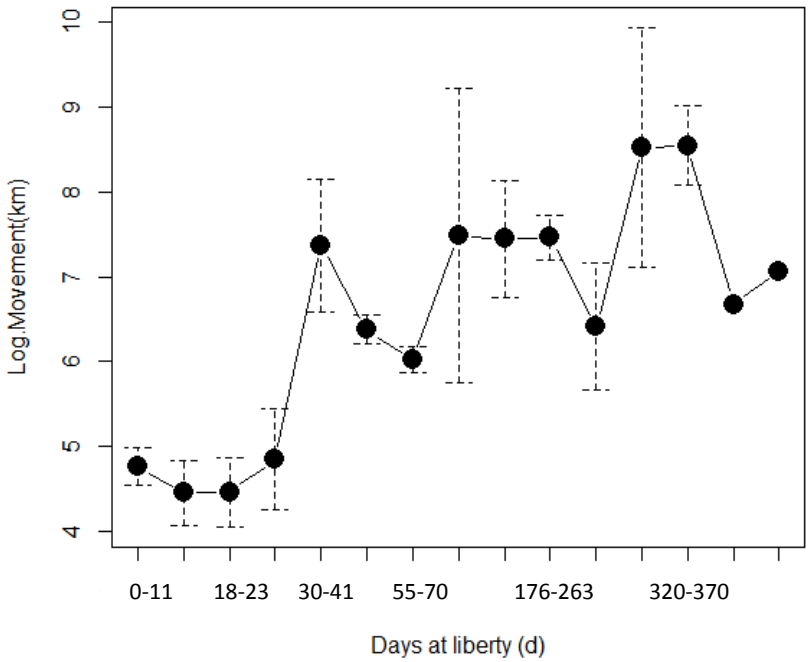


Figure 4.15 Plot of mean (± 95% C.I.) of Log_{10} transformed recapture distance (km) against time at liberty (days) for all recaptures. Time at liberty grouped into 15 bins using Jenks natural breaks classification (Jenks 1967).

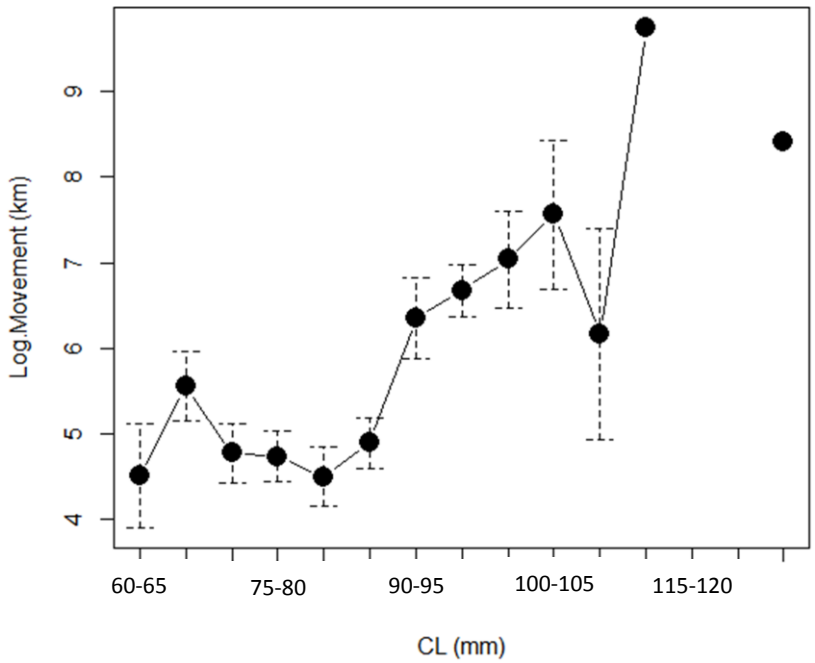


Figure 4.16 Plot of mean (± 95% C.I.) of Log_{10} transformed recapture distance (km) against CL (mm) for all recaptures. CL grouped into 15 bins of width 5 (mm).

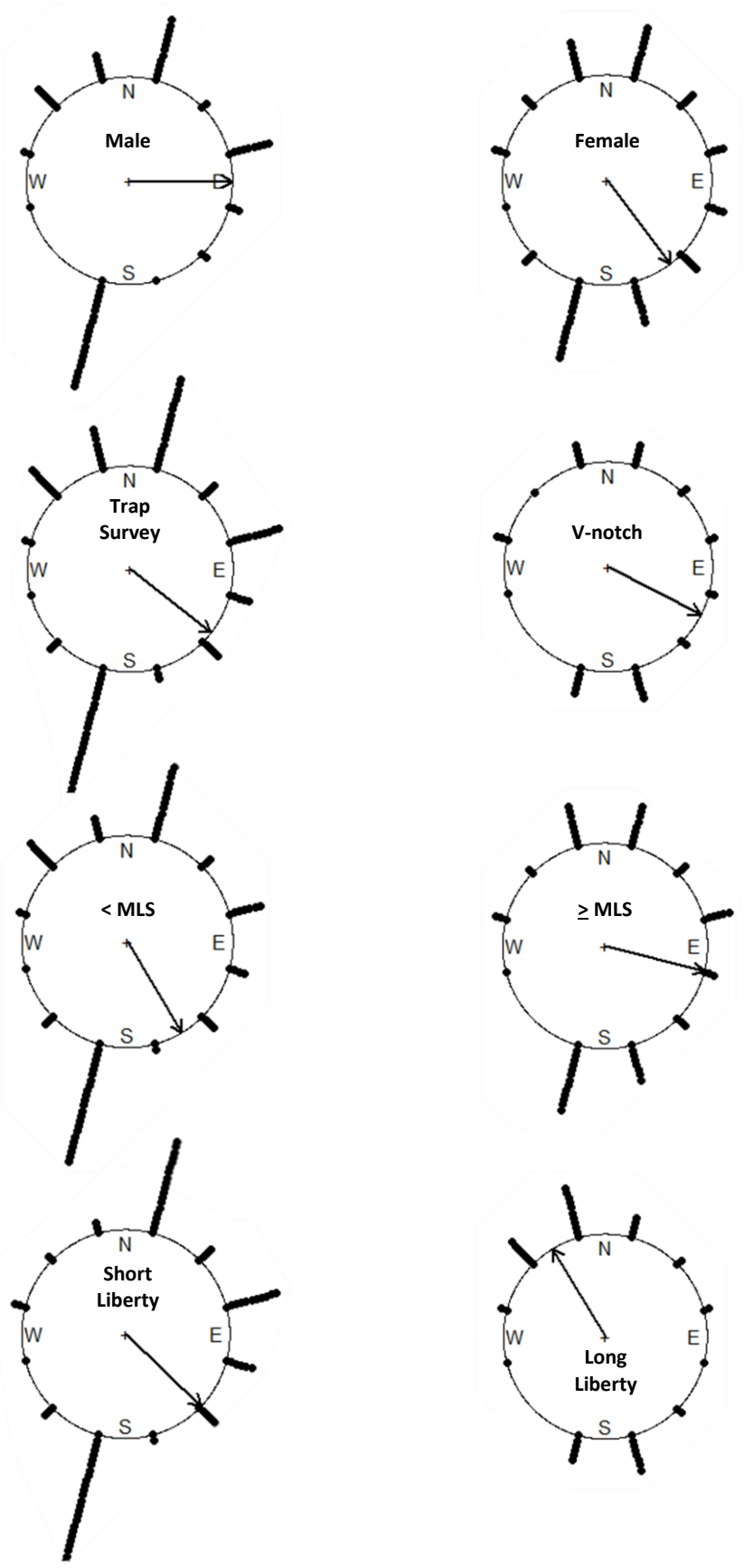


Figure 4.17 Frequency distribution of directions from release to last recapture positions of tagged lobsters, with bearings grouped into bins of 30 ^{o}. Mean bearing is also displayed as the arrow on the inside of the circle.

Watson's goodness of fit test showed that all groups circular distribution of direction moved, except v-notched lobsters, were significantly different from uniform distribution around the compass (Watson U^2: Table 4.7). There was a significant difference between the mean direction of male and female lobsters (ANOVA.circ$_1$: F = 19.41; p <0.001) and between 'short-time at liberty' and 'long-time at liberty' (ANOVA.circ$_1$: F = 47.16; p < 0.001). However, there was no significant difference in the two methods of collection or between size classes (Table 4.7) (Fig. 4.17).

Table 4.7 Mean distance moved, azimuth (mean bearing), circular variance and Watson's goodness of fit test results.

	V-notch	Trap survey	F	M	Berried	Short Liberty	Long Liberty	≥ MLS	< MLS
$\bar{x}$ distance (m)	5560.89	265.46	2911.18	307.10	5727.96	340.27	4176.70	3384.43	270.38
$\bar{x}$ bearing (°)	117.05	128.24	142.56	90.59	129.15	133.74	328.99	104.23	148.90
$\bar{x}$ Circular variance (r)	0.89	0.92	0.88	0.93	0.85	0.79	0.84	0.88	0.92
Watson U^2=	0.1097	0.46	0.2382	0.338	0.338	0.5987	0.2193	0.2079	0.3645
p =	p>0.1	p<0.01	p<0.025	p<0.01	p<0.01	p<0.01	p<0.05	p<0.05	p<0.01

4.4 Discussion

The fishery-independent trap data show catches were variously correlated with the three environmental variables. However, low catch rates and collinearity between the variables meant it was not possible to identify a predominant driver of catches from the models. There was significant spatial heterogeneity of numbers and sizes of lobster caught. With high numbers of small lobsters being caught at the inshore site, where there was shallow and hard reef substrate. Sex distributions were homogeneous.

Over 90% of recaptured lobsters moved less than 3km from their release location, suggesting high site fidelity. V-notched recaptures showed greatest movements; this was perhaps expected in light of their displacement from capture location (Vannini and Cannicci 1995). Larger lobsters generally travelled further and were recaptured in deeper water. Direction of movement was highly variable with overall mean direction

offshore and south, except those at liberty for longest that had mean direction north, against the general direction of water movement.

4.4.1 Fishery-independent trap data

Catches were relatively low in all locations, overall mean catch per trap was 0.48 individuals, but catches were highly aggregated spatially. Highest catch rates ($n \geq 4$) were always within 80m of reef and at shallow locations (< 30m). While traps set more than 100m from reefs were usually empty, empty traps occurred in all locations. Traps set within 10m of reef caught 61.5% (n = 532) of lobsters, while only 5% (n = 47) were caught 200m or further from reef. This would suggest some sort of control on catch rates by both depth and hardness. Spatial distribution of size was also heterogeneous, but was not obviously related to environmental variables measured. Smaller lobster were more common at inshore sites, approximately 77% of the catch at BL4 were < MLS, reducing to 61% and 57% at sites BL3 and BL2, respectively. Similar size distributions are seen for *H. americanus* (Cooper, Clifford *et al.* 1975), and have been attributed to environmental and habitat limitations (Howard 1980; Jury, Kinnison *et al.* 1994; Jury, Kinnison *et al.* 1994). There were no significant differences in sex distributions; catch rates of both sexes were similar across all areas.

Fishermen commonly set traps on or near hard substrate when targeting *H. gammarus*, and much of this effort is restricted to within the first 2 miles of shore (Turner, Gray *et al.* 2013). Greatest catches in this study came from BL4, which is distinct due to its wide range of substrate, greater amount of hard habitat and habitat edges, and shallow location within 2 miles of shore (Figs. 4.2 and 4.3). This suggests the site is more topographically complex than other sites. Complexity and areas with several habitat types are thought to be key determinants of lobster distribution (Selgrath, Hovel *et al.* 2007), with shelter-providing structures thought to be the most important determinant (Cobb 1971; Karnofsky, Atema *et al.* 1989; Hernkind, Butler Iv *et al.* 1997). Shallow sites may afford more shelter due to increased coverage of kelp, which is absent from deeper sites due to light limitations (Edwards 1980). However, factors such as complexity, shelter availability and kelp cover could not be quantified from the Olex data. Decreased offshore complexity may also explain the decreased frequency of

small lobsters offshore; large lobsters are less susceptible to predation and their association with shelter tends to relax, which could lead to them being able to explore and remain resident in offshore sites (Cooper and Uzmann 1971; Cooper, Clifford *et al.* 1975; Selgrath, Hovel *et al.* 2007). The strength of the inverse correlation between trap catch numbers and depth in selected models could reflect greater inshore catch rates; resulting in depth acting as a proxy for distance from shore. Distance to reef and hardness, however, were not significant determinants in the selected models, despite appearing to be correlated (Figs. 4.7 and 4.8). This is likely due to the nature of the data, and a lack of systematic structure in the habitat data. Both empty traps and low catches (0-3) occurred on a wide range of habitat hardness values, and distance to reef was naturally skewed towards 0 for all catches (0-6). Any effect of these two variables was therefore going to be difficult to observe, and any effect of hardness and distance to reef was likely to be obscured by their correlation with depth.

The high collinearity between variables, data nesting within sites, zero inflation, and weak ecological patterns, meant that the use of trap data to assess spatial patterns and environmental drivers of catches is problematic.

Collinearity was partly addressed using VIF to select variables for removal or standardisations, allowing the model to more successfully describe the data. However, this approach results in problems when identifying which covariates are driving the system; it causes the model to be unable to determine any individual covariate effects, or what effect is caused by a dropped variable. Instead it effectively replicates an overall effect of all covariates acting simultaneously. Any precise effect of an individually measured predictor will not be assessed without controlled studies; however, recreating natural habitat in *ex situ* studies of lobster behaviour is impossible.

The estimated value for the variance of the random effect for site was significant, but small. This is perhaps not surprising, since differences in the range of number of lobster caught per trap among sites were small. However, as it is significant, it indicates that beyond the three environmental variables modelled, there were likely further factors causing spatial differences in catch rates. Likely factors may include

lobster, predator and prey abundances at the site, or commercial fishing effort exerted within the site. The low number of environmental variables and the level of sampling were insufficient to detect its effect, several more controlled sites are required for future studies.

H. gammarus fisheries generally have low catch rates per trap (Bennett 1974a; Moland, Olsen *et al.* 2013) when compared to *H. americanus* (Estrella and McKiernan 1989; Miller and Rodger 1996; Jury, Howell *et al.* 2001); 73% of traps were empty upon hauling in this study. This zero inflation can be caused by lack of suitable habitat leading to an absence of lobster (i.e. 'real' zeroes) or despite the environment being suitable, by inadequate or troublesome sampling, such as unequal and incomplete effort, escapements, or lobsters remaining unobserved (i.e. 'false' zeroes). There are no simple solutions to using zero-inflated baited trap data, however, improvements in methodological design can help reduce or eliminate some of the problems encountered. Trapping survey methods should be extended to include a wider range of trap locations, with traps truly independent of each other, rather than being set in strings or arrays. This could be achieved via a random stratified approach to the sampling design, to reduce collinearity and site effects.

Due to the incomplete nature of the capture process, it is impossible to ascertain absence of lobster in an area from trap data alone. Catch data provide a measure of the catchability of the available population within the area of its influence; this is related to abundance, but not linearly (Addison and Bell 1997; Fogarty and Addison 1997). Correlations between abundance and CPUE have not been well established (Miller 1990). Certain habitats may reduce lobster catchability, thus leading to under- or over-estimation of abundances; the lack of lobster observations beyond 200 m from reef does not mean this environment is not frequented by lobster. This caveat of catch and abundance data is often seen in *H. americanus* fisheries, where despite greatest concentrations of lobster occurring on hard substrate, trap catch rates have been recorded as being equal or higher at soft sites (Lawton and Lavalli 1995; Tremblay and Smith 2001; Geraldi, Wahle *et al.* 2009; Tremblay, Smith *et al.* 2009). The manner in which lobsters utilise a habitat alters their catchability, and therefore the ability to detect them. The present analysis can only inform the distribution of catch rates,

which may be an index of abundance, but should be used with caution, especially when inferring the absence of lobsters in an area.

4.4.2 Movement

No significant correlation between distance moved and sex was observed. However, there was a weak positive correlation with size (Fig. 4.16), and distances travelled by lobster < MLS were significantly smaller ($\bar{x}_{77}$ = 0.27km) than those ≥ MLS ($\bar{x}_{61}$ = 3.38km). The restricted dispersal and strong site fidelity observed, corroborates other data on *H. gammarus* (Simpson 1961; Bannister, Addison *et al.* 1994; Jensen, Collins *et al.* 1994; Agnalt, Kristiansen *et al.* 2007; Moland, Olsen *et al.* 2011; Moland, Olsen *et al.* 2011a), however, effects of sex or size are unusual (Rowe 2001).

V-notch and berried lobsters travelled the greatest distances ($\bar{x}_{36}$ = 5.56 and 5.73km, respectively). Only few *H. gammarus* have previously been observed travelling over 15km in a season (Thomas 1954; Simpson 1961; Jensen, Collins *et al.* 1994; Smith, Collins *et al.* 1999). Individual variation in movement behaviour is common in mobile animals (Golet, Scopel *et al.* 2006; Scopel, Golet *et al.* 2009; McMahan, Brady *et al.* 2013), due to intra-population variation in fitness and boldness (Fraser, Gilliam *et al.* 2001), sometimes referred to as personalities (Gosling 2001). Highlighting the value of incorporating individual variation into methodologies.

As the release location was different from capture location for v-notched recaptures, there is potential for disorientation or homing behaviour to be exhibited; normal behaviour was unlikely. Homing in *H. gammarus* has rarely been studied, but has been reported for *H. americanus*, both over large and short distances (Pezzack and Duggan 1986; Karnofsky, Atema *et al.* 1989). However, very little is known about the prevalence or mechanisms of homing behaviour in crustaceans (Vannini and Cannicci 1995). Homing could have led to the dichotomous findings between ‘v-notch’ and ‘survey’ lobsters. However, another hypothesis may be that ovigerous females were migrating along temperature thresholds, associated with maximizing egg development (Crossin, Al-Ayoub *et al.* 1998); although temperature data are unavailable to test this, it is unlikely considering the variation in their movements. Contranatant migrations occur in ovigerous females (Meek 1925; Addison and Lovewell 1991), but are no longer

thought to occur in *H. gammarus* (Smith, Jensen *et al.* 2001), and again the variation in direction moved does not support this.

The difference between v-notch and survey lobsters may also be exaggerated by the disproportionate distribution and level of fishing effort surrounding the release locations of survey animals, therefore increasing the likelihood of recapture close to release location. Survey lobsters were more likely to be recaptured within the immediate vicinity due to higher than normal fishing effort being exerted by the scientific trap array, whereas v-notch lobsters were released away from traps. The study should be repeated to include non-ovigerous and male lobsters, and use known distances between capture and release locations to clarify if increased dispersion is a result of relocation and homing.

Even when displaced v-notched lobsters are omitted, there remain several key difficulties in analysis. Firstly, recapture rates were relatively low compared to previous studies that report rates of 28-53% (Smith, Jensen *et al.* 2001). However, previous studies often tagged and released thousands of lobsters into a single bay over a single or short tagging period. This study released approximately 1,500 lobsters throughout the entire district over the course of one month. In this study the spatial distribution of fishing effort, level of fishermen participation and number of unreported or inaccurate recaptures are uncertain, all of which could bias results, especially where lobsters were recaptured multiple times and not reported, which can alter behaviour, and where fishing effort is spatially heterogeneous; this will bias recapture rates in one area, even if more animals actually moved in the other direction. This is inevitable with recapture data.

The lower female than male recapture rates suggest significant differences in catchability between the sexes, as suggested elsewhere (Wiig, Moland *et al.* 2013). This could skew population parameters based on catch rates. V-notching programmes attempt to ensure large fecund females remain in the population; however the implications of removing or depleting males are unclear (Debuse, Addison *et al.* 1999; Debuse, Addison *et al.* 2003; Hunt, Breuker *et al.* 2009) and analogous measures for their protection have not been implemented. V-notching is gaining popularity as a conservation measure; not least because it increases stakeholder participation, which

can lead to voluntary v-notching and a greater sense of ownership of the stock. The effectiveness of V-notching to increase stock levels is yet to be verified.

Overall, the data presented here suggest that lobsters maintain high site fidelity, but larger individuals are capable of larger movements. To enable any understanding of natural lobster movements in the region, a much wider study would be required, to include the continued tagging of v-notch lobster, but to also include details of their capture location, so the occurrence of homing can be assessed. Increased fishermen involvement and training in reporting data and improved maps of spatial distribution of effort are also required.

4.5 Conclusion

Trap data remain essential for investigating shellfish, despite the caveats and uncertainties. However, particularly when using CPUE as an index of abundance, complex models may be required (e.g. zero inflation, unequal sampling and catchability) and difficulties arise in assessing effort per trap. Catch distribution is evidently affected by the interplay of depth, hardness, distance to shore, distance to reef, and likely other variables, such as available refuge (Howard 1980), prey abundance or diversity (O'Malley, Drazen *et al.* 2012), mates, competition topography, and fishing effort. As traps rely on lobsters' ability to detect the trap and willingness to enter it, they will not assess the complete range of movement and habitat utilisation. Further research using alternative methods, and utilising greater quality and detailed maps that include additional covariates are required to fully assess lobster movement and distribution.

Trap studies to determine distribution and movement of lobster within a confined area should aim to apply a stratified random sampling approach; fishing individual strings or traps in randomly generated locations. A computer model can be written to weight regions with variables that have been under-sampled, i.e. if too many soft shallow areas are being sampled, it can avoid them to some degree. Using an approach such as this, might avoid some of the problems of site effect, collinearity, and interactions between the variables. However, zero inflation is always likely to cause difficulties.

Despite problems with the method and data, this study offers some of the first European lobster movement data in Northumberland. Data are limited, but useful and highlight the variability in behaviour and the movement potential of European lobsters.

Chapter 5:

Investigating *Homarus gammarus* movement, behaviour and habitat use via acoustic telemetry

Chapter 5: Investigating *Homarus gammarus* movement, behaviour and habitat use via acoustic telemetry

5.1 Introduction

Most fisheries management decisions require some understanding of the distribution of the focal species. This is often inferred via spatial differences in fishing data and CPUE. However, numerous studies have concluded that CPUE is often a poor indicator of species abundance (Hilborn and Walters 1992; Addison 1995; Addison 1997; Fogarty and Addison 1997; Prince and Hilborn 1998; Harley, Myers *et al.* 2001); understanding predictors of spatial differences in abundance may be more effective for management. It is widely accepted that habitat and movement are key determinants of animal distribution, and therefore local abundance (Geraldi, Wahle *et al.* 2009), particularly for animals closely associated with the benthos. Understanding localised distributions is essential for the effective design of MPAs and no take zones, for example (Di Lorenzo, Anna *et al.* 2014). Predictability in the distribution of crustacean species over global ranges, suggest that distribution is regulated by a combination of environmental parameters, including temperature, salinity and depth (Ungaro, Marano *et al.* 2005). At more localised levels, fishing pressures and recruitment strength help determine distribution, but at a local scale, the distribution and composition of a mobile community will be explained by environmental variables alone (Townsend, Dolédec *et al.* 2003), such as the presence of substrates that provide suitable refuge from predation or increased availability of prey species.

Many environmental variables are changeable or difficult to map on the scale of most management. Therefore the physical substrate is often the most accessible and easily quantified environmental predictor for benthic species distribution (Pittman, Christensen *et al.* 2007). Ground discrimination techniques allow large areas to be accurately mapped and used to estimate distribution of species, provided there is existing knowledge of predictable behaviour (Wiley, McNyset *et al.* 2003; Holmes, Van Niel *et al.* 2008; Galparsoro, Borja *et al.* 2009; Chang, Chen *et al.* 2010).

Published data regarding *Homarus gammarus* use of habitats is limited. It is thought it spends most of its time in or near the shelter of rocky reefs (Howard 1980; Jensen, Collins *et al.* 1994), because trap catch rates are highest on or near hard substrates (Galparsoro, Borja *et al.* 2009). This is corroborated to some extent by extensive studies of *H. americanus* distribution and habitat use; the greatest concentrations of adults often observed on substrate with overlaying rock, boulders and cobble (Geraldi, Wahle *et al.* 2009). However, trap catches are sometimes higher on homogeneous soft sediments (Tremblay and Smith 2001; Selgrath, Hovel *et al.* 2007; Geraldi, Wahle *et al.* 2009). This highlights the dangers of estimating distribution from trap catches alone, as trapping techniques often assume catchability to be linear to abundance (Tremblay, Smith *et al.* 2006).

Adult *H. americanus* are most abundant at habitat edges, whereas smaller lobster are more common in the middle of cobble patches (Selgrath, Hovel *et al.* 2007), because they are more reliant on the shelter of appropriately sized refuges. Movements between habitat types involve trade-offs between foraging benefits and predation risks (Werner and Gilliam 1984); certain habitats, such as vegetated corridors, may act as links between one habitat and another (Micheli and Peterson 1999). If lobsters have separate uses for different habitat types, such as for foraging and transportation (Karnofsky, Atema *et al.* 1989; Hovel and Lipcius 2001; Selgrath, Hovel *et al.* 2007; Hovel and Wahle 2010), catchability will not remain constant (Tremblay and Smith 2001; Tremblay, Smith *et al.* 2006). They are less likely to be observed in traps taken from habitats not actively used for foraging, potentially leading to misinterpretation of CPUE data and erroneous distribution estimates.

Acoustic telemetry (AT) techniques offer an innovative means of continuous observation that could limit the need for observation via trap catches, and avoid difficulties presented by changeable catchability. This technology has the potential to address more complex behavioural, ecological and physiological questions at finer spatial and temporal scales. An array of acoustic receivers continuously maps the locations of tagged individuals *in situ* with minimal disturbance, permitting studies previously impossible using traditional techniques, by allowing movements to be

established regardless of the individual's willingness to enter a baited trap. This permits improved quantification of habitat utilisation, eliminating issues of fishing effort, catchability, species interaction and trap saturation that hinder the robustness of conclusions drawn from trapping surveys. Despite the obvious advantages, passive AT has rarely been applied in crustacean studies (Guerra-Castro, Carmona-Suarez *et al.* 2011), until recently (Watson, Golet *et al.* 2009; Moland, Olsen *et al.* 2011).

This chapter aims to establish the habitat utilisation of freely moving *H. gammarus*, using a VR2W VEMCO positioning system to monitor short-term movements. Objectives are to describe individual home-range size and habitat use, and relate this to season, sex and size; and identify patterns of activity and characteristics of movement behaviours on different substrates.

5.2 Methodology

5.2.1 Study site

The study was conducted between 2012 and 2013 from the 18.9m Research Vessel *Princess Royal*. The location of the AT array has been well studied in previous trapping experiments, and the habitats quantified by regular acoustic overpass (Olex). Positioned 2km East of Blyth (approx. 55°07'46 N, -01°26'89 W) (Fig. 5.1), the depth ranges from 15.5m at the south east to maximum depths of 31m at the west of the site. The site is composed of mixed hard and soft substrate, dominated by rock and cobble that form distinct patches of complex habitat. A large rocky-reef runs from the north-west to southern centre of the site and patches of coarse sand and mud are found throughout.

Substrate hardness data were collected continuously via the vessel's on-board mapping and navigation software, Olex 8.0. This measures relative change in substrate hardness by reporting backscatter values from the vessel's single-beam echo-sounder as a ratio of sent and received acoustic energy via proprietary algorithmic treatment of the sonogram. This translates linearly into a scale from 1 (low reflection) to 100 (0dB energy lost), although values above 60 are unlikely. As readings are impacted by environmental conditions such as sediment in the water column, only strong readings

are used by the software. Olex cannot use backscatter to assess bottom roughness, and only provides data as a proxy for habitat hardness. Previous studies reveal that there is little difference in broad scale habitat classification of Olex and multi-beam acoustic systems (Elvenes, Dolan *et al.* 2013), and Olex offers a reasonable approach to broad habitat discrimination.

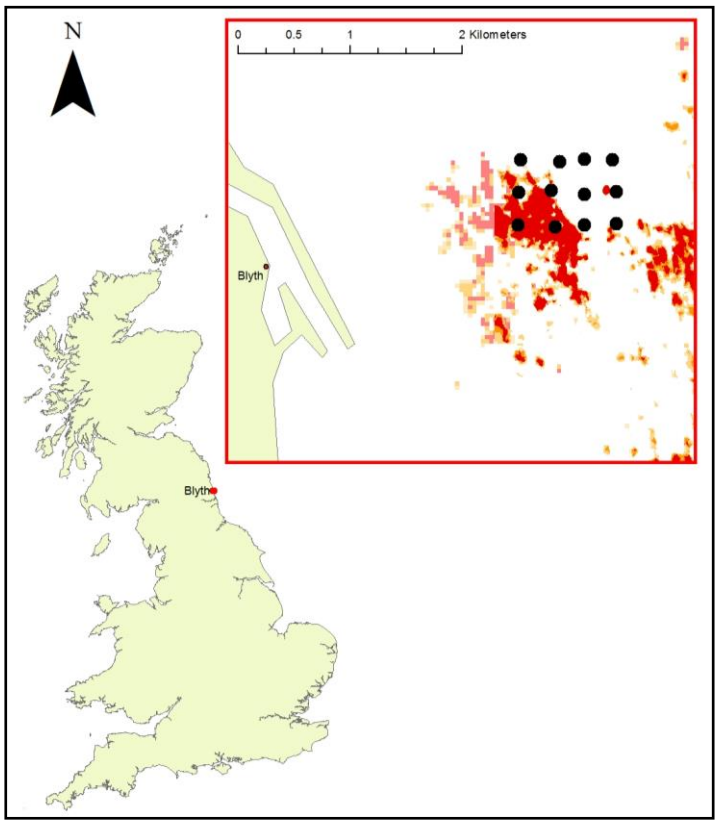


Figure 5.1 Locations of the 12 VR2W acoustic receivers are shown (●). Hard reefs are displayed in red, orange and yellow.

5.2.2 Data collection

A VEMCO Positioning System (VPS) (VEMCO Division, Amirix Systems Inc., Halifax, Canada) was used to monitor lobster positions over two distinct periods in 2013; 23 April 2013 to 03 June 2013 (summer) and 17 Sept 2013 to 20 Nov 2013 (termed, winter, but could be interpreted as autumn). VPS consists of an array of twelve VR2W single channel omni-directional acoustic receivers, moored in a grid arrangement (Fig. 5.1) at depths of 4m above the substrate. One V13 synchronisation tag (synctag) was moored with each receiver (Fig. 5.2 b) to allow for characterisation of variability in detection rate (Mathies, Ogburn *et al.* 2014). Synctags also allow for post-

hoc correction of clock drift and increase accuracy; clock skew is the difference between clocks at a point in time, clock drift is the rate of change in skew (Smith 2013). A single V13T reference tag was moored independently to the seafloor to adjust for movement of receivers and to record water temperature. The VPS has been shown to be more accurate than equivalent radio acoustic positioning (Andrews, Tolimieri *et al.* 2011).

Each VR2W hydrophone receiver detects acoustic signals at a restricted range of 69kHz; the same frequency as the signal emitted from V13 tags. This signal includes the tags individual ID number; the V13T tag also emits a temperature reading. These signals are repeated after a random delay between 500 and 700 seconds for the synchronisation tags and reference tags, and 200 and 400 seconds for animal tags, minimising the probability of tag signal collisions. To determine the distance VR2W's can accurately detect the V13 tag signal, a range-test was conducted prior to the study. As substrate complexity can interfere with an acoustic signal the range-test was first conducted over soft homogenous habitat and then hard complex habitat. The range-test consisted of nine VR2W receivers arranged in an 'L' shape, with receivers 100m apart. V13 tags with a fixed 5 second delay between signals, transmitting at the same signal strength as animal tags in the study, were placed at either end of the line of receivers.

Both hard and soft range-tests found that higher tides produced a decrease in detection rates, with 50-80% detection for hard and 60-100% detection for soft substrate during rising or falling tides. Background noise, wind and poor weather had no discernible effect, despite very strong winds being recorded. Tags were well suited to the location, with soft range-test having good range (>50% detection) up to 600m and very good range (>80% detection) at 300m. Hard range-test had very good range (>85% detection) up to 400m and poor range (>20% detection) up to 580m. Receivers were spaced conservatively, approximately 300m apart, to increase area of overlapping detection and likelihood of multiple receivers detecting tags. The complete array covered an area of 1.5km^2.

Five days prior to the setting of the VPS array (18 April 2013), two strings of eight standard commercial parlour traps were baited and set in the centre of the site, to catch a range of lobsters for tagging. Lobster from the subsequent catch were, measured, sexed, and fitted with a Hallprint, T-bar ID tag in the dorsal musculature behind the carapace to permit identification of the lobster (see; p.34), if it was subsequently recaptured in commercial or experimental traps. Each lobster was also fitted with a V13 coded transmitter (6g in water, ca. 1% body weight Fig. 5.2 a), attached by means of a cable tie and plastic tubing harness, between the denticles on the carpus of the largest claw (Moland, Olsen *et al.* 2011). Handling time for individual lobsters was no greater than 10 minutes. Lobsters were then released from their capture location with as little disturbance and time out of water as possible. As catch rates of lobster were low, as expected at this time of year, traps were reset and nine further lobsters were caught, tagged and released one day prior to the setting of the receivers. Catching, tagging and releasing the lobster prior to the start of the study allowed individuals to become accustomed to the tag, and resume their natural behaviours. Only positions gained at least 48 hours after first release were used in analysis.

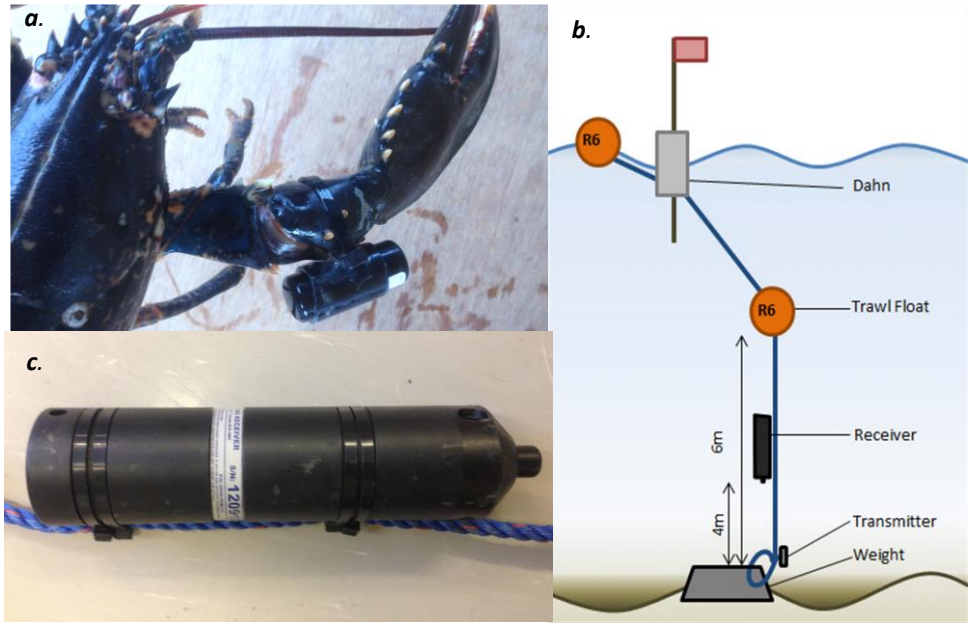


Figure 5.2 Images of **a.** V13 sync-tag (transmitter) attached to lobster; **b.** Receiver and transmitter (synctag) rigged to a hard trawl float and surface dahn and buoy; **c.** VR2W acoustic receiver.

Tagged lobsters ranged in size from 65 to 98mm carapace length (CL; $\bar{x}_{44}$ = 78mm), a size distribution similar to that of the natural population. All 44 lobsters tagged (21 female, four of which were ovigerous and 23 male) were in intermoult stage and had no recent signs of injury; however, six lobsters had one missing claw. There are no indications that tags impair lobster behaviour (Cowan, Watson *et al.* 2007; Moland, Olsen *et al.* 2011). Once tagged and released the V13 tags emit an acoustic 'ping' at 69kHz at a delay of 200-400 seconds. Considering their walking speeds (2.5m^{-min} (Aiken and Waddy 1995)) this provides high resolution data. The ping includes an ID number which allows identification of each specific tag. Tags stop pinging after 12months, to avoid tags lost, e.g. through ecdysis, impeding future data collection.

Positions are calculated by VPS, via hyperbolic positioning (time-difference-of-arrival; TDOA). When a transmission is received by three or more receivers, VPS takes differences between arrival times at pairs of receivers and calculates a single position by averaging all intermediate positions of receiver pairs, weighted by quality of intermediate positions. Summer and winter data stored within receivers was downloaded on 03 June 2013 and 20 Nov 2013, respectively.

For each animal tag calculated position, VPS provides an estimate of horizontal positioning error (HPE), which offers a level of confidence in the location of the estimated position. Positions with high HPE are likely to provide less information on the position of the animal (Smith 2013). HPE is based on the range of water temperature and salinity, the geometry of the tag and detecting receivers, and information on the error of VPS calculated positions for synctags and reference tags. HPE is calculated by VEMCO based on sensitivity of these calculations (Smith 2013). Temperature and salinity were assumed to remain constant; the V13T reference tag recorded a temperature of 7.2^{o}C and salinity was determined as 34ppt.

The method to relate HPE values as error sensitivity measurements, to error in absolute terms, involved examining the relationship between HPE and HPE in terms of metres (HPEm) for the stationary synctag transmitters of known location in the system. This was carried out by binning groups of calculated positions based on ranges of HPE of width 1, and for each bin calculating the 95% quantile. This approach was

found to be very similar to the twice distance root mean square approach commonly used (Misra and Enge 2006). A strong correlation was found, and the subsequent slope used to characterise HPE in terms of metres, deriving HPEm (Fig. 5.3). Since HPE is similarly calculated by VPS for synctags and animal tags, HPE characterisations are assumed also to apply to animal tags (Scheel and Bisson 2012; Coates, Hovel *et al.* 2013). The dataset was then filtered to remove erroneous high-error positions (HPE > 24) from analyses. HPE $\leq$ 24 represents a positional error of less than 30.34m in winter and 23.72m in summer. Mean HPEm of VPS from stationary synch tags was 4.59m (± $0.03_{s.e.}$) during the summer mean and 3.16m (± $0.01_{s.e.}$) during the winter.

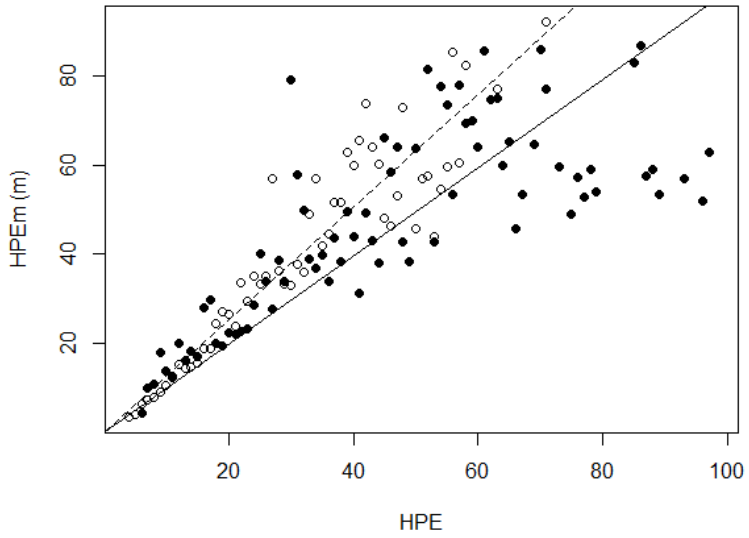


Figure 5.3 Plot of HPE and HPEm for VPS calculated synctag positions from summer (●) and winter (o). Each position is the 95% quantile value for bins of calculated positions (bin width = 1). Black line represents a linear regression forced through the axis for summer; $y = 0.9885x$; $R^2 = 0.8766$; $p < 0.001$, and the dashed line for winter; $y = 1.2642x$; $R^2 = 0.9658$; $p < 0.001$.

5.2.3 Statistical analysis

Positioning error estimates were generated for all tags by examining the relationship between the distances from the triangulated synctag positions to the true position measured in the field (Fig. 5.3). This estimate was used to filter the datasets and remove erroneous animal positions (HPE > 24) prior to analysis. Positional data collected by the receivers and processed by VEMCO were projected into ArcMap10.1, which along with the R software version 2.12.1, was used for all analysis. Each animal's utilisation distribution (UD) (Simpfendorfer, Heupel *et al.* 2002; Rogers and White

2007) was calculated, providing a probabilistic description of the space use of a tagged animal. This was based on density of detections using a kernel density estimator (KDE), which is less sensitive to outliers than other methods of home-range estimation (Seaman and Powell 1996). The density of positions was used to estimate home-ranges and gain an indication of habitat use and preference. A short-term home-range was defined as the smallest area containing 95% of the UD (95UD) for an individual; this was the area in which an individual can be expected to be found 95% of the time (Rodgers and Carr 2001). The core home-range was defined as the area containing 50% of the UD (50UD). To ensure individual home-ranges were comparable, kernel shape or search radius was standardised (h = 7.6m), and the cell-size of the output restricted to 0.1m (Kie, Matthiopoulos *et al.* 2010). These parameters gave the most appropriate and biologically meaningful KDE, and avoided over smoothing (Worton 1989; Van Der Veen and Logtmeijer 2005; Shimazaki and Shinomoto 2010).

Ten lobsters remained present when the array was reset during the winter period. Separate home-ranges were recorded for the summer and winter period for lobster that remained, allowing for direct seasonal comparisons between the home-range of these 10 lobsters. Linear regression was used to ensure that variation in the duration of tracking and number of positions did not bias the home-range estimates.

Diel patterns in movement and habitat use were analysed by categorising individual positions as day or night, defined by day lengths in Newcastle during the middle of the summer study period (day between 0600 and 1959, and night between 2000 and 0559). Rhythmic patterns in animal activity were inferred by pooling detection data for all synctags and animals into hourly bins; diel pattern of synctag detection frequency was used as control, with detection frequency used as a proxy for activity (Payne, Gillanders *et al.* 2010). Receiver positions were logged consistently hour by hour, therefore significant deviations in animal detection frequency were due to behavioural effects, rather than environmental factors or array errors (Lindholm, Auster *et al.* 2007).

Movement path metrics including turn angle, step length, and time interval were calculated via the Geospatial Modelling Environment (GME) platform version 0.7.2.1,

using R as the statistical engine (Fig. 5.4). Recorded positions map continuous movement as discrete points (Turchin 1998), each position having a fixed time-interval between consecutive positions; the shortest straight-line between consecutive positions were referred to as step-lengths. Step lengths were standardised by the step time-interval to create step-speed. Turning angles were defined as the angle between the bearing from (x-1) to (x), and the bearing from (x) and (x+1) (Fig. 5.4). Turning angle was constrained to positive values for analysis; distribution of turning angle was centred on 0 ^{o} (Martin, Tolon *et al.* 2009), thus 0^{o} shows high directionality continuing in straight line, 180^{o} was a 'U-turn', and 90^{o} could be either left or right turn perpendicular to original bearing, this prevents turns in opposite direction cancelling each other out when taking a mean. The sequence of step lengths, step-speeds, turning angles and their distributions provided the basis for the analysis of animal movement characteristics (Turchin 1998). Movement types have previously been identified as: intensive search movements, characterised by short step lengths and low directionality (due to high turning angles); and exploratory movement where step lengths are long and have high directionality (due to low turning angles)(Martin, Tolon *et al.* 2009). Analysis of movement metrics over different substrates was conducted by categorising metrics by the underlying substrate hardness of position(x) into categories of bin width 1. Due to restrictions of study site scale and the narrow range of depths within the site, depth was not included in any analysis.

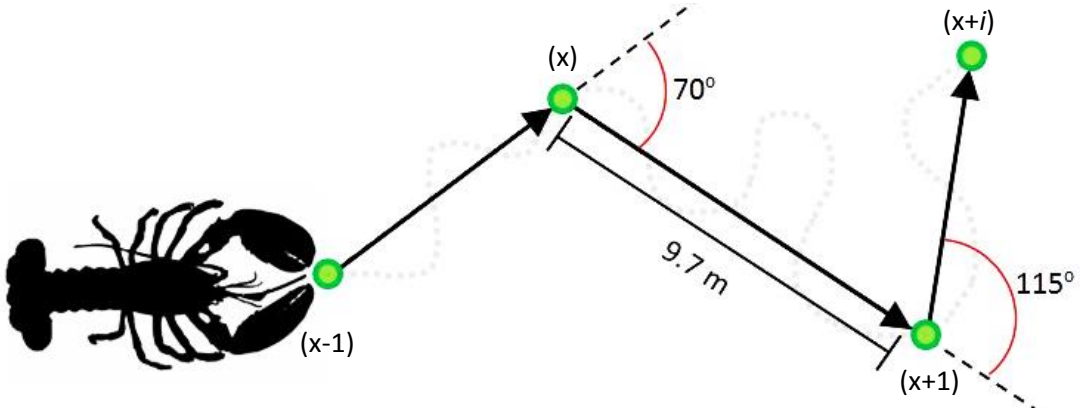


Figure 5.4 Movement of a tracked lobster; four recorded positions x-1 to x+i are shown (●), straight-lines between consecutive positions are referred to as step lengths (9.7 m), and the angles between the bearing of the previous step and the next step referred to as turn angles (70^{o} and 115^{o}).

5.3 Results

During the summer sampling period each receiver logged an average of 81,880 detections (83.6 per hour) of both synctags and lobster tags combined. Total number of detections ranged from 47,720 (receiver R01) to 126,199 (receiver R11). All synctags were well-detected across multiple receivers, with 91.7% of synctag transmissions logged on 3 or more receivers. During winter each receiver logged an average of 75,309 detections (57 per hour) of synctag and lobster tags combined. All synctags were well detected on multiple receivers, with each transmission detected over 6 times on average; 93.3% of synctag transmissions were logged on 3 or more receivers during the winter. Receiver time synchronization was excellent throughout both study periods, for all recovered receivers, meaning there was little clock drift to adjust against. There were short periods where no receiver time synchronization occurred, due to receiver movement or high error. These periods were removed from the analysis, along with positions with HPE > 24.

In the summer 27.8% of animal tag transmissions were detected on at least 3 receivers resulting in 60,982 animal tag positions being calculated by VPS for 44 different lobsters. Number of positions ranged from 15 (transmitter 28212) to 5,635 (transmitter 28180). During the winter period 24.0% of tag transmissions were detected on at least 3 receivers, resulting in 32,239 animal tag positions being calculated for 13 different lobsters. Number of positions ranged from 1 (transmitter 28158) to 8,448 (transmitter 28213).

Seven individual lobsters were excluded from summer home-range analyses as they either had tag malfunction prior to the onset of the study period or were not observed within the study area (n = 4), or there were an inadequate number of points for analysis (n = 3). Thus 37 individual home-ranges were estimated during the summer period (F= 18; M = 19). Twelve lobsters were observed during the winter study period, of these 2 individuals did not have an adequate number of points for analysis, thus 10 home-range estimates were gained (F = 2; M = 8). Only lobsters included in home-range analysis will be referred to from herein.

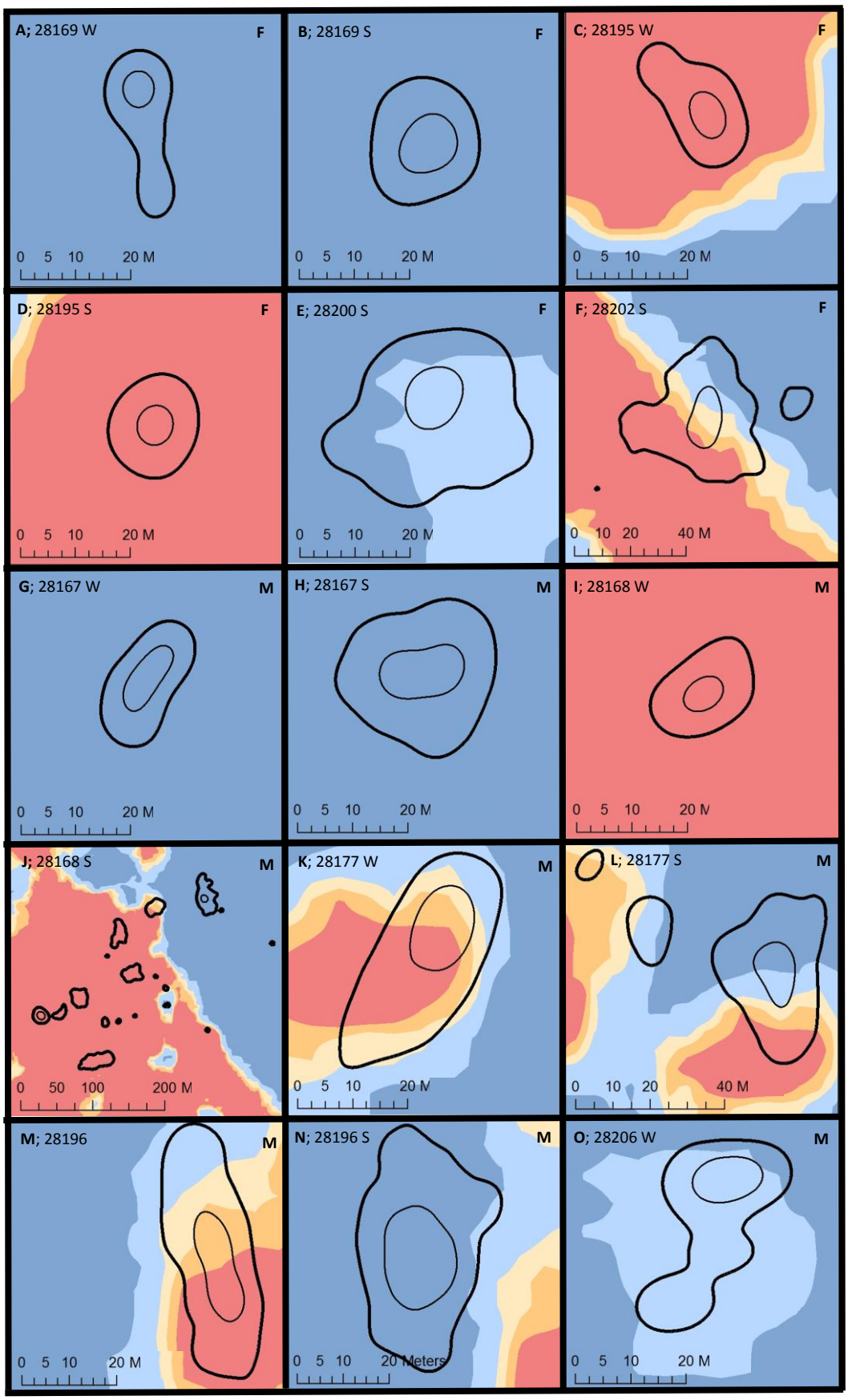


Figure 5.5 A-AU. Short-term total home-ranges (95UD) and core home-ranges (50UD) (n = 47).

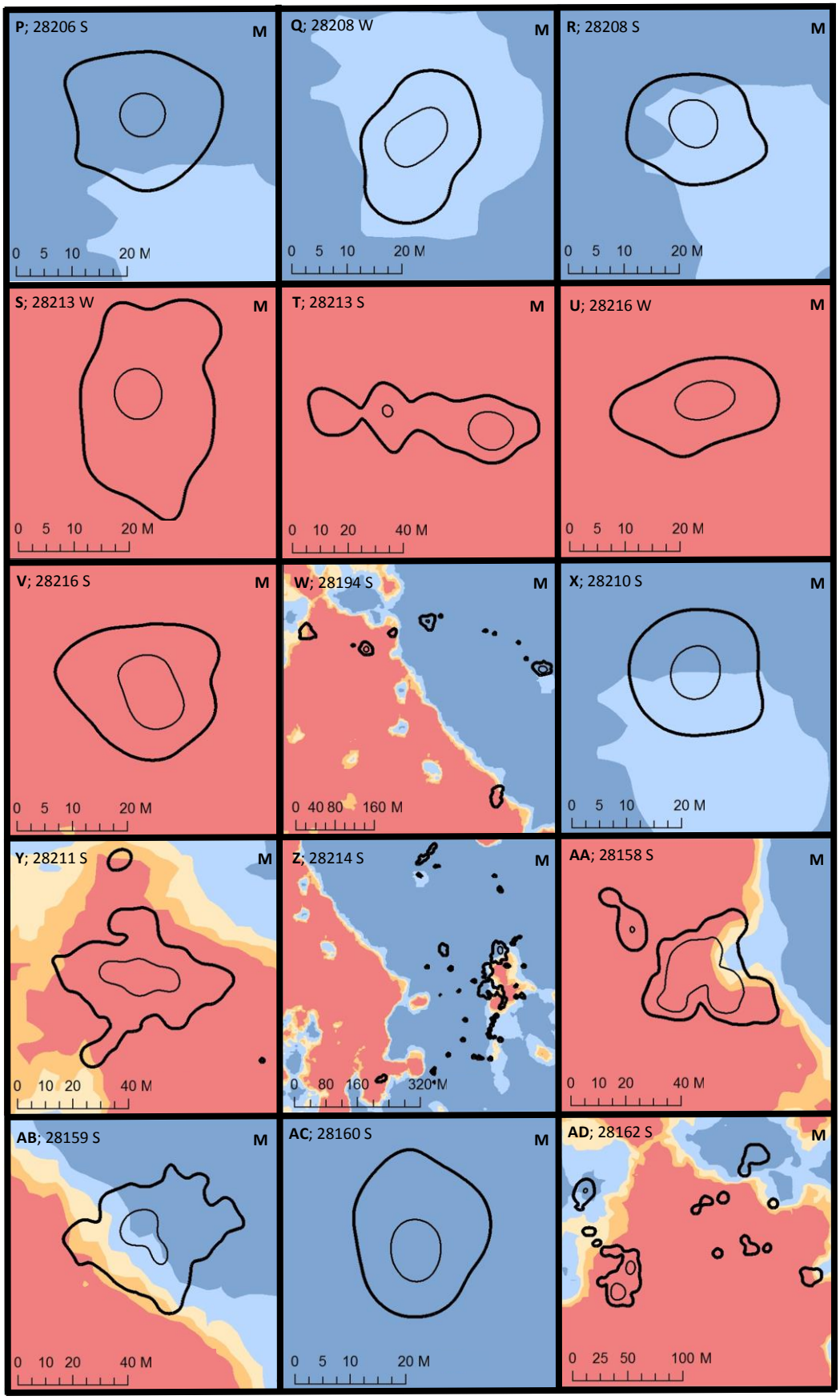


Figure 5.5 A-AU. Short-term total home-ranges (95UD) and core home-ranges (50UD) (n = 47).

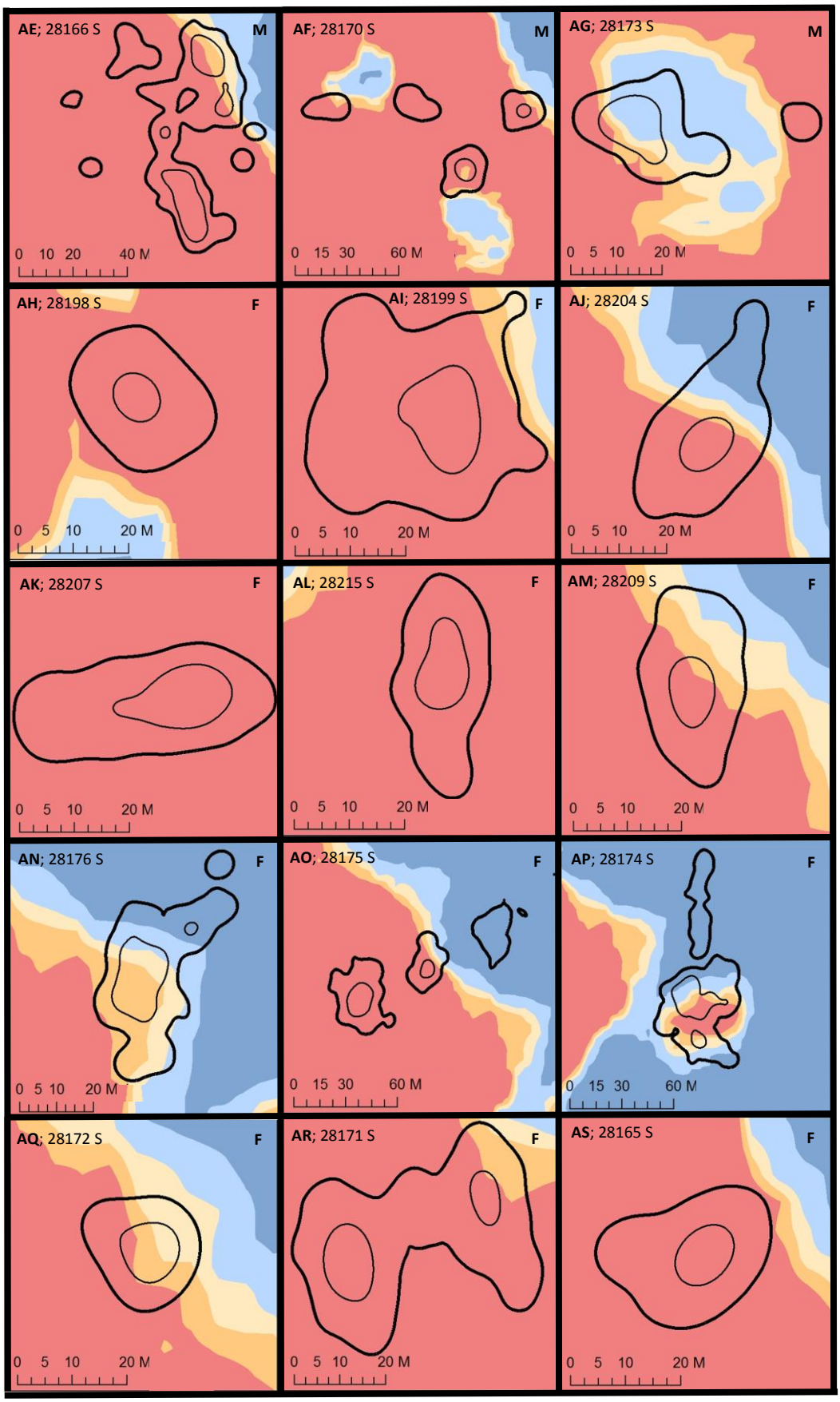


Figure 5.5. A-AU. Short-term total home-ranges (95UD) and core home-ranges (50UD) (n = 47).

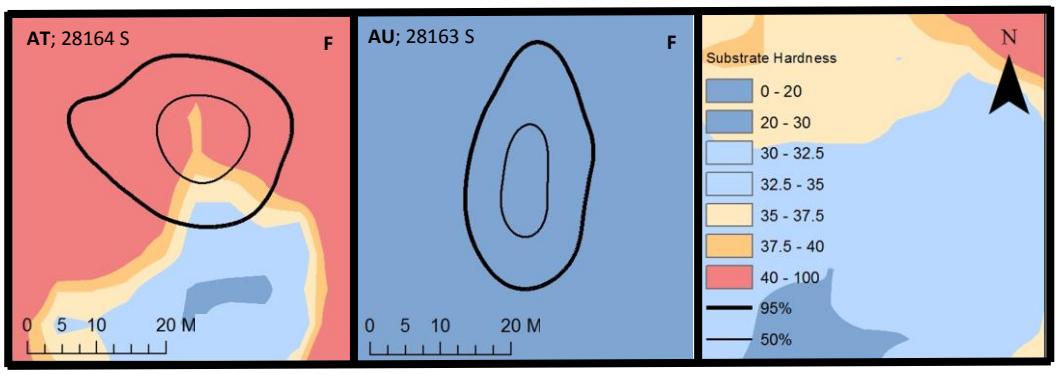


Figure 5.5 A-AU. Short-term total home-ranges (95UD) and core home-ranges (50UD) (n = 47) of tracked individual European lobster from continuous movement data during both Summer (S) and Winter (W) 2013. Each image is of an individual 95UD and 50UD home-range, overlaid on substrate hardness maps, showing soft substrates in blue, intermediate and mixed substrate in yellow and rocky reef in red. Each image has its own scale, states tag number in upper left, and sex of the individual in upper right.

Table 5.1 Summary of tagged lobster, number of positions (n) and days and their subsequent home-ranges during summer and winter.

Tag	Sex	CL	SUMMER						WINTER					
			n	Days	50UD (m^2)	95UD (m^2)	50UD hard (0-100)	95UD hard (0-100)	n	Days	50UD (m^2)	95UD (m^2)	50UD hard (0-100)	95UD hard (0-100)
28195	F	85	3969	16	37.50	243.99	47.52	47.76	1108	22	42.13	267.23	45.06	44.53
28206	M	73	2576	27	50.64	546.65	26.60	26.56	2983	64	82.81	504.33	31.52	31.60
28198	F	79	1304	41	58.23	492.16	42.55	45.18						
28208	M	77	1672	41	59.83	383.77	30.58	30.86	8074	62	84.59	439.21	32.96	32.15
28210	M	72	1878	41	69.30	463.83	31.32	29.52						
28160	M	76	1850	41	80.81	556.61	21.21	20.43						
28209	F	91	223	25	83.96	540.01	42.04	42.73						
28169	F	73	2990	25	86.28	364.94	20.21	17.53	173	30	29.41	237.08	18.00	17.53
28163	F	83	692	41	87.64	472.26	21.58	21.13						
28165	F	85	2210	39	88.57	570.77	50.17	54.17						
28200	F	87	1926	38	91.59	1205.57	31.38	30.38						
28172	F	76	714	39	91.65	341.82	38.32	41.37						
28204	F	86	1028	35	94.38	772.78	43.01	39.39						
28215	F	82	337	6	115.50	512.09	46.95	46.58						
28216	M	76	218	27	117.72	550.51	52.55	51.73	535	17	58.46	378.87	48.44	48.72
28167	M	72	1614	41	119.38	611.56	19.87	19.98	951	51	60.37	251.03	20.49	20.44
28164	F	74	642	41	131.46	573.71	41.58	42.91						
28177	M	71	1258	41	137.10	1153.77	29.84	30.03	2138	62	138.10	685.93	40.85	37.89
28207	F	86	431	41	168.29	770.05	51.90	50.49						
28170	M	75	1037	39	170.97	1841.16	40.56	45.86						
28168	M	69	1249	41	172.14	4718.43	36.95	44.00	6771	64	34.16	238.28	50.38	50.45
28213	M	74	1886	41	185.73	1357.62	53.69	51.49	8499	64	61.37	764.77	54.09	53.89
28214	M	77	1427	41	188.55	7721.69	26.73	28.73						
28159	M	78	1077	31	195.71	4313.78	29.74	23.88						
28199	F	71	913	40	197.05	1255.76	50.23	52.29						
28202	F	92	1146	26	201.65	2764.96	38.21	42.41						
28171	F	76	1313	37	205.88	1484.80	50.27	49.44						
28162	M	71	390	41	241.20	2929.95	48.64	44.17						
28176	F	74	97	36	256.09	1253.12	36.69	36.70						
28211	M	84	354	41	269.19	1814.33	52.99	48.96						
28196	M	76	528	37	277.81	1108.02	25.47	24.66	753	23	147.79	784.07	41.28	39.51
28175	F	65	232	39	290.49	2088.18	53.66	43.14						
28194	M	84	1099	41	301.15	3820.16	33.00	38.22						
28173	M	75	167	30	368.66	2146.95	37.11	38.65						
28166	M	71	127	3	452.24	2038.71	49.84	47.99						
28174	F	65	417	39	501.21	2864.76	36.38	31.12						
28158	M	98	191	22	556.61	2462.38	50.53	48.31						

The duration of tracking of each animal varied between individuals, and ranged from 3 to 41 days in the summer ($\bar{x}_{37}$ = 34 ± 1.6$_{s.e.}$) and 17 to 64 days during the winter ($\bar{x}_{10}$ = 46 ± 6.1$_{s.e.}$). There was also variation in the number of verified, accurate positions gained for each animal, which ranged from 97 to 3,969 in the summer ($\bar{x}_{37}$ = 1,113 ± 143$_{s.e.}$) and 173 to 8,499 in the winter ($\bar{x}_{10}$ = 3,199 ± 987$_{s.e.}$) (Table 5.1).

No significant correlation was found between the duration of tracking of individual lobsters in days, with size of either the 50UD home-range (R^2 = 0.006, p = 0.2788) or 95UD home-range (R^2 = -0.014, p = 0.4863). Duration tracked was also not correlated with size, sex, or number of observations. The number of positions for each individual was not significantly correlated with 95UD home-range size (R^2 = 0.005, p = 0.2852), however, it was negatively correlated with estimated size of the 50UD core home-range (R^2 = 0.3062, p < 0.001).

Summer home-ranges were estimated for 18 female and 19 male lobsters. The 95UD home-range area ranged from 243.99 to 2,864.76m^2 for females ($\bar{x}_{18}$ = 1,031.76 ± 184.51m$^2_{s.e.}$) and from 383.77 to 7,721.69m^2 for males ($\bar{x}_{19}$ = 2,133.68 ± 423.47m$^2_{s.e.}$). The 50UD core home-range sizes ranged from 37.50 to 51.21m^2 for females ($\bar{x}_{18}$ = 154.86 ± 25.51m$^2_{s.e.}$) and from 50.64 to 556.61m^2 for males ($\bar{x}_{19}$ = 211.30 ± 30.33m$^2_{s.e.}$). Underlying mean substrate hardness for 95UD home-ranges ranged from 17.53 to 54.17 for females ($\bar{x}_{18}$ = 40.82 ± 2.32$_{s.e.}$) and from 19.98 to 51.73 for males ($\bar{x}_{19}$ = 36.53 ± 2.47$_{s.e.}$). While 50UD core home-range hardness ranged from 20.21 to 53.66 for females ($\bar{x}_{18}$ = 41.26 ± 2.21$_{s.e.}$) and from 19.87 to 53.69 for males ($\bar{x}_{19}$ = 36.69 ± 2.55$_{s.e.}$) (Table 5.1).

Shapiro-Wilks tests showed 95UD and 50UD summer home-range area estimates for both sexes were non-normally distributed, while home-range hardness estimates for both sexes were normally distributed. Male and female 95UD home-range area estimates were significantly different (Kruskal-wallis$_1$: χ^2 = 4.2696; p < 0.05) (Fig. 5.6), but 50UD core home-range areas were not significantly different (Kruskal-wallis$_1$: χ^2 = 1.7073; p = 0.1913). Neither 95UD (t-test$_{34.963}$: t = 1.2304, p = 0.2268) or 50UD (t-test$_{34.54}$: t = 1.3155, p = 0.197) home-range hardness estimates were significantly

different between sexes, despite male mean hardness tending to be much lower than that of females (Fig. 5.7).

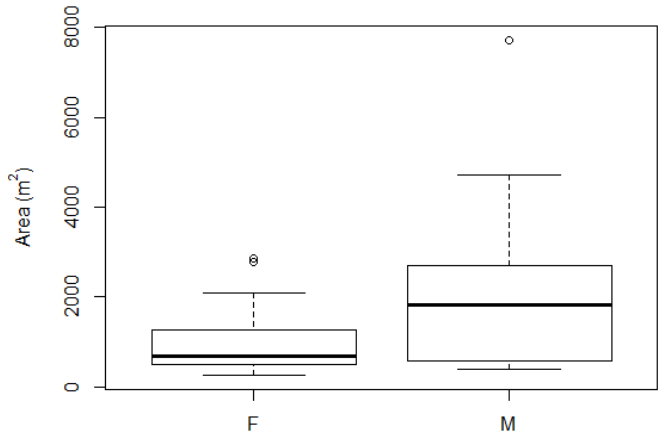


Figure 5.6 Boxplot of estimated 95UD summer home-range size of individual lobster (n=37), by Sex (F=18; M=19).

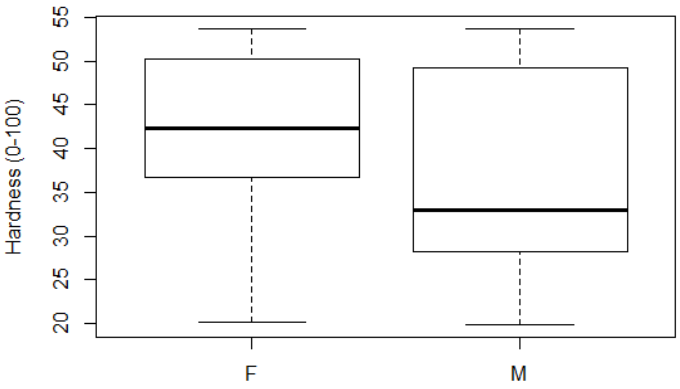


Figure 5.7 Boxplot of mean substrate hardness of 50UD summer core home-range of individual lobster (n=37), by Sex (F=18; M=19).

A log transform was used to normalise estimated areas of 95UD and 50UD summer home-range data. A linear regression model (LM1) was then implemented to first predict logUD50 home-range size based on sex, size and hardness ($LM1_{3and33}$: F = 2.578, p = 0.0703) (Table 5.2); only hardness was significant, with slight positive correlation. For the log95UD home-range size linear model ($LM2_{3and33}$: F = 2.198, p = 0.1068), only sex was significant, with males having larger 95UD home-range area (Table 5.3), however neither LM was significant.

Table 5.2 Results of fitted LM1 on 50UD: estimated coefficients values, relative error, t value and significance. Residual standard error: 0.821 on 33 degrees of freedom. Adjusted R^2 = 0.0908.

	Estimate	**Error**	***t*-value**	***p*-value**
Intercept	4.765759	1.172385	4.065	< 0.001
Sex M	0.377256	0.213423	1.768	0.0864
CL	-0.010869	-0.014313	-0.759	0.4530
Hardness	0.022865	0.009996	2.287	< 0.05

Table 5.3 Results of fitted LM2 on 95UD: estimated coefficients values, relative error, t value and significance. Residual standard error: 0.821 on 33 degrees of freedom. Adjusted R^2 = 0.0908.

	Estimate	**Error**	***t*-value**	***p*-value**
Intercept	6.679640	1.524786	4.381	< 0.001
Sex M	0.663183	0.280293	2.366	< 0.05
CL	-0.007478	0.019089	-0.392	0.6978
Hardness	0.014657	0.013292	1.103	0.2781

As some lobsters emigrated from the study area between the summer and winter study periods, analyses of any seasonal effect were restricted to those that remained within the site. Direct comparisons of home-ranges between seasons were conducted for the eight males and two female present throughout (Table 5.4).

Table 5.4 Summary of home-ranges of lobster observed in both periods (n = 10); mean home-range size and hardness ±s.e.

	50UD area (m^2)	**95UD area (m^2)**	**50UD hard (0-100)**	**95UD hard (0-100)**
Summer	124.41 ± 22.00	1,1103.93 ± 397.43	34.33 ± 3.83	34.46 ± 3.93
Winter	73.92 ± 12.22	455.08 ± 66.13	38.31 ± 3.69	37.67 ± 3.70

As 95UD summer home-range area data was non-normally distributed, between season comparisons of 95UD used a Wilcoxon singed ranks test. All other tests were conducted as parametric paired t-tests. Significant differences were observed between 50UD core home-range areas between seasons (t-$test_{10}$: $t = 2.4635$, $p < 0.05$) (Fig. 5.8), and between the 95UD home-range areas between seasons ($Wilcox_{10}$: $V = 51$, $p < 0.05$). Despite mean substrate hardness increasing during the winter, no significant difference was observed between the hardness of the 50UD core home-ranges (t-$test_{10}$ $t = 1.7766$, $p = 0.1094$), or the hardness of the 95UD home-range between seasons (t-$test_{10}$: $t = 1.8425$, $p = 0.09851$). No significant correlation was found between the size of a lobster and its subsequent mean substrate use, or the size of its home-range area for either 50UD or 95UD during summer and winter.

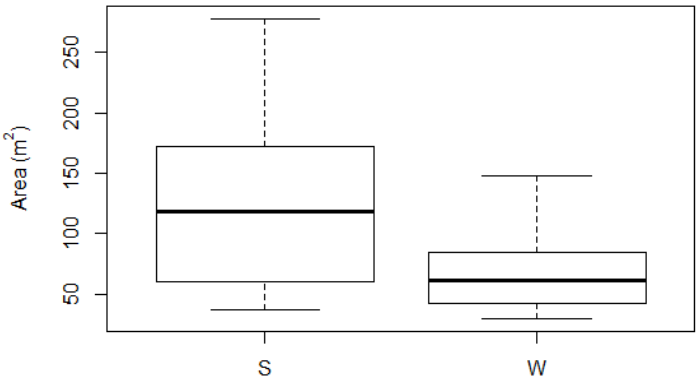


Figure 5.8 Boxplot of 50UD core home-range area of individual lobster (n=10) during summer and winter.

Of the 40 lobsters tracked during the summer, 29 were observed on substrate hardness <20 (14F and 15M). Cumulative time intervals for each substrate hardness value grouped within bins of width 1 were expressed as a percentage of the total time intervals recorded across all lobsters during the summer (Fig. 5.9). Total percentage times spent on substrate $\leq$ 20, $\leq$30, and $\geq$40 were 8.4%, 44% and 38% respectively. Most animals spent some time on soft (< 20) substrate, but this was rarely within their home-ranges.

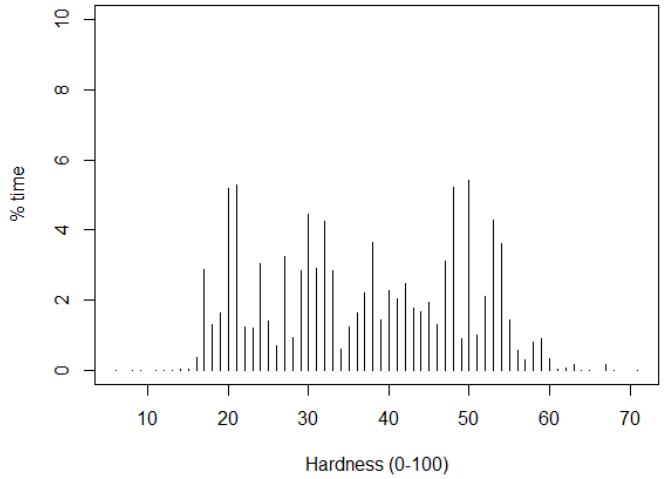


Figure 5.9 Plot of percentage of time spent on different substrate hardness', for all individuals (n = 40) pooled together across both study periods categorised by the underlying substrate hardness.

To highlight differences in lobster movement over different levels of substrate hardness, step-speed values between every consecutive position were pooled for all lobsters (n = 72,395) and grouped by underlying substrate to the nearest whole integer. Mean step-speed and mean turning angle (n = 72,393) were plotted for each substrate hardness integer (Figs. 5.10 and 5.11, respectively).

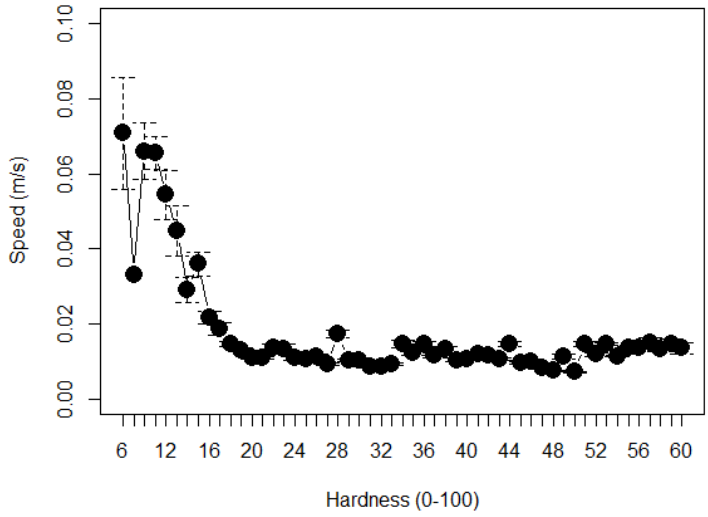


Figure 5.10 Plot of mean speed (m/s ± 95% CI) between all individual points, across all seasons categorised by the underlying substrate hardness (n=72,395).

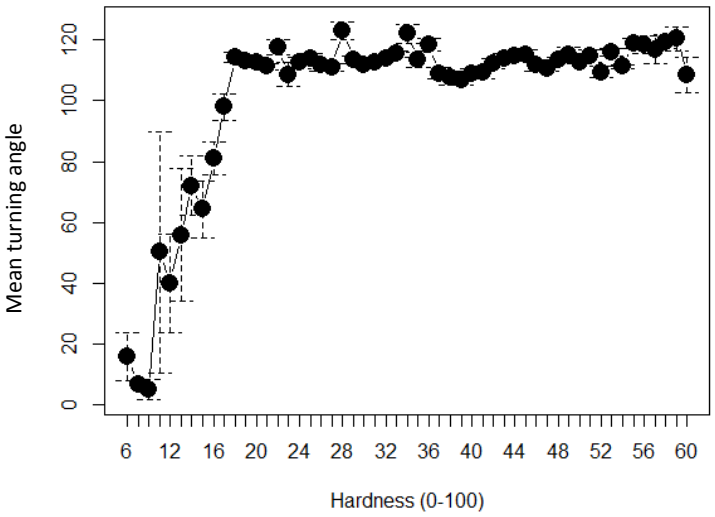


Figure 5.11 Plot of mean turning angle (^{o} ± 95% CI) between all individual points, across all seasons categorised by the underlying substrate hardness (n=72,393).

A change in movement behaviour was evident on soft ground. This effect was marked below substrate hardness value of ca. 18 (Figs. 5.10 and 5.11). Both high mean step-speed and high mean directionality (due to low turning angles) were observed when

lobsters were over soft substrate. Speed was positively skewed and observed values were small, therefore speed was converted into metres per hour to perform analysis and a constant added to each value so that the smallest value was 1. These were then $\log_{10}$ transformed. A linear regression model (LM3) was implemented to predict step-speed based on sex, size, hardness and turning angle ($LM3_{5and72,745}$: $F = 426.2$, $p <$ 0.001) (Table 5.5). All coefficients were found to be significantly correlated with step-speed. This predicted speeds over mixed substrate hardness to be lower than those over hard substrate, while soft substrate (≤ 20) speeds were predicted to be higher than on hard substrate. Males were expected to have mean speeds 0.06 times higher than females. Data from the 10 lobsters present during both summer and winter periods predicted no difference in the distribution of step-speed with hardness or turn angle with hardness, between the two seasons. Total distance travelled per day, calculated from cumulative step-lengths standardised by duration of tracking, showed no correlation with sex or size of the individual.

Table 5.5 Results of fitted LM on Speed (m/hr): estimated coefficients values, relative error, t value and significance. Residual standard error: 0.4979 on 72,745 degrees of freedom. Adjusted $R^2 = 0.02839$.

	Estimate	**Error**	***t*-value**	***p*-value**
Intercept	0.5282914	0.0329532	16.032	< 0.001
Hard mixed	-0.0170001	0.0038392	-4.428	< 0.001
Hard soft	0.1615958	0.0099903	16.175	< 0.001
CL	0.0079041	0.0004018	19.674	< 0.001
Sex M	0.0574658	0.0050291	11.427	< 0.001
Turning angle	0.0013015	0.0000330	39.440	< 0.001

Hourly summer detection ratios among animals and synctags indicated a significant difference in diel movement pattern (Kruskal-$Wallis_1$: $\chi^2 = 278.53$: $p = < 0.001$); lobsters were more active between 1500 and 0700 (Fig. 5.12). Winter detection frequencies between synctags and animal tags were also significantly different (Kruskal-$Wallis_1$: $\chi^2 =$ 19.4261: $p = < 0.001$), however, diel patterns of activity were not as clear as during the summer (Fig. 5.13). There were no significant differences between day and night for mean hardness, male and female activity, or substrate use of males and females, despite males using softer mean substrates during the night compared with day, and

females using harder mean substrate during the night compared with day. However, the range of hardness for positions was significantly different between day and night for all lobsters (Wilcoxon$_{78}$: $V = 232$, $p < 0.02$), with a wider range of substrate being used during the night, reflecting the increased movement activity.

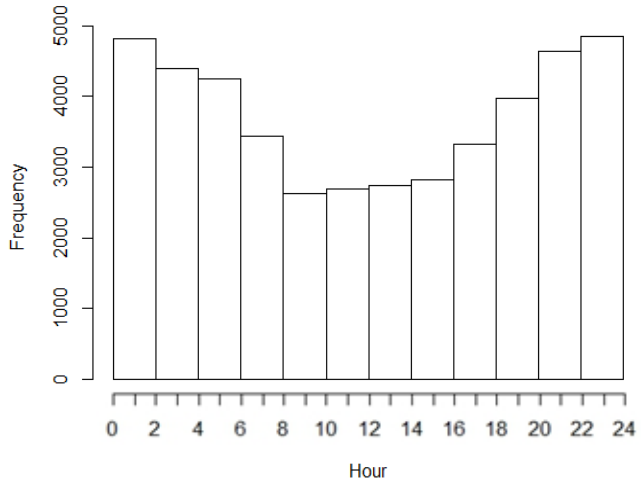


Figure 5.12 Histogram of summer detection frequency (n = 44,593) for all lobster tags (n = 40); categorised into 2 hour bins from 0000-0159 to 2200-2359.

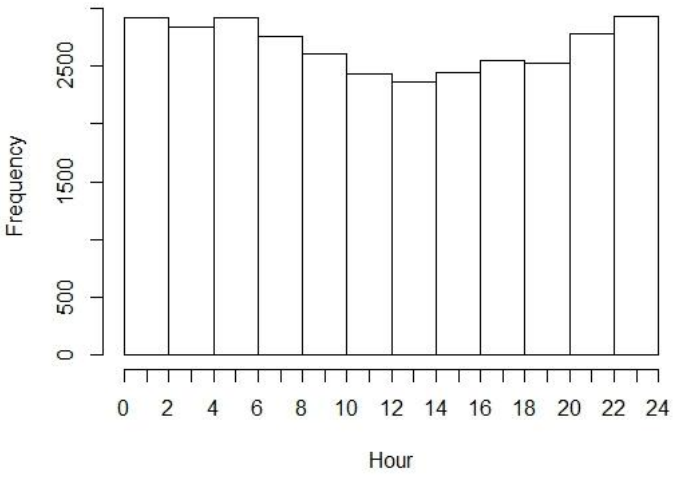


Figure 5.13 Histogram of winter detection frequency (n = 32,039) for all lobster tags (n = 10); categorised into 2 hour bins from 0000-0159 to 2200-2359.

Visual interpretation of summer movement paths showed 8 lobsters (21%; 6M and 2F) had multiple or fragmented home-ranges, while 22 tagged lobsters (59%; 10M and 12F) stayed in the same area throughout the entire period. Ten lobsters remained within the study area throughout both periods (27%; 8M and 2F). While 10 lobsters emigrated from the study period during the summer (27%; 5M and 5F); two migrated

south-west while 8 lobsters migrated due west. Only two migrations were observed during the winter, both were females migrating east.

5.4 Discussion

During the summer, male lobsters had significantly larger home-range areas than female. All lobsters had significantly reduced home-ranges during the winter; this was coupled with diel patterns of activity becoming less strict and a reduction in activity and movement rates. Home-range substrate hardness was not significantly different between sexes, sizes, seasons, or day and night, however, there was a significant increase in the range of substrate used by lobsters at night, suggesting increased excursions from shelter.

Lobsters spent the majority of time on mixed and hard substrates with mean movement characteristics of low directionality and speed and high turning angle, suggesting they were engaged in 'searching' behaviour on these substrates (Wiens, Schooley *et al.* 1997). However, most lobsters also spent time on soft substrate where movement changed towards 'exploratory' behaviour with, high directionality and speed (Jonsen, Myers *et al.* 2007). Utilisation of soft substrate corridors between patches of rock and cobble suggests high connectivity between discrete lobster habitats.

5.4.1 Home-range characteristics

Short-term home-range sizes reported in this study were relatively small; mean summer 95UD home-ranges of 1,032m^2 and 2,134m^2 and 50UD core home-ranges of 155m^2 and 211m^2 for females and males respectively. In comparison, previous *H. gammarus* home-range estimates have been much larger. Wiig *et al.* (2013) reported a mean summer 95UD home-range for males of 170,660m^2, declining to 123,004m^2 in winter. While, over the course of a year, Moland *et al.* (2011) found mean home-ranges of 23,411m^2 via minimum convex polygon and 19,879m^2 via UD. Neither study found correlations between home-range and size or sex. Much of the discrepancy between present and previous findings is likely attributable to methodology and

environment. Greater ranges are to be expected in such long-term and large-scale studies (Simpfendorfer, Heupel *et al.* 2002). The present study concentrates on accurate short-term movements within a restricted area, and does not observe long-term and large-scale movements. It is possible that the lobsters displaying fragmented home-ranges and those emigrating from the study site are indicating that a temporally and spatially increased study would discover larger home-ranges. Furthermore, cumulative centres of activity or active tracking lead to lower sampling rates and greatly decreased accuracy, causing over-estimation of home-ranges. The minimum convex polygon technique employed also has a tendency to over-estimate; in this study minimum convex polygon would have over-estimated home-ranges to 39,356m^2 and 8,803m^2 for males and females respectively. However, methodological differences do not exclude the possibility of biological or behavioural differences between lobster in the present study and Norwegian populations of lobster studied within Wiig *et al.* (2013) and Moland *et al.* (2011); closed seasons to fishing, lower catches and greater availability of hard habitat within Norwegian waters may lead to increased individual range of movement.

It is generally postulated that *H. gammarus* have more restricted dispersal and lower movement rates, compared with *H. americanus* (Smith, Jensen *et al.* 2001; Agnalt, Kristiansen *et al.* 2007; Moland, Olsen *et al.* 2011). However, results here compare well with a study using similar techniques to elucidate short-term *H. americanus* movements, which estimated 95UD and 50UD home-range sizes to be 760m^2 and 74m^2 respectively (n = 32) (Scopel, Golet *et al.* 2009), with no correlation between lobster size and home-range size was reported. This supports the hypothesis that methodology, study length and study area, have an influence on home-range size estimation.

Although differences between home-range substrate hardness were not significant, it was apparent that as a home-range extended it generally included a wider range of substrate; softer substrates being along the periphery of the home-ranges. Previous studies show lobsters reside predominantly in shelter-providing habitat (Steneck 2006), areas of high kernel density generally consisting of hard substrate, whereas

home-range peripheries consist of unstructured soft substrate (McMahan, Brady *et al.* 2013). This further suggests that the hard substrate is used to provide shelter, i.e. the centre of their home-range, and the surrounding substrates are used for other activities.

Duration tracked was not correlated with size, sex, or number of observations; which justifies comparing home-ranges and data between individuals studied for different durations. Home-range area significantly declined during winter; however core home-range did not. This would imply that short movements away from shelter and near-by foraging, albeit less frequent, remains vital during winter, but excursions further away from shelter are restricted. Multiple and fragmented home-ranges were not observed during the winter, perhaps as potential gains of longer movements are outweighed by potential losses (Levin, Cohen *et al.* 1984; Miller, Crowder *et al.* 1985). There is evidence in *H. americanus* of lobster overwintering, finding suitable habitat to do so, and remaining there until summer months, when larger more fragmented movement is undertaken (Thomas 1968; Karnofsky, Atema *et al.* 1989; Factor 1995). Maine temperatures are much lower in winter than UK, so sustained zero-movement is expected. However, this could also be an artefact of methodology, because animals present during both periods by definition exhibited non-transient behaviour. Small-scale seasonal comparisons of the same lobsters are biased towards individuals with restricted movement. However, they still provide a meaningful comparison of paired seasonal home-range data. This shows a non-significant reduction in the use of soft substrates between summer and winter, a product of the reduced 95UD home-range area.

5.4.2 Movement characteristics

Lobsters exhibited low rates of short-term movement with small home-ranges restricted to hard and mixed substrate. ‘Homing’ behaviour, consisting of regular back and forth movement to a centre of activity, was common. However, nomadic behaviour was also observed; 21% of tagged lobsters had fragmented or multiple home-ranges, with size of home range remaining fairly consistent from one to the next and 73% migrating outside the 1.5km^2 study area prior to winter. Except for

differences of 95UD home-range areas between sexes and predictors of step-speed, there was no significant predictor of movement behaviour. This adds credence to the hypothesis that populations are governed by individual personalities in the form of variation in boldness, risk-taking, habitat-use, exploration and movement tendencies (Fraser, Gilliam *et al.* 2001; Golet, Scopel *et al.* 2006; Wolf, van Doorn *et al.* 2007; Scopel, Golet *et al.* 2009; McMahan, Brady *et al.* 2013). However the complexity of individual behaviour and the high intra-population variation requires high repetition and large cohorts of tagged animals in telemetry.

Typically lobsters are categorised as transient or resident. These two types have been recorded many times previously, primarily in *H. americanus* (Cooper and Uzmann 1980; Ennis 1984; Karnofsky, Atema *et al.* 1989; Scopel, Golet *et al.* 2009) but also in *H. gammarus* (Dybern, Jacobsson *et al.* 1967; Dybern 1973; Smith, Collins *et al.* 1999; Moland, Olsen *et al.* 2011; Moland, Olsen *et al.* 2011a): residents remained within the area of release, whereas transient lobsters moved rapidly from release site, sometimes returning later in the year (Pezzack and Duggan 1986; Geraldi, Wahle *et al.* 2009). This dichotomy of movement behaviour has not been explained by size or sex and is likely an individual's response to seasonal limitations of habitat or mate availability (Bowlby, Hanson *et al.* 2007), reflecting a trade-off to fitness (Dieckmann, O'Hara *et al.* 1999). It is likely that individuals alter movement strategies in response to current health, reproductive stage, moult stage, local food, shelter and mate availability (Ennis 1984; Ennis 1984; Atema 1986). Seasonal movement towards the end of summer may be driven by the need to secure suitable over-wintering shelter before reducing movement through colder months (Bowlby, Hanson *et al.* 2007; Bowlby, Hanson *et al.* 2008). Large population-wide movements are likely to be driven by large-scale environmental variables, such as bottom temperature (Aiken and Waddy 1986; Drinkwater, Harding *et al.* 1996; Schmalenbach and Buchholz 2013), where long-term fitness benefits of movement outweigh the fitness cost of remaining stationary (Levin, Cohen *et al.* 1984; Miller, Crowder *et al.* 1985). Understanding decisions to alter behaviour between resident and transient is one key to understanding lobster movements.

Mobility has previously been shown to correlate positively with catchability and a propensity for increased trap interaction (Bowlby, Hanson *et al.* 2007; Wiig, Moland *et al.* 2013). The reduced mobility of animals during colder months could explain seasonal reductions in lobster landings i.e. rather than being due to reduced abundances as lobster move offshore, as sometimes anecdotally described by fishermen within the Northumberland district, it could be due to restricted movement and subsequent reduced lobster-trap interaction. It also suggests that any study using traps to catch animals for tagging is biased towards disperser characteristics and animals with higher catchability.

While *H. gammarus* is generally considered to migrate less and have more restricted long-term home-ranges than *H. americanus*, exploratory movements of *H. gammarus* have been recorded (Jensen, Collins *et al.* 1994);, this highlights potential connectivity between discrete areas of lobster habitat. Selection would be expected to favour the least energetically expensive mode of movement (Zollner and Lima 1999) via soft substrate corridors (Beier and Noss 1998; Micheli and Peterson 1999; Hovel and Lipcius 2001). Utilisation of soft substrate as a means of exploratory movement was recorded in this study. Parameters of movement path metrics (step-speed and turning angle) showed sharp reductions between 0 and 20 substrate hardness values, with no difference above 20. Increased speed and directionality over soft substrate are indicative of lobsters' dependency on the shelter-providing qualities of hard substrates. Movement on unstructured soft substrate could be considered high-risk, due to increased susceptibility to predation (Spanier, McKenzie *et al.* 1998; Micheli and Peterson 1999; Gilliam and Fraser 2001; Hovel and Wahle 2010). Therefore fast, highly directional movement towards shelter-providing substrate is expected. In contrast, movement on hard substrate will naturally tend to be slower, with larger (tighter) turning angles, due to the increased energetics and difficulties of traversing this substrate (Schippers, Verboom *et al.* 1996; Wiens, Schooley *et al.* 1997). It may also be an indication of increased foraging or searching behaviour, investigating shelter, and interacting with conspecifics (Skajaa, Fernö *et al.* 1998; Watson, Vetrovs *et al.* 1999; Patterson, Thomas *et al.* 2008). This sharp reduction in speed but increased turning angle on hard substrate will alter catchability, with movement behaviour linked to

probability of detecting, finding and entering a baited trap. These findings suggest that population assessments will benefit from considering overall substrate patterns and nonlinear responses of animals to them.

Seasonal reductions in *H. gammarus* movements have long been known anecdotally, and have been recorded previously in the UK (Smith, Collins *et al.* 1998; Smith, Collins *et al.* 1999; Smith, Jensen *et al.* 2001), where they are strongly correlated with water temperature (Smith, Collins *et al.* 1999). Summer excursions outside of shelter were previously thought to be exclusively nocturnal, but relax with greater turbidity and lower light levels (Smith, Collins *et al.* 1999). The present study also showed a strong diel pattern of activity during the summer, which relaxed during the winter. However exploratory movements still occurred during daylight in both seasons. The present study site, is relatively deep and turbid, therefore diel patterns may be less clear than at shallow inshore sites. Trap entry rates may remain constant throughout the diel cycle (Jury, Howell *et al.* 2001), and previous studies have even shown largest movements to occur during the day (McMahan, Brady *et al.* 2013). Therefore diel cycles were not as key to lobster behaviour and distribution as habitat, or seasonal and temperature driven cycles.

5.4.3 Assumptions and uncertainties

One of the strongest aspects of this study, other than the high accuracy and detection rate of the equipment, was the high sampling rate and large sample size (n = 40); this lends itself to more suitable and accurate use of KDE home-range estimation (Millspaugh and Marzluff 2001). The wide range of sex and size of the tagged population enabled size effects on movement and behaviour to be explored. However, individual 'personalities' (Dingemanse and Réale 2005) were not obvious and may have masked size or sex correlation. Size of the area studied made it possible for high resolution positions to be logged with very high rate of detection. However the area under surveillance was limited, due to restrictions in equipment, therefore large-scale movements were impossible to observe, and for some transient lobsters, home-ranges would have been under-estimated. The transient nature of portions of the population relative to the area of the site caused winter replication to be low, and sex ratio to be

skewed in favour of males. For future studies, continuous tracking between seasons or increasing the study area would help improve understanding of emigration and connectivity between patches of hard substrate.

Substrate topography is likely to play a key role in determining animal movement patterns and directions. It is clear from the present study that substrate hardness restricts or dictates movement behaviours. Improved bathymetric data could highlight various features or contours that are influencing shape and size of home-range or movement paths. Range-tests on the array showed detection rates increased on soft or flat substrate, which could lead to a biasing of positions and movements. However this was offset by the number of positions gained and the high frequency of animal positions logged, regardless of distance, speed or substrate (Heupel, Semmens *et al.* 2006; Welsh, Fox *et al.* 2012; Cagua, Berumen *et al.* 2013; Roy, Beguin *et al.* 2014).

There were also limitations in the accuracy and resolution of the substrate hardness maps. Olex provides a useful means of mapping broad scale hardness and depth (resolution 5m), but did not reveal fine detail to the same resolution as animal positional data (resolution ca. 3m). Shelter-providing structures need only be small for a single lobster, and these can be missed, leading to inaccurate assumptions of lobster substrate use.

KDE home-range estimation is a key area of potential error in the analysis. An often cited drawback is the choice of smoothing parameter (*h*) (Worton 1995; Seaman and Powell 1996; Kernohan, Gitzen *et al.* 2001), which aims to reduce variability of home-ranges at the cost of increasing bias (Fieberg 2007). To ensure individual home-ranges were comparable, *h* was fixed at 7.6m. This biases some estimates upwards and others downwards with more fragmentation. Non-statistical methods for smoothing parameter selection can be less robust than statistical methods. However, biological and behavioural factors or the nature of the data can be used to guide decisions (Laver 2005). Smoothing parameters should not be equal to or smaller than the distance typically travelled in the given sampling interval, re-sightings within the search radius of *h* should only occur if the animal choses to remain or if it subsequently returned to the area. Considering reported lobster walking speeds (< $2.5m^{-min}$), animals could

travel ca. $7.5m^{-3\ min}$; a biologically and methodologically meaningful value for *h*. It is also twice the mean winter HPEm; while giving the most appropriate KDE, and avoiding over-smoothing (Worton 1989; Van Der Veen and Logtmeijer 2005; Shimazaki and Shinomoto 2010). Selection of *h* is low in comparison to previous studies (Wiig et al (2013); *h* = 50; Moland *et al.* (2011); *h* = 25), however here the scale and accuracy of the method meant a smaller parameter was appropriate. For large cohorts and high sampling rates it is considered better to smooth less in order to reduce bias (Fieberg 2007). Previous studies have demonstrated that using least-squares cross-validation for each individual will not always be a suitable method for selecting *h* automatically (Silverman 1986; Gitzen, Millspaugh *et al.* 2006; Wiig, Moland *et al.* 2013), and KDE methods are considered efficient even with unequal sampling of individuals (Börger, Franconi *et al.* 2006), therefore the present methods employed are considered robust.

Assumptions were made regarding movement path metrics. Step-speed will have often been underestimated, because it assumed a straight-line between positions in reality it was an estimate of the slowest possible speed of the lobster (Turchin 1998). Deviations from the straight line bearing were assumed to be proportional in all step lengths. The high replication in this study reduced uncertainty about mean step-speed and turning angle estimation. A random walk model might have been implemented to simulate natural movements, however, animals that alter movement behaviour over time may not be suited to conventional correlated random walk model analysis, without incorporating behavioural heterogeneity between and within individuals (Morales and Ellner 2002).

5.5 Conclusion

This study demonstrates the capabilities of a fixed acoustic telemetry array for quantifying the fine-scale movements of marine animals within a heterogeneous study site. It provides the UK's first acoustic telemetry study of lobsters, which will inform the future application of the technique. There was high variability between lobster movement behaviours, with no correlation with size. Over short periods lobsters had restricted home-ranges, showing high site fidelity. In contrast to previous lobster movement studies, males had greater short-term exploratory and risk-taking

behaviour, with greater mean 95UD home-range, and a tendency to use a wider range of substrate. Within sexes variation also existed, with more males remaining resident within the array.

Movement behaviours were strongly influenced by substrate, with higher probability of being found on mixed and hard substrates, particularly at habitat edges. However, soft substrate areas were utilised by transient portions of the population as corridor between areas of shelter-providing substrate. Movement path metrics changed to reflect this behavioural difference. This work shows the potential connectivity between distinct patches of hard substrate is high, while lower temperatures were associated with more restricted lobster movements and habitat utilisation, probably causing a drop in catchability and connectivity.

These data illustrate both the residential and the transient nature of lobster movements. Understanding the complexity of individual behaviour, primarily drivers of the decision to be transient or resident, is the greatest challenge in translating these data into management. Behavioural decisions are complex, caused by numerous variables including fitness and interactions with surrounding members of the population, not necessarily sex, size or season. However, this study provides essential data on spatial structure of the landscape, and how lobsters interact and use it. The high rate of emigration from the site indicates that limited management, such as small reserves, may not alone fully protect adult lobsters and that other management measures are essential.

Chapter 6:

Thesis overview, limitations and wider implications

Chapter 6: Thesis overview, limitations and wider implications

This thesis has examined the abundance, behaviour, catchability and movement of *Homarus gammarus* off the coast of Northumberland, UK. Multiple approaches, including fishery-independent trap-studies, CMR and acoustic telemetry were employed, and have provided some of the first data of their kind on European lobster. This chapter provides an overview of the thesis, highlighting the key findings, providing an explanation of results and in light of the unique nature of the work, resulting changes to the current knowledge are discussed. Limitations of the study are reviewed and caveats to the interpretation of results provided. The work is placed within the wider context of lobster research and management with an overview of the significance of findings and implications for their application. Finally, outstanding research questions are identified and recommendations for future work are made on this basis.

6.1 Key findings and contributions to knowledge

The current trend of UK inshore fisheries management is towards decentralisation and increased regional responsibility for monitoring and regulating stocks (McCay and Jentoft 1996; Symes 1997; Symes and Phillipson 1997; Gray and Hatchard 2003; Griffin 2013; Jentoft and Knol 2014). This was made clear with the establishment of regional IFCAs in 2011, as part of the Marine and Coastal Access Act 2009, with a remit to '*manage a sustainable marine environment and inshore fisheries, by securing the right balance between social, environmental and economic benefits*'. This trend towards devolved management is likely to continue, and the recognition of biological and environmental spatial variability has increased the importance of regionally specific data (Koeller 1999; Tully, O'Donovan *et al.* 2000; Lizarraga-Cubedo, Tuck *et al.* 2003). However, such data are currently scarce. Prior to this thesis, few fisheries-independent studies of lobster within the Northumberland district had been conducted (Nichols and Lawton 1978; Brown 1982; Turner, Hardy *et al.* 2009). Self-reported commercial catch and effort data and limited vessel sightings were some of the only available information (CEFAS 2011; Turner, Gray *et al.* 2013; Turner, Polunin *et al.* 2014). This thesis' approach allowed greater understanding of how both traps

and remote-tracking provide independent views and interpretations of the same behaviours within the study area. In some instances, findings are corroborated between these approaches and in others they are contradicted. The novel achievements lie in the thesis' estimations of catchability, abundance, fidelity and movement of the European lobster at a local scale .

6.1.1 Catchability and abundance

One of the most striking findings was the significant difference between the catchability of male and female lobsters. Males were almost three times more susceptible to trapping than females throughout the study. Acoustic telemetry demonstrated that larger male home-range sizes are a behavioural cause that could contribute to this. Their home-ranges extend over a larger area and include a wider range of substrates than females; this is consistent with the hypothesis that wider dispersing lobsters have increased catchability (Bowlby, Hanson *et al.* 2007). Another contributory factor might be dominance behaviour, with subordinate individuals avoiding traps due to presence of dominant individuals (Summerlin and Wolfe 1973; Cobb and Tamm 1975), or due to increased energy expenditure (Wiig, Moland *et al.* 2013). Increased male boldness and exploratory behaviour increase the number of traps encountered and the frequency of trap interaction, leading to greater probabilities of capture (Wiig, Moland *et al.* 2013).

Crespin (2008) stated that, heterogeneity of catchability may reflect hidden features of the population. Dichotomous catchability caused CMR estimates of female populations to be exaggerated. This implies that lobster populations off the coast of Blyth are heavily skewed towards females, despite sex proportions of both fishery-independent and commercial catches being consistently equal (NIFCA data). These observations are attributable to the greater male catchability. However, additional factors are likely to be acting upon catch and catchability estimates, such as decreased likelihood of same sex pairings, creating an increase in the occurrence of individual lobsters and mixed sex pairings. This may lead to an unequal sex distribution appearing homogeneous, as seen in abundance data (Addison and Bell 1997). Increased male catchability could lead to fishery selection favouring the removal of males, driving the population further

in favour of females (Conover and Van Voorhees 1990; Allendorf and Hard 2009). UK *H. gammarus* catchabilities between portions of the population have been little considered, limiting the evidence and understanding to underpin management.

The short-term CMR approach is the first application of its kind to European lobster and it corroborated the common understanding that European lobsters have strong attachment to the site that they occupy (Smith, Jensen *et al.* 2001; Moland, Olsen *et al.* 2011; Moland, Olsen *et al.* 2011a). However, this single CMR study significantly impacts current knowledge only at the regional scale, albeit further replication over seasons, years, habitats and regions is desirable to clarify patterns. CMR can map distributions and provide further information on survival, emigration, site fidelity and density. It provides a useful baseline that catch data alone cannot provide, and the first nominal density estimates of UK lobster. CMR methods have the potential to be greatly improved by coupling outputs with acoustic telemetry findings. Mean home-range sizes for each sex could be used to produce unique capture areas for each sex; subsequently scaling abundance estimates to densities (Bell, Addison *et al.* 2001; Watson, Golet *et al.* 2009). These unique capture areas result in population estimates further skewed in favour of females; as female catches were theoretically drawn from a smaller capture area. However, without direct observations (not catch observations) of sex ratios in the study area, findings are difficult to verify. It is possible that findings could be explained by either intrinsic or extrinsic means, reflect as skewed population sex proportions and catchability behaviour (intrinsic), or limitations of the model design (extrinsic) (Crespin, Choquet *et al.* 2008).

Another aspect of catchability highlighted in this study is animal interactions around traps. Interactions between *H. gammarus* and *C. pagurus* were observed to have a dramatic impact on the subsequent ingress of *C. pagurus*. This could occur for two reasons: slight differences in habitat preference of the two species, and probably more importantly, avoidance behaviour of *C. pagurus* (Richards and Cobb 1987). Avoidance may be due to adult *H. gammarus* preying on juvenile *C. pagurus* (Evans and Mann 1977; Lawton 1987; Mente, Houlihan *et al.* 2001); lobster avoidance behaviour would increase crab survivability when young. Given the high prevalence and importance of mixed species trap fisheries within the UK, it is surprising that only one previous *in situ*

study focussed on lobster-crab interactions and catches (Addison 1995). The presence of one *H. gammarus* within a trap effectively halts the effort exerted by that trap upon *C. pagurus*. It is important that this information be utilised in *C. pagurus* stock assessments (Millar 1990; Carvalho, Ahrens *et al.* 2014), otherwise in these fisheries they will grossly underestimate crab stocks in some areas (Harley, Myers *et al.* 2001; Watson and Jury 2013).

6.1.2 Movement and behaviour

Estimates of *H. gammarus* site fidelity (philopatry) are often based on catch data alone and are rarely verified by other approaches. This study offers corroborating evidence of site fidelity between traps and telemetry within the same area. Both methods showed strong agreement that lobsters have high short-term site fidelity, with a minimum of 82% population site fidelity over 35 days from CMR and 84% population site fidelity over 45 days from telemetry. This confirms the European lobster's high site fidelity and low population turnover (Smith, Collins *et al.* 1998; Moland, Olsen *et al.* 2011; Schmalenbach, Mehrtens *et al.* 2011; Moland, Olsen *et al.* 2011a; Wiig, Moland *et al.* 2013). This may be partly due to their high reliance on shelter-providing refuge and strong diel cycles of activity (Howard 1980; Jensen, Collins *et al.* 1994; Smith, Collins *et al.* 1998; Smith, Collins *et al.* 1999), leading to small daily movements restricted to on or near shelter-providing habitat (Geraldi, Wahle *et al.* 2009; Moland, Olsen *et al.* 2011). Restricted movement could lead to adult lobster populations being more susceptible to localised changes of fishing effort and regulation, that even spatially restricted MPAs or other regulations are likely to have localised impacts (Rowe 2001) and regional management bye laws are likely effective. However, the present fidelity estimates only allow for a narrow understanding of lobster movement and behaviour, as they are restricted by their spatial and temporal resolution, and are likely to underestimate the transient portion of highly mobile lobsters.

Comparing results acquired using different techniques across the study reveals further details of movement and space and habitat utilisation. Traps set over soft substrate revealed little about lobster abundance, due to low lobster catch rates and

catchability, high trap saturation by crabs and difficulties in analysis. Significantly here, telemetry revealed that lobsters spent significant portions of time on soft substrate, but rarely within their restricted home-ranges. While it is understood that adult lobsters must use soft substrates due to occasional trap observation and the colonisation of artificial reefs removed from natural lobster habitat (Jensen, Collins *et al.* 1994; Smith, Collins *et al.* 1998; Galparsoro, Borja *et al.* 2009). Regular utilisation of soft sediments had yet to be demonstrated within the UK, probably due to the general use of baited traps as a sampling tool and reduced catchability over soft substrate (Tremblay and Smith 2001; Frusher and Hoenig 2003; Tremblay, Smith *et al.* 2006; Tremblay, Smith *et al.* 2009; Courchene and Stokesbury 2011; Hosack, Peters *et al.* 2013), coupled with the manner in which lobsters appear to utilise soft substrates, possibly as transit corridors (Beier and Noss 1998; Micheli and Peterson 1999; Debinski and Holt 2000; Gilliam and Fraser 2001). Acoustically tracked lobster altered their movement characteristics dramatically over soft substrates: from slow low-directionality movement typical of searching behaviour on hard and mixed substrate, to fast highly-directional movement on soft ground typical of exploratory behaviour (Turchin 1991; Wiens, Schooley *et al.* 1997). Typically searching behaviour is seen in animals encountering high prey densities or changes in habitat, that cause them to display area-restricted search behaviours, distinct from exploratory behaviour (Jonsen, Myers *et al.* 2007). Exploratory behaviour was observed on soft substrate patches possibly acting as corridors for small-scale migratory behaviour, allowing low energy movements and connecting distinct habitat patches (Zollner and Lima 1999), highlighting potential connectivity of lobster populations (Beier and Noss 1998; Turchin 1998; Geraldi, Wahle *et al.* 2009).

The benefit of movement between distinct patches must ultimately outweigh the cost of remaining resident within shelter (Levin, Cohen *et al.* 1984; Miller, Crowder *et al.* 1985); this could be driven by shortages of food, shelter, or increased competition for mates (Croft, Albanese *et al.* 2003; Pittman and McAlpine 2003; Austin, Bowen *et al.* 2004; Edgar, Barrett *et al.* 2004; Bowler and Benton 2005; Darden and Croft 2008). It is likely that these changes in movement characteristics may also cause a reduction in catchability over soft substrate, rendering the use of baited traps as monitoring tools

over these habitats less effective, as they under-estimate lobster presence (Tremblay and Smith 2001; Geraldi, Wahle *et al.* 2009; Courchene and Stokesbury 2011). This further highlights the need for managers and researchers to accept that baited traps sample only portions of the population at large, requiring studies to either increase in length of time or incorporate additional methods.

While home-range size, step-speed and turn-angle, varied with sex and substrate hardness, the overall distance and direction of movements are not so easily predicted. Despite, weak patterns suggesting larger lobsters are capable of the fastest and greatest movements, the literature often reports no relationship with size or sex, but rather with habitat (Rowe 2001; Golet, Scopel *et al.* 2006; Moland, Olsen *et al.* 2011a). Significant variability in individual lobster movement behaviour was observed in this study.

Movement behavioural types can be broadly categorised as residents (displaying area-restricted back and forth movement) and transients (displaying high mobility between fragmented or multiple home-ranges) (Bowlby, Hanson *et al.* 2007; Geraldi, Wahle *et al.* 2009). To date, these movement categories had rarely been displayed in *Homarus gammarus*. This variation was clearly seen in both telemetry and recapture studies; one individual was recaptured within 10m over three consecutive years, while another individual reportedly travelled over 60km in a single year. Variance is likely due to an individual's fitness and personality traits (Quinn and Brodeur 1991; Dieckmann, O'Hara *et al.* 1999; Skalski and Gilliam 2000; Fraser, Gilliam *et al.* 2001), which will influence habitat-utilisation and catchability as well as movement (Bowlby, Hanson *et al.* 2008; McMahan, Brady *et al.* 2013). Lobsters may undergo series of short-term behavioural changes; periods of searching behaviour within a home-range might result in higher catchability, while periods of transient behaviour, exploring new habitat for prey, mates, or shelter, might result in decreased catchability. There are also periods where they remain within shelter for long periods, most likely periods of vulnerability, such as spawning or ecdysis, where catchability is zero (Dunnington, Wahle *et al.* 2005).

Unpredictable variation of individual animal behaviours can have dramatic consequences for management and conservation approaches, as it cannot be assumed

that measures will impact all portions of the population equally (Shumway 1999; Lizarraga-Cubedo, Tuck *et al.* 2003; Egli and Babcock 2004; Botsford, Brumbaugh *et al.* 2009; Moland, Olsen *et al.* 2011a). For example, a small MPA may only offer protection to the resident portion of the population, or if the MPA is positioned on 'over-wintering' grounds may only protect lobster at the time of year they require least protection (Thomas 1968; Karnofsky, Atema *et al.* 1989). 'Personality profiles' have been used in large terrestrial mammal management, categorising portions of the population and analysing them individually and as a whole (Gold and Maple 1994; King and Figueredo 1997; Freeman and Gosling 2010). Furthermore there could be selective pressures acting differently on transient and catchable portions of the stock, favouring individuals with lower catchabilities. This further highlights the importance of applying a multiple-methods approach with various degrees of reliance on trapping of lobsters. The use of traps to gain data and samples biases data in favour of lobsters currently in a catchable state.

6.2 Limitations

Conducting work within the marine environment is often challenging, particularly in the North Sea. Poor weather, loss of equipment, limited vessel availability and interactions with other sea users impacted data collection during this study. Vessel availability led to surveys being conducted towards the end of the year, while locations of vessels, finances and logistics of sampling distant, multiple or long-term study sites, limited the study's extent. However, advances in passive tracking technology have helped alleviate some of these difficulties as once set, arrays remain *in situ* collecting data for extended periods. However, passive tracking is not without limitations (Catipovic 1990; Biesinger, Bolker *et al.* 2013). These will be discussed alongside more general limitations of the study in the following section.

6.2.1 Acoustic work

The study is somewhat limited in its temporal and spatial extent and resolution. This is often unavoidable when working with mobile marine animals (Kilfoyle and Baggeroer 2000; Eggleston, Herrnkind *et al.* 2013). The number of traps and acoustic

receivers available to the study also limited spatial coverage and resolution. Therefore it was appropriate to restrict studies to the vicinity of Blyth, which avoided large-scale spatial variability and limited the uncertainties introduced into analyses, while allowing for fine resolution assessments over small spatial scales. However, these spatial constraints must be borne in mind when interpreting the present results. Findings may be applied to European lobster populations more widely; however, it should not be taken for granted that they are directly applicable due to variations of biology, behaviour, environment and fisheries, between regions (Howard 1980; Tully and Ceidigh 1987; Lizarraga-Cubedo, Tuck *et al.* 2003; Woll, van der Meeren *et al.* 2006; Agnalt, Farestveit *et al.* 2009; O'Malley, Drazen *et al.* 2012).

6.2.2 Trap studies

Catchability and logistical limitations are largely unavoidable for studying commercial crustacea, especially as direct observations are often impossible. Baited traps create a selection bias in favour of animals in a 'catchable' state (White 1982; Krouse 1989; Miller 1990). Catchability of *Homarus* gammarus is understudied and lacks predictability. Further studies are required to either address catchability rates or to increase replication. Unequal soak times and effective effort exerted by traps are also effectively unavoidable in the North Sea, and weather limits most offshore studies. Estimating effective effort from trap catch data (Chapter 2) proved a relatively reliable method for scaling unequal soak times. The distribution of commercial fishing effort and extent of recapture reporting are also spatially heterogeneous (Turner, Gray *et al.* 2013; Turner, Polunin *et al.* 2014), and will bias results, but remain relatively uncertain. Uncertainties involved when using baited traps as a sampling tool raise two main questions, for this and previous studies (Smith and Tremblay 2003): to what degree is the entire population sampled, and can baited traps be more effectively implemented as a sole sampling tool?

A further limitation is the definition of environmental and habitat variables (Kenny, Cato *et al.* 2003; Elvenes, Dolan *et al.* 2013). Pre-existing habitat maps within the study area were unavailable or spatially inappropriate; therefore analysis was limited to substrate hardness data collected using commercial Olex systems. Ideally a higher

resolution metric for complexity or habitat type is required. Known to be important predictor of lobster abundance and distribution (Tremblay and Smith 2001; Galparsoro, Borja *et al.* 2009; Geraldi, Wahle *et al.* 2009; Tremblay, Smith *et al.* 2009; Chang, Chen *et al.* 2010; Hovel and Wahle 2010; Courchene and Stokesbury 2011), hardness values alone could be usefully augmented with multi-beam data of habitat structure for example. Olex data were deemed sufficient for the purpose of this study, but future work should consider methods that can reveal more habitat detail. Olex spatial resolution (ca. 5m) is not sufficient to identify small structures; for example, boulders on soft sediments of sufficient size to shelter lobster may be overlooked. Therefore, increased resolution and additional backscatter based parameters offered by more advanced acoustic systems (Kenny, Cato *et al.* 2003; Anderson, Van Holliday *et al.* 2008) would considerably enhance habitat discrimination.

Many of the limitations highlighted are somewhat unavoidable consequences of data collection in a temperate and turbid aquatic environment. However, impacts can be managed to some extent. Improvements in the trap survey design were made throughout the study: for example, increasing distance between traps to reduce trap interaction, maintaining equal soak time to minimise differences in effort and extending study periods to gain greater recapture numbers. Fishery-independent trap surveys should aim to use single traps distributed in a random stratified design (Smith and Tremblay 2003), with short (<48 hours) equal soak times (Bennett 1974a; Bennett and Brown 1979; Miller and Rodger 1996; Fogarty and Addison 1997). This would help avoid pseudo-replication (Hurlbert 1984), collinearity among variables, confounding environmental factors and site effects (Ewers and Didham 2006; Courchene and Stokesbury 2011). CMR methods were also refined and improved throughout the course of the study, via the application of permanent tags, increased effort and decreased soak times. The final method presented for 2012 is considered robust and the data sufficient for accurate CMR modelling. Early sampling suffered from too few captures and recaptures, caused by insufficient levels of sampling during winter, when movement and catchability are lowest. Such difficulties and limitations should be kept in mind when conclusions regarding a mobile and changeable population are drawn from catch data.

6.3 Wider implications

The findings presented have potentially important implications for understanding *H. gammarus*, associated fisheries and future management. Recent *H. gammarus* studies have been limited to analysis of commercial landings data or *ex situ* studies focused on aquaculture, genetics, physiology, diseases and pathology. Numerous gaps remain in the availability of data relevant to current management (Phillips 2013). In addition to the typically limited, and potentially inadequate, existing regulations, the work in this thesis suggests that the behaviour of lobsters and the sampling characteristics of traps may limit the capacity of the fishery to monitor stocks effectively and without bias. This not only threatens our capacity to manage stocks proactively, but may prevent fishers from responding reactively to changes in the relative abundance and dominance of individual species in a mixed fishery. (Berkes, Colding *et al.* 2000; Folke, Colding *et al.* 2003; Mahon, McConney *et al.* 2008; Miller and Breen 2010). Examples of the potentially detrimental impacts of reactive rather than proactive management can be seen in other clawed lobster fisheries. For example, the unprecedented increase and northward movement of *H. americanus* landings has resulted in hundreds of publications per year and greater monitoring and regulation efforts (Holland 2011), whereas in Norway the stock of *H. gammarus* subsided into a terminal decline that, initially, was not arrested owing to weak or inadequate management (Moksness 2004; van der Meeren, Knutsen *et al.* 2010), and even when regulation was later implemented, subsequent recovery has still been slow (Agnalt, Jørstad *et al.* 2004). Conversely, other lobster fisheries introduce pre-emptive regulation; for example, the *Panulirus cygnus* industry in Western Australia has long been regulated proactively in response to biological and population parameters (Caputi, Chubb *et al.* 1995; Caputi, de Lestang *et al.* 2014). This fishery has avoided any serious stock collapse to date. With this in mind, increased monitoring and data collection, particularly of larvae and pre-recruits, should be the aim of UK shellfish management, in order to help predict, prevent or manage changes that may occur.

This study begins to address the need for regional and national data collection. While there is some scope for transferability of findings to the wider UK population, the main

use of the data in this thesis should be as regionally specific reference points for continued and future monitoring efforts (Phillips 2005). Stock assessments should aim to be specific to biologically determined regions (Begg, Friedland *et al.* 1999; Cotter, Burt *et al.* 2004), or at least use localised parameters to account for potential spatial variability; these may be gained through spatially and temporally specific fishery-independent studies (Courchene and Stokesbury 2011). This would allow regionally specific management measures or regulations to be implemented in response to cues from the local population. This study provides the first density, site fidelity, catchability and home-range points of reference for Northumberland lobster; these are potentially useful as baselines for managers to monitor spatial or temporal patterns especially. However, because findings are specific to the method, study site and time of sampling, any extrapolation to regional or UK lobster populations may not be appropriate and should ideally be tested through replicated studies in the future.

CMR should be seen as an analysis procedure to inform managers or scientists of population processes gained from standard catch and recapture data, not as a stand-alone method for stock assessment. The approach can be applied during periodic fishery-independent trap and tagging surveys. Over time it should be possible to compare CMR outputs and local landings. Fishery-independent CMR also allows managers to assess the portion of the population below MLS (Cowan, Solow *et al.* 2001). Such data are unavailable from commercial landings, but are vital as it indicates the short-term future strength of the fishery. Continued tagging of lobsters for CMR studies at the same sites would also allow estimation of long-term migration, site fidelity, growth, and changes in density, recruitment, and possibly enable predictions of future landings, identifying years or regions of concern. With sufficient baseline data, CMR can also be applied to the monitoring of offshore installations, habitat and stock enhancement programs or conservation areas (Bannister, Addison *et al.* 1994; Jensen, Collins *et al.* 1994; Castro, Cobb *et al.* 2001; Dunnington, Wahle *et al.* 2005; Mills, Gardner *et al.* 2006; Schwartz, Luikart *et al.* 2007; Goni, Hilborn *et al.* 2010; Moland, Olsen *et al.* 2011; Schmalenbach, Mehrtens *et al.* 2011; Meisingset 2013; Moland, Olsen *et al.* 2013).

Reported changes in catchability due to soak time, differences between sexes, likelihood of sex-pairings, and inter-specific interactions, are all significant for the analysis of any trap catch data (Addison 1995; Hosack, Peters *et al.* 2013). The need for post-hoc standardisation of catch and effort data is well documented (Smith and Jamieson 1989; Maunder and Punt 2004), or at least their effects need to be considered. It is not appropriate to simply compare catches from traps directly (Starr and Vignaux 1997), as evidence suggests CPUE should not be modelled assuming proportionality to abundance (Harley, Myers *et al.* 2001; Watson and Jury 2013). Ignoring effects of variable catchability may cause spatial homogeneities to be overlooked. Aggregations of lobsters, whether by sex, size or catchability, may lead to portions of the stock being more or less vulnerable to targeted fishing (Kelly, MacDiarmid *et al.* 1999; Berkeley, Hixon *et al.* 2004; Sadovy and Domeier 2005), so are important to understand for management. Non-proportional demographics within catches have been reported (Miller 1990; Addison and Bell 1997). These can be particularly damaging when CPUE remains high while abundance declines, known as 'hyper-stability' (Hilborn and Walters 1992; Ward, Askey *et al.* 2013). Hyper-stability leads to overestimation of abundance (Crecco and Overholtz 1990), and subsequently mismanagement. With this in mind, it is vital to identify spatial relationships between fishing effort, CPUE, catchability, and sex and size aggregations of lobster populations (Steneck 2006; Myers, Smith *et al.* 2014). This should also be coupled with spatial understanding of the species composition of catches and fishermen behaviour (Wilen, Smith *et al.* 2002; Turner, Gray *et al.* 2013; Wiig, Moland *et al.* 2013; Carvalho, Ahrens *et al.* 2014; Turner, Polunin *et al.* 2014). For example, the inhibitory effect of *H. gammarus* presence on *C. pagurus* catches must be taken into consideration for UK stock assessments, to avoid under-estimating crab CPUE and abundance. This requires crab and lobster commercial landings data to have some spatial reference and be specific to the vessel, and occasion or individual trap-haul. Catchability parameters reported in this study may be used as a reference point by managers and researchers within the region, and techniques can be applied to any trap fishery data.

Identification of stock limits, or the 'unit stock', is also vital in order to more efficiently implement regulations, monitor enhancement or conservation programs and conduct

stock assessment (Begg, Friedland *et al.* 1999; Begg and Waldman 1999; Cadrin, Kerr *et al.* 2013). The majority of lobsters in this study were highly site specific, implying that localised management could be effective (Rowe 2001; Moland, Olsen *et al.* 2013). However, despite uncertainties, long distance recaptures and soft substrate exploratory behaviours highlight the potential for connectivity and wider dispersal of lobsters between populations or jurisdictional boundaries (Sale, Cowen *et al.* 2005; Bowlby, Hanson *et al.* 2008; Xue, Incze *et al.* 2008; Incze, Xue *et al.* 2010). On a local scale the potential for disorientation or homing behaviour of displaced V-notched lobsters should be addressed, and any negative impacts investigated (Herrnkind 1980).

Lobsters' use of habitat is a key determinant of distribution, movement and abundance (Courchene and Stokesbury 2011). These data are useful for stock assessments, marine spatial planning, and the design and implementation of spatial closures. The reported soft substrate utilisation requires management to take into consideration the importance and distribution of these habitats for maintaining lobster connectivity. It is also important to understand rates of emigration and site fidelity, particularly from habitats regularly targeted by fishermen, as they will affect conservation objectives. For example, high rates of emigration via soft substrates may not allow for complete protection in closed areas, but benefits to the adjacent fishery may be more likely (Kramer and Chapman 1999; Chapman and Kramer 2000; Jennings 2000; Edgar, Barrett *et al.* 2004; Moland, Olsen *et al.* 2011a). If closures aim for complete protection they may need to include several habitat patches. The study also highlights and reiterates the fact that fishery-independent catch rates and commercial landings are only representative of portions of the population at any one time.

6.4 Future considerations

Though this study addressed several key questions, new areas of interest were also highlighted. Firstly, can the difference in catchability between males and females be corroborated? Despite, similar findings reported from Norwegian studies (Wiig, Moland *et al.* 2013), catchability differences have not previously been linked to a skewed sex ratio. Therefore the sex skew inferred from modelling the Blyth lobster populations requires validation. Visual census via dive surveys could achieve this, while

remaining unaffected by catchability effects; however, these are not straight forward in the North Sea. If a population sex skew is discovered, the effect on behaviour and reproductive strength should be investigated. Increased catchability and less protection afforded to males could have major impacts on their mortality rates (Moland, Ulmestrand *et al.* 2013). This can lead to changes in fitness and selection pressure favouring smaller or slower growing males (Sato and Goshima 2006; Sato and Goshima 2007). The impact of strong size selective harvesting on reproduction and population parameters remains poorly understood for *Homarus* spp, but examples in other species exist (Baskett, Levin *et al.* 2005; Fenberg and Roy 2008; Allendorf and Hard 2009). If this is discovered to be the case in the UK, managers may need to re-address the level of male protection or regional MLS based on local size at maturity and fecundity (De Lestang, Caputi *et al.* 2009).

Maturity, sex and size frequency distributions are important areas of research for the Northumberland lobster stock, particularly as literature consistently reports smallest size at maturity within the North Sea (Free, Tyler *et al.* 1992; Tully 2001; Lizarraga-Cubedo, Tuck *et al.* 2003; Laurens, Fifas *et al.* 2009). There are also reports of increased male extraction rates over the past three years within Northumberland (CEFAS 2011). Small-skewed size distributions were also observed, with 78% of all lobster caught within the study being below MLS. However, this does not mean that these observations are a result of overexploitation. It should be investigated if local lobster populations are naturally skewed toward smaller lobster, i.e. if local environmental conditions lead to slower growth rates, allowing lobster to mature earlier. If regional differences are found, it could lead to EU-wide regulations, such as MLS, differing in effectiveness between regions. This further demonstrates the need for parameters such as sea temperature, local growth rates and size at maturity to be taken into account in stock assessment.

A further key determinant of stock structure and stock response to fishing pressures and conservation measures is movement, particularly the proportions of resident and transient behaviours exhibited. It would be useful to know the drivers of movement behaviour, particularly what prompts a switch between these behaviours. However,

there are numerous difficulties in quantifying these drivers, especially as they are likely to be subtle and not obvious to observation (Crespin, Choquet *et al.* 2008), or an interaction of numerous factors. Better understanding of environmental influences in combination with detailed habitat maps would greatly increase understanding of distribution. This could lead to advances in stock enhancement, conservation and management. Factors causing migration or higher densities could be monitored or managed in order to promote or suppress emigration or increase the carrying capacity of the habitat (Caddy and Stamatopoulos 1990; Addison and Bannister 1994).

A future application of acoustic telemetry would be to precisely understand movements and distributions, home-range size, trap interaction and catchability throughout the region and wider UK (Skajaa, Fernö *et al.* 1998; Watson, Golet *et al.* 2009; Di Lorenzo, Anna *et al.* 2014). This could be achieved through large-scale and long-term acoustic tagging studies, tagging both traps and lobster, and could incorporate habitat manipulation, to assess animal responses.

Another key area of research emerging in the UK is that of population genetics (André and Knutsen 2010; Huserbråten, Moland *et al.* 2013; Neenan, Hodgson *et al.* 2014), however, to date work remains largely unpublished. Data to support this could be collected during the annual V-notching programme. Genetic data from all the removed V-notch tissue could help identify UK stock distributions and phenotype distribution, adding to genetic databases that are being built throughout the UK. This database coupled with T-bar tagging would build a picture of female movement, how often they mate, number of male partners etc. Over time it could enable an indication to be got of the success of the V-notch programme, through monitoring the proportion of genes passed down by the V-notched animals into the landings. The use of T-bar tags should continue within the region, particularly with commercial fishermen involvement, where an economic incentive in order to gain recaptures can raise initial interest. This exercise is useful not only for the biological and behavioural data; but also as it increases stakeholder participation and connects scientist, manager and resource user. This in turn can improve management and increase the level of acceptance of future regulation, making the fishery more resilient to future changes.

Despite an increase in conservation programmes and bye-law regulations, the lack of proven effective measures means the level of control and understanding managers have of the UK lobster stock should be appraised. It is important that they identify what data are essential or useful and what data are missing. This might include priority data on EBP recruits, sources and sinks of larvae and post-larvae and identification of local breeding stock (Tully and Ceidigh 1987; Wahle and Incze 1997; Linnane, Ball *et al.* 2001; Mercer, Bannister *et al.* 2001; Sheehy and Prior 2008). Some areas are already being explored, such as stock structure and enhancement success via genetics. While in its infancy, it is beginning to provide data around the UK and spatial variation in egg-size, fecundity and size at maturity have been studied to some extent, and may soon be incorporated into stock assessments (Ulrich, Muller *et al.* 2001; Jørstad, Farestveit *et al.* 2005).

However, much of the research focus in the UK remains upon stock enhancement, aquaculture and *ex situ* studies. While important, greater effort could be implemented into *in situ* studies of behaviour and population parameters of adult lobsters, to ensure the continued sustainability of remaining natural stocks; this might help avoid the need for extensive enhancement programs, the impacts of which remain unclear (Araki and Schmid 2010). It should be kept in mind that UK, and specifically Northumberland, lobster landings are currently considered stable (CEFAS 2011). As one of the last regions within the species' range to maintain such landings (Phillips 2013), and given the location within the centre of the species range, it is vital to maintain the fishery at sustainable levels in order to enable the continued extraction of the resource on an EU wide scale.

6.5 Concluding remarks

This thesis provides some of Europe's first high-resolution lobster data gained from short-term CJS style CMR and VPS acoustic telemetry tracking. It offers novel insights into European lobster behaviour and catchability, and both approaches have great scope for extended future application. As pressures on shellfish increase, and possible effects of climate change begin to take effect, it is desirable to find ways of sustaining harvests of the stocks, and this requires more detailed regionally specific

data. The lack of these data should be recognised and research needs to continue to provide time-series and comparisons for this and future studies.

Measurements of lobster catches indicate differences in population structure between areas. The most likely factors driving this difference are habitat, movement, ambient environment and fishing pressure. However, stocks are often grouped by jurisdictional limits, rather than biophysical regions. It seems important that there be a move toward locally specific monitoring and management, informed by local environmental, biological, anthropogenic and population data. Inferences from other lobster species or from distinctly different areas should be avoided. However, the limited knowledge of some local lobster populations is likely to impede the development of the evidence-based regional-specific measures that are necessary for the future safeguarding of stocks.

Key findings from this work could aid future management decisions by providing a baseline and a framework of methods for data collection, allowing changes in the population dynamics, behaviour, and distribution of individuals, size frequencies and catch rates to be monitored.

Chapter 7:

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Appendix I: Publications, oral and poster presentations during PhD

Skerritt, D.J., Fitzsimmons, C., Polunin, N.V.C., Berney, P., Hardy, M.H. (2012) Investigating the impact of offshore wind farms on European Lobster (Homarus gammarus) and brown Crab (Cancer pagurus) fisheries. Report to the Marine Management Organisation June 2012. http://webarchive.nationalarchives.gov.uk/20130303193519/http://www.marinemanagement.org.uk///fisheries/funding/documents/fcf-lobstercrab.pdf

Skerritt, D.J., Fitzsimmons, C., Hardy, M.H., Polunin, N.V.C. (2013) Mapping European lobster (*Homarus gammarus*) movement and habitat-use via acoustic telemetry – Implications for management. Progress report to the Marine Management Organisation. Oct 2013. www.gov.uk/government/uploads/system/uploads/attachment_data/file/312996/fcf-europeanlobsters.pdf

Skerritt, D.J., Fitzsimmons, C., Polunin, N.V.C. Investigating European lobster (*Homarus gammarus*) populations in Northumberland, UK, via acoustic telemetry – Movement & Habitat-utilisation. The 10th International Conference and Workshop on Lobster Biology and Management. May 2014. Cancun. Mexico. Oral presentation.

Skerritt, D.J., Fitzsimmons, C., Polunin, N.V.C. Investigating European lobster (*Homarus gammarus*) movement & habitat-utilisation via acoustic telemetry. IMBER Open Science Conference. June 2014. Bergen, Norway. Oral presentation.

Skerritt, D.J., Fitzsimmons, C., Polunin, N.V.C. Investigating European lobster (*Homarus gammarus*) movement & habitat utilisation using acoustic telemetry. Institute of Fisheries Management Tagging & Telemetry Workshop. July, 2014. Leeds, UK. Oral presentation.

Skerritt, D.J., Fitzsimmons, C., Polunin, N.V.C., M.**C**. Bell. Estimating *Homarus gammarus* densities from continuous, short-term mark-recapture catch data**.** Institute of Fisheries Management Tagging & Telemetry Workshop. July, 2014. Leeds, UK. Poster presentation.

Appendix II: Successful grants written during PhD

Marine Management Organisation. Fisheries Challenge Fund. FES 255. Investigating the impact of offshore wind farms on European Lobster (*Homarus gammarus*) and brown Crab (*Cancer pagurus*) fisheries. (2010). **£38,574**.

Marine Management Organisation. Fisheries Challenge Fund. FES 289. Mapping Crustacean habitat-use and movement via acoustic telemetry - Implications for management. BH120694. (2012). **£46,641**.

British Ecological Society - Training and Travel Grant. (2014). Grant number: 4959-5999. **£500**.

Newcastle University - Student Conference Funding. (2014). **£1,665.**

Appendix III: CMR population modelling code

The following R code was provided by Dr Mike Bell.

```
##-------------------------------------------------------------------------
## R IMPLEMENTATION OF CORMACK-JOLLY-SEBER MODEL FOR MARK RECAPTURE DATA
##-------------------------------------------------------------------------
## Load required packages for variance-covariance estimation
require(MASS)     ## for ginv() function
require(Matrix)   ## for rankMatrix() function
require(maxLik)   ## maximum likelihood estimation
require(numDeriv) ## numerical derivatives for gradient and hessian estimation
## N.B. numDeriv must be loaded AFTER maxLik so that hessian function from maxLik is
masked
## by hessian function from numDeriv rather than vice versa
##-------------------------------------------------------------------------
## Likelihood and data transformation functions
## Returns log-likelihood for group structured CJS model
loglikCJS<-
function(p,PhiDesign,PDesign,marray,effort,dt,NRphi,NPphi,NRp,NPp,Ngroups,Nocc)
{
  ## Assemble structural parameters from design matrices
  mu<-c()
  for(i in 1:NRphi) {
    logit<-0
    for(j in 1:NPphi) {
      logit<-logit+p[j]*PhiDesign[i,j]
    }
    mu[i]<-(-log(1/(1+exp(-logit))))
  }
  q<-c()
  for(i in 1:NRp) {
    logit<-0
    for(j in 1:NPp) {
      logit<-logit+p[NPphi+j]*PDesign[i,j]
    }
    q[i]<-(-log(1-1/(1+exp(-logit))))
  }
  ## Convert into terms for the m-array probabilities
  ii<-0
  Pavailable<-c()
  Pcapture<-c()
  for(i in 1:Ngroups) {
    for(j in 1:Nocc) {
      ii<-ii+1
      F<-effort[j]*q[ii]
      Z<-F+dt[j]*mu[ii]
      Pavailable[ii]<-exp(-Z)
      Pcapture[ii]<-(1-Pavailable[ii])*F/Z
    }
  }
  ## Calculate likelihood
  LL<-0
  for(k in 1:Ngroups) {
    for(i in 1:Nocc) {
      NRprob<-1
      for(j in i:Nocc) {
        mprob<-Pcapture[(k-1)*Nocc+j]
        if(j>i) {
          j2<-j-1
          for(jj in i:j2) {
            mprob<-mprob*Pavailable[(k-1)*Nocc+jj]
          }
        }
        NRprob<-NRprob-mprob
        LL<-LL+marray[j,i,k]*log(mprob)
      }
```

```
      LL<-LL+marray[Nocc+1,i,k]*log(NRprob)
    }
  }

  return(LL)

}
## Convert logistic to continuous parameters
Logistic2Log<-function(p,NPphi,NPp)
{
  l<-c()
  for(i in 1:NPphi) {
    l[i]<-(-log(1/(1+exp(-p[i]))))
  }
  for(i in 1:NPp) {
    l[NPphi+i]<-(-log(1-1/(1+exp(-p[NPphi+i]))))
  }
  return(l)
}
## Convert continuous to logistic parameters
Log2Logistic<-function(l,NPphi,NPp)
{
  p<-c()
  for(i in 1:NPphi) {
    x<-exp(-l[i])
    if(x>0.999999999) {
      x<-0.999999999
    } else if(x<(1-0.999999999)) {
        x<-1-0.999999999
    }
    p[i]<-log(x/(1-x))
  }
  for(i in 1:NPp) {
    x<-1-exp(-l[NPphi+i])
    if(x>0.999999999) {
      x<-0.999999999
    }
    else if(x<(1-0.999999999)) {
        x<-1-0.999999999
    }
    p[NPphi+i]<-log(x/(1-x))
  }
  return(p)
}
## Convert logistic to sine transformed parameters
Logistic2Sin<-function(p,NPphi,NPp)
{
  s<-c()
  for(i in 1:NPphi) {
    x<-1/(1+exp(-p[i]))
    s[i]<-asin(2*x-1)
  }
  for(i in 1:NPp) {
    x<-1/(1+exp(-p[NPphi+i]))
    s[NPphi+i]<-asin(2*x-1)
  }
  return(s)
}
## Convert sine transformed to logistic parameters
Sin2Logistic<-function(s,NPphi,NPp)
{
  p<-c()
  for(i in 1:NPphi) {
    x<-(sin(s[i])+1)/2
    if(x>0.999999999) {
      x<-0.999999999
    } else if(x<(1-0.999999999)) {
```

```
        x<-1-0.999999999
    }
    p[i]<-log(x/(1-x))
  }
  for(i in 1:NPp) {
    x<-(sin(s[NPphi+i])+1)/2
    if(x>0.999999999) {
      x<-0.999999999
    }
    else if(x<(1-0.999999999)) {
        x<-1-0.999999999
    }
    p[NPphi+i]<-log(x/(1-x))
  }
  return(p)
}
## Likelihood function for model parameterised as continuous rate parameters
loglikCJSlog<-
function(p,PhiDesign,PDesign,marray,effort,dt,NRphi,NPphi,NRp,NPp,Ngroups,Nocc)
{
  ## Convert continuous back to logistic parameters so that design matrices work OK
  lp<-c()
  lp<-Log2Logistic(p,NPphi,NPp)

  ## Assemble structural parameters from design matrices
  mu<-c()
  for(i in 1:NRphi) {
    logit<-0
    for(j in 1:NPphi) {
      logit<-logit+lp[j]*PhiDesign[i,j]
    }
    mu[i]<-(-log(1/(1+exp(-logit))))
  }
  q<-c()
  for(i in 1:NRp) {
    logit<-0
    for(j in 1:NPp) {
      logit<-logit+lp[NPphi+j]*PDesign[i,j]
    }
    q[i]<-(-log(1-1/(1+exp(-logit))))
  }
  ## Convert into terms for the m-array probabilities
  ii<-0
  Pavailable<-c()
  Pcapture<-c()
  for(i in 1:Ngroups) {
    for(j in 1:Nocc) {
      ii<-ii+1
      F<-effort[j]*q[ii]
      Z<-F+dt[j]*mu[ii]
      Pavailable[ii]<-exp(-Z)
      Pcapture[ii]<-(1-Pavailable[ii])*F/Z
    }
  }
  ## Calculate likelihood
  LL<-0
  for(k in 1:Ngroups) {
    for(i in 1:Nocc) {
      NRprob<-1
      for(j in i:Nocc) {
        mprob<-Pcapture[(k-1)*Nocc+j]
        if(j>i) {
          j2<-j-1
          for(jj in i:j2) {
            mprob<-mprob*Pavailable[(k-1)*Nocc+jj]
          }
        }
```

```
        NRprob<-NRprob-mprob
        LL<-LL+marray[j,i,k]*log(mprob)
      }
      LL<-LL+marray[Nocc+1,i,k]*log(NRprob)
    }
  }
  return(LL)
}
## Likelihood function for model parameterised as sine transforms
loglikCJSsin<-
function(p,PhiDesign,PDesign,marray,effort,dt,NRphi,NPphi,NRp,NPp,Ngroups,Nocc)
{
  ## Convert continuous back to logistic parameters so that design matrices work OK
  lp<-c()
  lp<-Sin2Logistic(p,NPphi,NPp)

  ## Assemble structural parameters from design matrices
  mu<-c()
  for(i in 1:NRphi) {
    logit<-0
    for(j in 1:NPphi) {
      logit<-logit+lp[j]*PhiDesign[i,j]
    }
    mu[i]<-(-log(1/(1+exp(-logit))))
  }
  q<-c()
  for(i in 1:NRp) {
    logit<-0
    for(j in 1:NPp) {
      logit<-logit+lp[NPphi+j]*PDesign[i,j]
    }
    q[i]<-(-log(1-1/(1+exp(-logit))))
  }
  ## Convert into terms for the m-array probabilities
  ii<-0
  Pavailable<-c()
  Pcapture<-c()
  for(i in 1:Ngroups) {
    for(j in 1:Nocc) {
      ii<-ii+1
      F<-effort[j]*q[ii]
      Z<-F+dt[j]*mu[ii]
      Pavailable[ii]<-exp(-Z)
      Pcapture[ii]<-(1-Pavailable[ii])*F/Z
    }
  }
  ## Calculate likelihood
  LL<-0
  for(k in 1:Ngroups) {
    for(i in 1:Nocc) {
      NRprob<-1
      for(j in i:Nocc) {
        mprob<-Pcapture[(k-1)*Nocc+j]
        if(j>i) {
          j2<-j-1
          for(jj in i:j2) {
            mprob<-mprob*Pavailable[(k-1)*Nocc+jj]
          }
        }
        NRprob<-NRprob-mprob
        LL<-LL+marray[j,i,k]*log(mprob)
      }
      LL<-LL+marray[Nocc+1,i,k]*log(NRprob)
    }
  }

  return(LL)
```

```
}
##-------------------------------------------------------------------------------------
## Gradient and hessian functions
gradCJS<-
function(p,PhiDesign,PDesign,marray,effort,dt,NRphi,NPphi,NRp,NPp,Ngroups,Nocc)
{
  g<-
grad(loglikCJS,p,PhiDesign=PhiDesign,PDesign=PDesign,marray=marray,effort=effort,
          dt=dt,NRphi=NRphi,NPphi=NPphi,NRp=NRp,NPp=NPp,Ngroups=Ngroups,Nocc=Nocc)
  return(g)
}
hessCJS<-
function(p,PhiDesign,PDesign,marray,effort,dt,NRphi,NPphi,NRp,NPp,Ngroups,Nocc)
{
  h<-
hessian(loglikCJS,p,PhiDesign=PhiDesign,PDesign=PDesign,marray=marray,effort=effort,
             dt=dt,NRphi=NRphi,NPphi=NPphi,NRp=NRp,NPp=NPp,Ngroups=Ngroups,Nocc=Nocc)
  return(h)
}
##-------------------------------------------------------------------------------------
## Partial derivatives for calculating standard error of N
Nderiv<-function(f,q,t,mu,C)
{
  F<-f*q
  M<-t*mu
  Z<-F+M
  eM<-exp(M)
  eZ<-exp(Z)
  e2Z<-exp(2*Z)
  eF<-exp(F)
  n<-(-(M*e2Z+(F*F*eM+M*F*eM-M*eM)*eF)*C)
  d<-q*F*e2Z-2*q*F*eZ+q*F
  dNdq<-n/d
  n<-(t*eZ+((-t*M-t)*eM-F*t*eM)*eF)*C
  d<-F*e2Z-2*F*eZ+F
  dNdmu<-n/d
  dNdC<-(Z*eZ)/(F*eZ+F)
  return(list(dq=dNdq,dmu=dNdmu,dC=dNdC))
}

## Calculate N
Nhat<-function(f,q,t,mu,C)
{
  F<-f*q
  M<-t*mu
  Z<-F+M
  N<-C/((1-exp(-Z))*F/Z)
  return(N)
}

## Estimate standard error of N by delta method
Ndelta<-function(f,q,t,mu,C,varq,varmu,varc,covarqmu)
{
  dN<-Nderiv(f,q,t,mu,C)
  d<-c(dN$dq,dN$dmu,dN$dC)
  v<-array(c(varq,covarqmu,0,covarqmu,varmu,0,0,0,varc),dim=c(3,3))
  se<-sqrt(d%*%v%*%d)
  return(se)
}

## Convert logistic parameters to mu and q values
## Calculate logistic parameters from model terms
ConvertParms<-function(p,PhiDesign,PDesign,NRphi,NPphi,NRp,NPp)
{

  ## Assemble mu and q arrays from design matrices
```

```
  mu<-c()
  Slogistic<-c()
  for(i in 1:NRphi) {
    logit<-0
    for(j in 1:NPphi) {
      logit<-logit+p[j]*PhiDesign[i,j]
    }
    mu[i]<-(-log(1/(1+exp(-logit))))
    Slogistic[i]<-logit
  }
  q<-c()
  Plogistic<-c()
  for(i in 1:NRp) {
    logit<-0
    for(j in 1:NPp) {
      logit<-logit+p[NPphi+j]*PDesign[i,j]
    }
    q[i]<-(-log(1-1/(1+exp(-logit))))
    Plogistic[i]<-logit
  }
  return(list(mu=mu,q=q,logitS=Slogistic,logitP=Plogistic))
}

## Convert covariance matrix between logistic and log (mu and q) pararameters
## Calculate covariance matrix for stuctural paramaters on a logistic scale for CIs
ConvertCovar<-function(p,cov,PhiDesign,PDesign,NRphi,NPphi,NRp,NPp)
{

  ## Assemble partial derivatives from design matrices
  partial.qmu<-c(rep(0,times=(NRphi+NRp)*(NPphi+NPp)))
  dim(partial.qmu)<-c(NRphi+NRp,NPphi+NPp)
  partial.logistic<-c(rep(0,times=(NRphi+NRp)*(NPphi+NPp)))
  dim(partial.logistic)<-c(NRphi+NRp,NPphi+NPp)
  for(i in 1:NRphi) {
    logit<-0
    for(j in 1:NPphi) {
      logit<-logit+p[j]*PhiDesign[i,j]
    }
    for(j in 1:NPphi) {
      partial.qmu[i,j]<-PhiDesign[i,j]/(exp(logit)+1)
      partial.logistic[i,j]<-PhiDesign[i,j]
    }
  }
  for(i in 1:NRp) {
    logit<-0
    for(j in 1:NPp) {
      logit<-logit+p[NPphi+j]*PDesign[i,j]
    }
    for(j in 1:NPp) {
      partial.qmu[i+NRphi,j+NPphi]<-PDesign[i,j]*exp(logit)/(exp(logit)+1)
      partial.logistic[i+NRphi,j+NPphi]<-PDesign[i,j]
    }
  }

  ## Calculate the new covariance matrices
  cov.qmu<-array(c(rep(0,times=(NRphi+NRp)*(NRphi+NRp))),dim=c(NRphi+NRp,NRphi+NRp))
  cov.qmu<-partial.qmu%*%cov%*%t(partial.qmu)
  cov.logistic<-
array(c(rep(0,times=(NRphi+NRp)*(NRphi+NRp))),dim=c(NRphi+NRp,NRphi+NRp))
  cov.logistic<-partial.logistic%*%cov%*%t(partial.logistic)

  return(list(cov.qmu=cov.qmu,cov.logistic=cov.logistic))
}
##-------------------------------------------------------------------------------
## Fit the model and calculate model statistics
```

```
FitCJS<-
function(p,PhiDesign,PDesign,marray,effort,dt,NRphi,NPphi,NRp,NPp,Ngroups,Nocc)
{
  ## fit the model using logistic link function
  CJS<-maxLik(loglikCJS,grad=gradCJS,hess=hessCJS,start=p,method="BFGS",
          PhiDesign=PhiDesign,PDesign=PDesign,
          marray=marray,effort=effort,dt=dt,
          NRphi=NRphi,NPphi=NPphi,NRp=NRp,NPp=NPp,
          Ngroups=Ngroups,Nocc=Nocc)

  ## invert the model hessian to get variance-covariance matrix and parameter SEs
  var<-ginv(-CJS$hessian)
  se<-sqrt(diag(var))

  ## estimate number of model parameters using three different link functions
  rank1<-rankMatrix(CJS$hessian,method="maybeGrad")
  l<-Logistic2Log(CJS$estimate,NPphi,NPp)
  h<-hessian(loglikCJSlog,x=l,
          PhiDesign=PhiDesign,PDesign=PDesign,
          marray=marray,effort=effort,dt=dt,
          NRphi=NRphi,NPphi=NPphi,NRp=NRp,NPp=NPp,
          Ngroups=Ngroups,Nocc=Nocc)
  rank2<-rankMatrix(h,method="maybeGrad")
  s<-Logistic2Log(CJS$estimate,NPphi,NPp)
  h<-hessian(loglikCJSsin,x=s,
          PhiDesign=PhiDesign,PDesign=PDesign,
          marray=marray,effort=effort,dt=dt,
          NRphi=NRphi,NPphi=NPphi,NRp=NRp,NPp=NPp,
          Ngroups=Ngroups,Nocc=Nocc)
  rank3<-rankMatrix(h,method="maybeGrad")
  np<-max(rank1,rank2,rank3)
  AIC<-(-2*CJS$maximum)+2*np
  AICc<-AIC+2*np*(np-1)/(sum(marray)-np-1)

  return(list(CJS=CJS,var=var,se=se,np=np,AIC=AIC,AICc=AICc,
              PhiDesign=PhiDesign,PDesign=PDesign,effort=effort,dt=dt,
              NRphi=NRphi,NPphi=NPphi,NRp=NRp,NPp=NPp,Ngroups=Ngroups,Nocc=Nocc))
}
##------------------------------------------------------------------------------------
## Estimate population size from catch data
EstimateN<-function(C,Cvar,CJS)
{
  ## C is a vector of catch data (numbers) of length NPphi*Ngroups
  ## Cvar is a vector of variances for the catch data
  ## CJS is a fitted model object returned by FitCJS

  ## Convert the parameters to mu and q vectors and logistic structural parameters
  parm<-ConvertParms(CJS$CJS$estimate,PhiDesign=CJS$PhiDesign,PDesign=CJS$PDesign,
                     NRphi=CJS$NRphi,NPphi=CJS$NPphi,NRp=CJS$NRp,NPp=CJS$NPp)
  q<-parm$q
  mu<-parm$mu
  logitS<-parm$logitS
  logitP<-parm$logitP
  ## Convert the covariance matrix to the mu and q parameters
  var2<-
ConvertCovar(CJS$CJS$estimate,CJS$var,PhiDesign=CJS$PhiDesign,PDesign=CJS$PDesign,
                     NRphi=CJS$NRphi,NPphi=CJS$NPphi,NRp=CJS$NRp,NPp=CJS$NPp)
  ## Get SEs for the mu and q parameters and structural logistic parameters
  mu.se<-c()
  q.se<-c()
  logitS.se<-c()
  logitP.se<-c()
  for(i in 1:CJS$NRphi) {
    mu.se[i]<-sqrt(var2$cov.qmu[i,i])
    logitS.se[i]<-sqrt(var2$cov.logistic[i,i])
  }
  for(i in 1:CJS$NRp) {
```

```
    q.se[i]<-sqrt(var2$cov.qmu[CJS$NRphi+i,CJS$NRphi+i])
    logitP.se[i]<-sqrt(var2$cov.logistic[CJS$NRphi+i,CJS$NRphi+i])
  }
  ## Calculate 95% CI for structural parameters, based on logistic SEs
  logitS.l95<-logitS-1.96*logitS.se
  logitS.u95<-logitS+1.96*logitS.se
  mu.l95<-(-log(1/(1+exp(-logitS.u95))))
  mu.u95<-(-log(1/(1+exp(-logitS.l95))))
  logitP.l95<-logitP-1.96*logitP.se
  logitP.u95<-logitP+1.96*logitP.se
  q.l95<-(-log(1-1/(1+exp(-logitP.l95))))
  q.u95<-(-log(1-1/(1+exp(-logitP.u95))))
  ## Calculate the population estimates
  ## Calculate 95% C.I. for N assuming it is log-normally distributed
  N<-c()
  N.se<-c()
  N.l95<-c()
  N.u95<-c()
  ii<-0
  for(i in 1:CJS$NRphi) {
    ii<-ii+1
    if(ii>CJS$Nocc) {
      ii<-1
    }
    N[i]<-Nhat(CJS$effort[ii],q[i],CJS$dt[ii],mu[i],C[i])
    N.se[i]<-Ndelta(CJS$effort[ii],q[i],CJS$dt[ii],mu[i],C[i],

var2$cov.qmu[i,i],var2$cov.qmu[CJS$NRphi+i,CJS$NRphi+i],Cvar[i],var2$cov.qmu[i,CJS$NR
phi+i])
    selog<-sqrt((1/N[i])*(1/N[i])*N.se[i]*N.se[i])
    N.l95[i]<-exp(log(N[i])-1.96*selog)
    N.u95[i]<-exp(log(N[i])+1.96*selog)
  }
  return(list(mu=mu,mu.se=mu.se,mu.l95=mu.l95,mu.u95=mu.u95,
              q=q,q.se=q.se,q.l95=q.l95,q.u95=q.u95,

    logitS=logitS,logitS.se=logitS.se,logitS.l95=logitS.l95,logitS.u95=logitS.u95,

logitP=logitP,logitP.se=logitP.se,logitP.l95=logitP.l95,logitP.u95=logitP.u95,
              N=N,N.se=N.se,N.l95=N.l95,N.u95=N.u95))
}
```

Appendix IV: CMR population modelling output

```
> ## ------------------------------------------------------------------------
> ## CMR modelling output
> ## Northumberland lobster data for 2012
> ##------------------------------------------------------------------------
> ## Dimensions
> Nocc<-8
> Ngroups=2
>
> ## Read in m-arrays
> m<-scan(nmax=144)
1: 3 7 3 4 2 1 1 0 38
10: 0 1 3 2 2 2 1 1 25
19: 0 0 2 5 0 1 2 3 23
28: 0 0 0 1 1 1 3 0 28
37: 0 0 0 0 3 0 2 0 23
46: 0 0 0 0 0 0 0 1 58
55: 0 0 0 0 0 0 4 0 35
64: 0 0 0 0 0 0 0 0 38
73: 1 0 1 1 0 2 0 0 45
82: 0 1 0 1 1 1 3 1 32
91: 0 0 1 0 1 0 0 0 23
100: 0 0 0 1 0 1 1 0 29
109: 0 0 0 0 0 0 0 0 28
118: 0 0 0 0 0 1 1 1 60
127: 0 0 0 0 0 0 1 0 32
136: 0 0 0 0 0 0 0 1 37
Read 144 items
> dim(m)<-c(9,8,2)
>
> totaln<-sum(m)
>
> ## Read in effort and soak time data
> effort<-scan(nmax=8)
1: 2.611115377 3.256596476 2.611115377 4.713186849
5: 3.256596476 2.611115377 3.256596476 1.864227026
Read 8 items
> dt<-scan(nmax=8)
1: 3 4 3 7 4 3 4 2
Read 8 items
> ## Read in catch data
> C<-scan(nmax=16)
1: 37 36 34 23 60 40 37 18
9: 40 26 30 28 65 33 38 21
Read 16 items
>
> ## Calculate catch variances under an assumption of 20% CV
> Cvar<-(C*0.2)^2
>
> ##-------------------------------------------------------------------------------
> ## Model specification
> ## group*time
> NRgxt=16
> NPgxt=16
> gxtDesign<-scan(nmax=256)
1: 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
17: 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0
33: 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
49: 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0
65: 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0
81: 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0
97: 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0
113: 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0
129: 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0
145: 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0
```

```
161: 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0
177: 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0
193: 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0
209: 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0
225: 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
241: 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
Read 256 items
> dim(gxtDesign)<-c(16,16)
> gxtDesign<-t(gxtDesign)
> ################################
> ## group*time (last parameter constrained)
> NRgxtc=16
> NPgxtc=14
> gxtcDesign<-scan(nmax=224)
1: 1 0 0 0 0 0 0 0 0 0 0 0 0 0
15: 0 1 0 0 0 0 0 0 0 0 0 0 0 0
29: 0 0 1 0 0 0 0 0 0 0 0 0 0 0
43: 0 0 0 1 0 0 0 0 0 0 0 0 0 0
57: 0 0 0 0 1 0 0 0 0 0 0 0 0 0
71: 0 0 0 0 0 1 0 0 0 0 0 0 0 0
85: 0 0 0 0 0 0 1 0 0 0 0 0 0 0
99: 0 0 0 0 0 0 0 1 0 0 0 0 0 0
113: 0 0 0 0 0 0 0 0 1 0 0 0 0 0
127: 0 0 0 0 0 0 0 0 0 1 0 0 0 0
141: 0 0 0 0 0 0 0 0 0 0 1 0 0 0
155: 0 0 0 0 0 0 0 0 0 0 0 1 0 0
169: 0 0 0 0 0 0 0 0 0 0 0 0 1 0
183: 0 0 0 0 0 0 0 0 0 0 0 0 0 1
197: 0 0 0 0 0 0 0 0 0 0 0 0 0 0
211: 0 0 0 0 0 0 0 0 0 0 0 0 0 1
Read 224 items
> dim(gxtcDesign)<-c(14,16)
> gxtcDesign<-t(gxtcDesign)
> ################################
> ## group+time
> NRgat=16
> NPgat=9
> gatDesign<-scan(nmax=144)
1: 1 0 0 0 0 0 0 0 0
10: 0 1 0 0 0 0 0 0 0
19: 0 0 1 0 0 0 0 0 0
28: 0 0 0 1 0 0 0 0 0
37: 0 0 0 0 1 0 0 0 0
46: 0 0 0 0 0 1 0 0 0
55: 0 0 0 0 0 0 1 0 0
64: 0 0 0 0 0 0 0 1 0
73: 1 0 0 0 0 0 0 0 1
82: 0 1 0 0 0 0 0 0 1
91: 0 0 1 0 0 0 0 0 1
100: 0 0 0 1 0 0 0 0 1
109: 0 0 0 0 1 0 0 0 1
118: 0 0 0 0 0 1 0 0 1
127: 0 0 0 0 0 0 1 0 1
136: 0 0 0 0 0 0 0 1 1
Read 144 items
> dim(gatDesign)<-c(9,16)
> gatDesign<-t(gatDesign)
> ################################
> ## time
> NRt=16
> NPt=8
> tDesign<-scan(nmax=128)
1: 1 0 0 0 0 0 0 0
9: 0 1 0 0 0 0 0 0
17: 0 0 1 0 0 0 0 0
25: 0 0 0 1 0 0 0 0
33: 0 0 0 0 1 0 0 0
```

```
41: 0 0 0 0 0 1 0 0
49: 0 0 0 0 0 0 1 0
57: 0 0 0 0 0 0 0 1
65: 1 0 0 0 0 0 0 0
73: 0 1 0 0 0 0 0 0
81: 0 0 1 0 0 0 0 0
89: 0 0 0 1 0 0 0 0
97: 0 0 0 0 1 0 0 0
105: 0 0 0 0 0 1 0 0
113: 0 0 0 0 0 0 1 0
121: 0 0 0 0 0 0 0 1
Read 128 items
> dim(tDesign)<-c(8,16)
> tDesign<-t(tDesign)
> ################################
> ## time (last parameter constrained)
> NRtc=16
> NPtc=7
> tcDesign<-scan(nmax=112)
1: 1 0 0 0 0 0 0
8: 0 1 0 0 0 0 0
15: 0 0 1 0 0 0 0
22: 0 0 0 1 0 0 0
29: 0 0 0 0 1 0 0
36: 0 0 0 0 0 1 0
43: 0 0 0 0 0 0 1
50: 0 0 0 0 0 0 1
57: 1 0 0 0 0 0 0
64: 0 1 0 0 0 0 0
71: 0 0 1 0 0 0 0
78: 0 0 0 1 0 0 0
85: 0 0 0 0 1 0 0
92: 0 0 0 0 0 1 0
99: 0 0 0 0 0 0 1
106: 0 0 0 0 0 0 1
Read 112 items
> dim(tcDesign)<-c(7,16)
> tcDesign<-t(tcDesign)
> ################################
> ## group
> NRg=16
> NPg=2
> gDesign<-scan(nmax=32)
1: 1 0
3: 1 0
5: 1 0
7: 1 0
9: 1 0
11: 1 0
13: 1 0
15: 1 0
17: 0 1
19: 0 1
21: 0 1
23: 0 1
25: 0 1
27: 0 1
29: 0 1
31: 0 1
Read 32 items
> dim(gDesign)<-c(2,16)
> gDesign<-t(gDesign)
> ################################
> ## constant
> NRc=16
> NPc=1
> cDesign<-scan(nmax=16)
```

```
1: 1
2: 1
3: 1
4: 1
5: 1
6: 1
7: 1
8: 1
9: 1
10: 1
11: 1
12: 1
13: 1
14: 1
15: 1
16: 1
Read 16 items
> dim(cDesign)<-c(1,16)
> cDesign<-t(cDesign)
> ################################
>
> ##------------------------------------------------------------------------------------
> ## Estimate Model Phi(group*time),P(group*time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=14),rep(-2,times=16))
>
> ## Fit the model
> SgxtPgxt<-FitCJS(p,
+           PhiDesign=gxtcDesign,PDesign=gxtDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRgxtc,NPphi=NPgxtc,NRp=NRgxt,NPp=NPgxt,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SgxtPgxt)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -356.04
> np
[1] 30
> AIC
[1] 772.0801
> AICc
[1] 774.9419
> detach(SgxtPgxt)
>
> ## Estimate population size from catch
> NSgxtPgxt<-EstimateN(C,Cvar,SgxtPgxt)
> attach(NSgxtPgxt)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N       N.se        N.l95        N.u95
 [1,]  727.6690   470.2710 2.050300e+02 2.582560e+03
 [2,]  418.5001   173.7856 1.854473e+02 9.444315e+02
 [3,]  514.2424   201.8957 2.382172e+02 1.110101e+03
 [4,]  281.7473   115.7848 1.259069e+02 6.304777e+02
 [5,] 1222.5024   517.7308 5.330384e+02 2.803761e+03
 [6,] 1712.0561 30431.7490 1.268109e-12 2.311423e+18
 [7,]  597.9007   381.6018 1.711400e+02 2.088847e+03
 [8,]  846.2765   539.9820 2.423136e+02 2.955607e+03
 [9,] 1999.8710 37658.8647 1.870819e-13 2.137825e+19
[10,] 1897.4297  2381.4880 1.621035e+02 2.220952e+04
[11,] 1454.6629  1208.0524 2.856623e+02 7.407503e+03
[12,] 1185.1091  1033.1947 2.146126e+02 6.544273e+03
```

```
[13,] 4939.2627  4318.7397 8.899876e+02 2.741197e+04
[14,] 1405.7100  1040.8394 3.293239e+02 6.000235e+03
[15,] 1526.2441 34732.2655 6.497360e-17 3.585180e+22
[16,]  798.0601 12502.4634 3.688160e-11 1.726877e+16
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se       mu.l95       mu.u95
 [1,] 1.242564e-07 2.286490e-13 1.242560e-07 1.242569e-07
 [2,] 1.331385e-07 1.137705e-10 1.329157e-07 1.333616e-07
 [3,] 2.000222e-11 4.423164e-16 2.000133e-11 2.000289e-11
 [4,] 6.696956e-10 1.952468e-13 6.693130e-10 6.700784e-10
 [5,] 3.720579e-12 7.875003e-16 3.719025e-12 3.722134e-12
 [6,] 6.593512e-02 1.800869e-01 2.698099e-04 2.902251e+00
 [7,] 1.397650e-09 3.824492e-13 1.396900e-09 1.398400e-09
 [8,] 1.397650e-09 3.824492e-13 1.396900e-09 1.398400e-09
 [9,] 1.305745e-01 1.784896e-01 7.972468e-03 1.232740e+00
[10,] 1.045297e-11 6.870127e-16 1.045164e-11 1.045430e-11
[11,] 5.256151e-11 4.451403e-14 5.247425e-11 5.264877e-11
[12,] 6.146195e-12 3.019128e-15 6.140422e-12 6.152190e-12
[13,] 3.041929e-08 6.732663e-12 3.040610e-08 3.043249e-08
[14,] 7.431192e-06 4.966097e-03 0.000000e+00          Inf
[15,] 2.779812e-01 2.984793e-01 2.835987e-02 1.519524e+00
[16,] 2.779812e-01 2.984793e-01 2.835987e-02 1.519524e+00
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q         q.se         q.l95      q.u95
 [1,] 0.019985938 0.011540215 0.0064156807 0.06139140
 [2,] 0.027620322 0.009768553 0.0137726379 0.05501339
 [3,] 0.026197145 0.009263829 0.0130661440 0.05218447
 [4,] 0.018068173 0.005217383 0.0102468656 0.03176531
 [5,] 0.015453245 0.005464130 0.0077159368 0.03083061
 [6,] 0.009986761 0.005181764 0.0036052671 0.02750947
 [7,] 0.019615819 0.010524840 0.0068261581 0.05570998
 [8,] 0.011532449 0.006933168 0.0035396588 0.03724040
 [9,] 0.009364260 0.009651026 0.0012354973 0.06915191
[10,] 0.004236784 0.004359355 0.0005625158 0.03153485
[11,] 0.007980868 0.005829213 0.0019017756 0.03317211
[12,] 0.005073022 0.003013755 0.0015814476 0.01621117
[13,] 0.004067811 0.002915029 0.0009972328 0.01651522
[14,] 0.009097986 0.004139647 0.0037242528 0.02214013
[15,] 0.012886292 0.008250519 0.0036611576 0.04484059
[16,] 0.018693027 0.023087154 0.0016376529 0.19657485
> detach(NSgxtPgxt)
>
> ##-------------------------------------------------------------------------------
> ## Estimate Model Phi(group*time),P(group+time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=16),rep(-2,times=9))
>
> ## Fit the model
> SgxtPgat<-FitCJS(p,
+           PhiDesign=gxtDesign,PDesign=gatDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRgxt,NPphi=NPgxt,NRp=NRgat,NPp=NPgat,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SgxtPgat)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -357.656
> np
[1] 25
> AIC
```

```
[1] 765.3121
> AICc
[1] 767.2697
> detach(SgxtPgat)
>
> ## Estimate population size from catch
> NSgxtPgat<-EstimateN(C,Cvar,SgxtPgat)
> attach(NSgxtPgat)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N       N.se        N.l95        N.u95
 [1,]  684.2895   385.0253 2.271383e+02 2.061529e+03
 [2,]  477.4842   191.7732 2.173114e+02 1.049145e+03
 [3,]  532.5560   191.1725 2.635132e+02 1.076287e+03
 [4,]  297.6192   113.7111 1.407464e+02 6.293390e+02
 [5,] 1314.5555   512.5626 6.121785e+02 2.822798e+03
 [6,] 1264.2409 11077.7109 4.397178e-05 3.634843e+10
 [7,]  441.8873   208.3061 1.754070e+02 1.113207e+03
 [8,]  671.6291 29520.5635 2.588283e-35 1.742799e+40
 [9,] 2476.7990 53543.7976 9.820988e-16 6.246351e+21
[10,]  897.7207   469.2991 3.222201e+02 2.501093e+03
[11,] 1227.4858   576.2465 4.891142e+02 3.080510e+03
[12,]  944.6458   503.7726 3.321400e+02 2.686686e+03
[13,] 3754.9208  1847.8223 1.431235e+03 9.851233e+03
[14,] 2143.7695   959.6842 8.914983e+02 5.155083e+03
[15,] 1650.9767 40775.0748 1.565903e-18 1.740672e+24
[16,] 1042.4767  1024.6685 1.518414e+02 7.157190e+03
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se       mu.l95       mu.u95
 [1,] 2.987460e-07 3.209955e-04 0.000000e+00          Inf
 [2,] 3.597225e-07 2.625755e-04 0.000000e+00          Inf
 [3,] 5.874932e-10 1.157749e-12 5.852283e-10 5.897667e-10
 [4,] 1.041389e-13 1.390785e-16 1.039169e-13 1.043610e-13
 [5,] 9.556766e-10 1.855344e-12 9.520469e-10 9.593200e-10
 [6,] 1.757117e-01 1.420281e-01 3.356959e-02 7.327853e-01
 [7,] 2.131935e-08 9.998810e-11 2.112428e-08 2.151623e-08
 [8,] 7.850739e-01 1.304799e+00 1.076842e-02 4.885551e+00
 [9,] 1.703258e-01 1.740910e-01 2.079868e-02 9.710341e-01
[10,] 1.888922e-10 3.671155e-13 1.881739e-10 1.896132e-10
[11,] 4.397829e-10 7.058823e-14 4.396445e-10 4.399212e-10
[12,] 2.049028e-12 3.182383e-15 2.042810e-12 2.055245e-12
[13,] 4.232299e-10 8.911235e-13 4.214871e-10 4.249803e-10
[14,] 1.176609e-08 1.431123e-11 1.173807e-08 1.179417e-08
[15,] 1.809935e-01 2.525800e-01 9.925885e-03 1.598638e+00
[16,] 4.367939e-04 3.166304e-06 4.306318e-04 4.430441e-04
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q         q.se        q.l95       q.u95
 [1,] 0.021288776 0.010717173 0.007906193 0.05669043
 [2,] 0.024070804 0.008183732 0.012335247 0.04671363
 [3,] 0.025265882 0.008158881 0.013389328 0.04743024
 [4,] 0.017064761 0.004570298 0.010085439 0.02880484
 [5,] 0.014345425 0.004661634 0.007578590 0.02707305
 [6,] 0.015887032 0.005805987 0.007749160 0.03243352
 [7,] 0.026852000 0.010767724 0.012196234 0.05861044
 [8,] 0.029082518 0.027323219 0.004545331 0.17491840
 [9,] 0.007974740 0.004583276 0.002580598 0.02450673
[10,] 0.009024735 0.003897963 0.003865777 0.02099653
[11,] 0.009476341 0.003920265 0.004207027 0.02127565
[12,] 0.006383983 0.002327111 0.003122629 0.01302946
[13,] 0.005362101 0.002167170 0.002426710 0.01182725
[14,] 0.005941199 0.002332924 0.002749965 0.01281209
[15,] 0.010076236 0.004392299 0.004281877 0.02361962
[16,] 0.010920853 0.010545401 0.001636159 0.07104931
> detach(NSgxtPgat)
> ##---------------------------------------------------------------------------
```

```
> ## Estimate Model Phi(group*time),P(group)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=16),rep(-2,times=2))
>
> ## Fit the model
> SgxtPg<-FitCJS(p,
+           PhiDesign=gxtDesign,PDesign=gDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRgxt,NPphi=NPgxt,NRp=NRg,NPp=NPg,
+           Ngroups=Ngroups,Nocc=Nocc)
Warning message:
In sqrt(diag(var)) : NaNs produced
>
> ## Model selection criteria
> attach(SgxtPg)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -359.5337
> np
[1] 18
> AIC
[1] 755.0674
> AICc
[1] 756.0545
> detach(SgxtPg)
>
> ## Estimate population size from catch
> NSgxtPg<-EstimateN(C,Cvar,SgxtPg)
Warning messages:
1: In sqrt(var2$cov.qmu[i, i]) : NaNs produced
2: In sqrt(var2$cov.logistic[i, i]) : NaNs produced
3: In sqrt(d %*% v %*% d) : NaNs produced
> attach(NSgxtPg)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N        N.se        N.l95        N.u95
 [1,]  761.8211   129.74638 5.456089e+02 1.063713e+03
 [2,]  597.9489   109.01802 4.182829e+02 8.547870e+02
 [3,]  700.0517   119.22709 5.013693e+02 9.774678e+02
 [4,]  267.6041    57.75735 1.752966e+02 4.085189e+02
 [5,]  996.5801   180.35598 6.989776e+02 1.420892e+03
 [6,]  965.7566  5146.55499 2.809943e-02 3.319233e+07
 [7,]  614.5577   111.21956 4.310361e+02 8.762170e+02
 [8,]  768.6975 22545.53779 8.316731e-23 7.104904e+27
 [9,] 2800.8839 69069.09773 2.860827e-18 2.742197e+24
[10,] 1166.0892   391.10570 6.042741e+02 2.250244e+03
[11,] 1674.3652   525.79656 9.047835e+02 3.098530e+03
[12,]  872.0585   351.42600 3.958388e+02 1.921201e+03
[13,] 2915.2221   976.48979 1.511979e+03 5.620791e+03
[14,] 1841.8121   636.14251 9.359311e+02 3.624489e+03
[15,] 1844.4917 38067.54112 4.989199e-15 6.819030e+20
[16,] 1639.5610         NaN          NaN          NaN
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se       mu.l95       mu.u95
 [1,] 1.047643e-07 3.708583e-10 1.040399e-07 1.054937e-07
 [2,] 6.950212e-07 4.582546e-04 0.000000e+00          Inf
 [3,] 9.997725e-09 5.830998e-12 9.986303e-09 1.000916e-08
 [4,] 1.355820e-07 7.262672e-10 1.341660e-07 1.370130e-07
 [5,] 5.827457e-09 1.650566e-12 5.824223e-09 5.830693e-09
 [6,] 1.100983e-01 1.042113e-01 1.627420e-02 6.019158e-01
 [7,] 1.182587e-11 3.256562e-15 1.181966e-11 1.183231e-11
 [8,] 4.333029e-01 5.678338e-01 2.263471e-02 2.628170e+00
 [9,] 1.579087e-01 1.722034e-01 1.682653e-02 1.002251e+00
```

```
[10,] 1.861871e-07 1.224460e-04 0.000000e+00          Inf
[11,] 4.148015e-12 7.466528e-16 4.146461e-12 4.149348e-12
[12,] 5.875245e-09 1.019238e-12 5.873248e-09 5.877243e-09
[13,] 1.518257e-08 9.108455e-12 1.516473e-08 1.520043e-08
[14,] 3.774794e-06 1.011744e-03 0.000000e+00 5.128455e+02
[15,] 4.021958e-02 1.446318e-01 3.091731e-05 4.015922e+00
[16,] 1.320634e-03          NaN          NaN          NaN
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q        q.se       q.l95      q.u95
 [1,] 0.019067290 0.002896738 0.014151552 0.02566879
 [2,] 0.019067290 0.002896738 0.014151552 0.02566879
 [3,] 0.019067290 0.002896738 0.014151552 0.02566879
 [4,] 0.019067290 0.002896738 0.014151552 0.02566879
 [5,] 0.019067290 0.002896738 0.014151552 0.02566879
 [6,] 0.019067290 0.002896738 0.014151552 0.02566879
 [7,] 0.019067290 0.002896738 0.014151552 0.02566879
 [8,] 0.019067290 0.002896738 0.014151552 0.02566879
 [9,] 0.006924127 0.001909686 0.004031001 0.01188141
[10,] 0.006924127 0.001909686 0.004031001 0.01188141
[11,] 0.006924127 0.001909686 0.004031001 0.01188141
[12,] 0.006924127 0.001909686 0.004031001 0.01188141
[13,] 0.006924127 0.001909686 0.004031001 0.01188141
[14,] 0.006924127 0.001909686 0.004031001 0.01188141
[15,] 0.006924127 0.001909686 0.004031001 0.01188141
[16,] 0.006924127 0.001909686 0.004031001 0.01188141
> detach(NSgxtPg)
>
> ##-------------------------------------------------------------------------------------
> ## Estimate Model Phi(group*time),P(time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=16),rep(-2,times=8))
>
> ## Fit the model
> SgxtPt<-FitCJS(p,
+           PhiDesign=gxtDesign,PDesign=tDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRgxt,NPphi=NPgxt,NRp=NRt,NPp=NPt,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SgxtPt)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -362.8761
> np
[1] 24
> AIC
[1] 773.7522
> AICc
[1] 775.5503
> detach(SgxtPt)
>
> ## Estimate population size from catch
> NSgxtPt<-EstimateN(C,Cvar,SgxtPt)
> attach(NSgxtPt)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N       N.se        N.l95        N.u95
 [1,]  837.7500   475.4505 2.754361e+02 2.548050e+03
 [2,]  602.7769   242.9637 2.735603e+02 1.328190e+03
 [3,]  667.9049   241.1407 3.291477e+02 1.355310e+03
 [4,]  378.2297   148.8292 1.749086e+02 8.178999e+02
 [5,] 1726.0607   677.4110 7.998099e+02 3.724992e+03
```

```
 [6,] 1632.1338 23175.7596 1.335837e-09 1.994150e+15
 [7,]  683.1149   323.4789 2.700303e+02 1.728124e+03
 [8,]  917.8944 55927.7755 1.252259e-49 6.728083e+54
 [9,] 1432.0580 13840.4303 8.495525e-06 2.413965e+11
[10,]  435.3449   180.4877 1.931662e+02 9.811509e+02
[11,]  637.7254  3463.7204 1.518313e-02 2.678590e+07
[12,]  460.4536   181.1832 2.129324e+02 9.957034e+02
[13,] 1869.8994   733.8554 8.664669e+02 4.035381e+03
[14,] 1288.5377   976.3670 2.918113e+02 5.689736e+03
[15,] 1240.1282 16464.2645 6.201343e-09 2.479975e+14
[16,]  658.7832   561.5232 1.239354e+02 3.501786e+03
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se       mu.l95       mu.u95
 [1,] 1.107758e-11 1.686595e-17 1.107758e-11 1.107758e-11
 [2,] 3.147369e-09 3.713419e-14 3.147296e-09 3.147442e-09
 [3,] 5.173417e-12 7.898993e-18 5.173417e-12 5.173417e-12
 [4,] 7.604117e-11 1.296928e-16 7.604095e-11 7.604140e-11
 [5,] 8.806289e-13 2.795522e-19 8.806289e-13 8.806289e-13
 [6,] 2.969865e-02 1.431973e-01 2.059010e-06 6.092012e+00
 [7,] 2.998402e-11 5.732841e-16 2.998291e-11 2.998513e-11
 [8,] 5.361380e-01 1.073278e+00 4.451187e-03 4.734491e+00
 [9,] 3.359172e-01 1.704038e-01 1.167443e-01 8.272667e-01
[10,] 7.026994e-06 1.934499e-03 0.000000e+00 5.277151e+02
[11,] 5.380867e-02 1.117301e-01 8.451431e-04 1.529233e+00
[12,] 9.222886e-09 1.587938e-11 9.191815e-09 9.254063e-09
[13,] 7.876089e-08 3.156912e-10 7.814456e-08 7.938208e-08
[14,] 1.090811e-05 6.622786e-03 0.000000e+00          Inf
[15,] 3.217686e-01 2.321596e-01 7.009941e-02 1.093275e+00
[16,] 4.607794e-06 2.184422e-10 4.607366e-06 4.608222e-06
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
               q         q.se       q.l95      q.u95
 [1,] 0.01729948 0.008740991 0.006405805 0.04629488
 [2,] 0.01890974 0.006399772 0.009724523 0.03661339
 [3,] 0.02000940 0.006454224 0.010615848 0.03756030
 [4,] 0.01331096 0.003639132 0.007782917 0.02272111
 [5,] 0.01086404 0.003533288 0.005737990 0.02052270
 [6,] 0.00993618 0.003400040 0.005076336 0.01940369
 [7,] 0.01709936 0.006778822 0.007845959 0.03706569
 [8,] 0.01737784 0.014036730 0.003543673 0.08301838
 [9,] 0.01729948 0.008740991 0.006405805 0.04629488
[10,] 0.01890974 0.006399772 0.009724523 0.03661339
[11,] 0.02000940 0.006454224 0.010615848 0.03756030
[12,] 0.01331096 0.003639132 0.007782917 0.02272111
[13,] 0.01086404 0.003533288 0.005737990 0.02052270
[14,] 0.00993618 0.003400040 0.005076336 0.01940369
[15,] 0.01709936 0.006778822 0.007845959 0.03706569
[16,] 0.01737784 0.014036730 0.003543673 0.08301838
> detach(NSgxtPt)
>
> ##------------------------------------------------------------------------------
> ## Estimate Model Phi(group*time),P(constant)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=16),rep(-2,times=1))
>
> ## Fit the model
> SgxtP<-FitCJS(p,
+           PhiDesign=gxtDesign,PDesign=cDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRgxt,NPphi=NPgxt,NRp=NRc,NPp=NPc,
+           Ngroups=Ngroups,Nocc=Nocc)
Warning message:
In sqrt(diag(var)) : NaNs produced
>
> ## Model selection criteria
```

```
> attach(SgxtP)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -364.954
> np
[1] 17
> AIC
[1] 763.9081
> AICc
[1] 764.7841
> detach(SgxtP)
>
> ## Estimate population size from catch
> NSgxtP<-EstimateN(C,Cvar,SgxtP)
Warning messages:
1: In sqrt(var2$cov.qmu[i, i]) : NaNs produced
2: In sqrt(var2$cov.logistic[i, i]) : NaNs produced
3: In sqrt(d %*% v %*% d) : NaNs produced
> attach(NSgxtP)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N        N.se        N.l95        N.u95
 [1,]  997.1346   164.41697 7.217670e+02 1.377560e+03
 [2,]  781.5210   139.94115 5.501987e+02 1.110099e+03
 [3,]  916.2974   154.32645 6.586748e+02 1.274682e+03
 [4,]  348.6318    73.95701 2.300350e+02 5.283722e+02
 [5,] 1302.5703   250.38552 8.936689e+02 1.898566e+03
 [6,] 1107.2663  7736.31891 1.250011e-03 9.808226e+08
 [7,]  803.2177   144.94913 5.639260e+02 1.144048e+03
 [8,]  942.3785 35962.91197 3.091711e-30 2.872446e+35
 [9,] 1629.1831 18762.00297 2.565549e-07 1.034569e+13
[10,]  564.4411   128.31836 3.614976e+02 8.813163e+02
[11,]  874.3781  8662.34573 3.227051e-06 2.369151e+11
[12,]  444.0410  2342.35803 1.436061e-02 1.373009e+07
[13,] 1527.1343 13154.33839 7.107443e-05 3.281263e+10
[14,]  890.1498         NaN          NaN          NaN
[15,] 1208.9846 16329.38009 3.848527e-09 3.797930e+14
[16,]  817.0388 44038.09091 1.076339e-43 6.202063e+48
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se       mu.l95      mu.u95
 [1,] 2.743326e-06 0.0004185286 0.000000e+00 286.2165031
 [2,] 1.205903e-05 0.0007140670 0.000000e+00 104.7350241
 [3,] 1.122514e-05 0.0006708052 0.000000e+00 105.7313425
 [4,] 1.714135e-05 0.0007532758 0.000000e+00  75.1588129
 [5,] 2.567671e-05 0.0012655327 0.000000e+00  86.0341891
 [6,] 1.806631e-02 0.1035411271 2.178346e-07   7.3308661
 [7,] 4.340690e-06 0.0007669856 0.000000e+00 333.9787746
 [8,] 3.550219e-01 0.5592674078 1.082091e-02   2.8733881
 [9,] 2.994578e-01 0.1694832650 9.231943e-02   0.8154961
[10,] 2.031860e-05 0.0021977668 0.000000e+00 201.2021259
[11,] 5.327963e-02 0.1461911957 2.186511e-04   2.6875138
[12,] 1.317967e-02 0.0791244831 9.521724e-08   7.5226802
[13,] 4.039187e-02 0.1276817283 7.406429e-05   3.1754859
[14,] 6.163254e-04          NaN          NaN         NaN
[15,] 2.069238e-01 0.1996319841 2.794610e-02   1.0524984
[16,] 3.602658e-02 0.7910649512 0.000000e+00  40.5117829
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
               q        q.se      q.l95      q.u95
 [1,] 0.01448134 0.002087214 0.01091459 0.01920251
 [2,] 0.01448134 0.002087214 0.01091459 0.01920251
 [3,] 0.01448134 0.002087214 0.01091459 0.01920251
 [4,] 0.01448134 0.002087214 0.01091459 0.01920251
 [5,] 0.01448134 0.002087214 0.01091459 0.01920251
```

```
 [6,] 0.01448134 0.002087214 0.01091459 0.01920251
 [7,] 0.01448134 0.002087214 0.01091459 0.01920251
 [8,] 0.01448134 0.002087214 0.01091459 0.01920251
 [9,] 0.01448134 0.002087214 0.01091459 0.01920251
[10,] 0.01448134 0.002087214 0.01091459 0.01920251
[11,] 0.01448134 0.002087214 0.01091459 0.01920251
[12,] 0.01448134 0.002087214 0.01091459 0.01920251
[13,] 0.01448134 0.002087214 0.01091459 0.01920251
[14,] 0.01448134 0.002087214 0.01091459 0.01920251
[15,] 0.01448134 0.002087214 0.01091459 0.01920251
[16,] 0.01448134 0.002087214 0.01091459 0.01920251
> detach(NSgxtP)
>
> ##------------------------------------------------------------------------------
> ## Estimate Model Phi(group+time),P(group*time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=9),rep(-2,times=16))
>
> ## Fit the model
> SgatPgxt<-FitCJS(p,
+           PhiDesign=gatDesign,PDesign=gxtDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRgat,NPphi=NPgat,NRp=NRgxt,NPp=NPgxt,
+           Ngroups=Ngroups,Nocc=Nocc)
Warning message:
In sqrt(diag(var)) : NaNs produced
>
> ## Model selection criteria
> attach(SgatPgxt)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -356.1043
> np
[1] 25
> AIC
[1] 762.2085
> AICc
[1] 764.1661
> detach(SgatPgxt)
>
> ## Estimate population size from catch
> NSgatPgxt<-EstimateN(C,Cvar,SgatPgxt)
Warning messages:
1: In sqrt(var2$cov.qmu[i, i]) : NaNs produced
2: In sqrt(var2$cov.logistic[i, i]) : NaNs produced
3: In sqrt(var2$cov.qmu[i, i]) : NaNs produced
4: In sqrt(var2$cov.logistic[i, i]) : NaNs produced
5: In sqrt(var2$cov.qmu[i, i]) : NaNs produced
6: In sqrt(var2$cov.logistic[i, i]) : NaNs produced
7: In sqrt(var2$cov.qmu[i, i]) : NaNs produced
8: In sqrt(var2$cov.logistic[i, i]) : NaNs produced
> attach(NSgatPgxt)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N        N.se        N.l95        N.u95
 [1,]  727.6574    470.2627 2.050271e+02 2.582513e+03
 [2,]  418.5086    173.7922 1.854485e+02 9.444643e+02
 [3,]  514.2518    201.9014 2.382198e+02 1.110130e+03
 [4,]  281.7368    115.7781 1.259044e+02 6.304436e+02
 [5,] 1222.5384    517.7541 5.330472e+02 2.803879e+03
 [6,] 1712.0072    869.3360 6.328023e+02 4.631729e+03
 [7,]  705.9340    234.1436 3.684963e+02 1.352369e+03
 [8,]  982.8033    477.0452 3.795704e+02 2.544725e+03
 [9,] 1999.4796  37659.7610 1.855356e-13 2.154799e+19
```

```
[10,] 1897.1737   2380.9534 1.621173e+02 2.220163e+04
[11,] 1454.4777   1207.8176 2.856571e+02 7.405751e+03
[12,] 1185.0413   1034.2763 2.141958e+02 6.556257e+03
[13,] 4939.0584   4878.0246 7.127641e+02 3.422493e+04
[14,] 1405.6699   3199.4377 1.623426e+01 1.217122e+05
[15,] 1525.7121  34716.4281 6.526314e-17 3.566787e+22
[16,]  797.4040 793465.3475 0.000000e+00          Inf
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se       mu.l95       mu.u95
 [1,] 6.449526e-09          NaN          NaN          NaN
 [2,] 4.440892e-16 7.712451e-18 4.440892e-16 4.440892e-16
 [3,] 4.440892e-16 2.521888e-18 4.440892e-16 4.440892e-16
 [4,] 5.551115e-14 1.150166e-11 0.000000e+00 3.763750e+02
 [5,] 4.478640e-13 8.838750e-11 0.000000e+00 3.582950e+02
 [6,] 6.001200e-12 9.543354e-10 0.000000e+00 2.858498e+02
 [7,] 1.483024e-08          NaN          NaN          NaN
 [8,] 6.816369e-06 1.009593e-03 0.000000e+00 2.784063e+02
 [9,] 1.304973e-01 1.785450e-01 7.947879e-03 1.234044e+00
[10,] 1.033954e-08          NaN          NaN          NaN
[11,] 7.858273e-09          NaN          NaN          NaN
[12,] 1.197426e-06 2.495103e-04 0.000000e+00 3.947744e+02
[13,] 9.681823e-06 1.918143e-03 0.000000e+00 3.767678e+02
[14,] 1.296960e-04 2.074927e-02 0.000000e+00 3.046384e+02
[15,] 2.780324e-01 2.985797e-01 2.835386e-02 1.520022e+00
[16,] 4.999399e+00 1.482629e+02 0.000000e+00 2.975605e+02
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q         q.se        q.l95      q.u95
 [1,] 0.019986263 0.011540309 0.0064158442 0.06139183
 [2,] 0.027619723 0.009768443 0.0137722398 0.05501260
 [3,] 0.026196652 0.009263737 0.0130658169 0.05218381
 [4,] 0.018068872 0.005217484 0.0102473750 0.03176619
 [5,] 0.015452778 0.005464046 0.0077156244 0.03082999
 [6,] 0.009054239 0.004049282 0.0037634875 0.02170251
 [7,] 0.016531477 0.004585851 0.0095881947 0.02843176
 [8,] 0.009915573 0.004434461 0.0041210143 0.02376163
 [9,] 0.009365094 0.009651226 0.0012357778 0.06914868
[10,] 0.004237360 0.004359574 0.0005626895 0.03153372
[11,] 0.007981894 0.005829586 0.0019021962 0.03317332
[12,] 0.005073337 0.003013864 0.0015815932 0.01621169
[13,] 0.004068059 0.002915168 0.0009973121 0.01651592
[14,] 0.009099931 0.004149830 0.0037175753 0.02218895
[15,] 0.012891951 0.008260625 0.0036591353 0.04490366
[16,] 0.145076157 4.303715139 0.0000000000        Inf
> detach(NSgatPgxt)
>
> ##-------------------------------------------------------------------------------
> ## Estimate Model Phi(group+time),P(group+time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=9),rep(-2,times=9))
>
> ## Fit the model
> SgatPgat<-FitCJS(p,
+           PhiDesign=gatDesign,PDesign=gatDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRgat,NPphi=NPgat,NRp=NRgat,NPp=NPgat,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SgatPgat)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -358.4215
```

```
> np
[1] 18
> AIC
[1] 752.843
> AICc
[1] 753.8301
> detach(SgatPgat)
>
> ## Estimate population size from catch
> NSgatPgat<-EstimateN(C,Cvar,SgatPgat)
> attach(NSgatPgat)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N       N.se        N.l95        N.u95
 [1,]  689.0615   387.2524 2.290204e+02 2.073203e+03
 [2,]  481.8993   193.2234 2.196091e+02 1.057456e+03
 [3,]  530.5494   190.0349 2.629254e+02 1.070580e+03
 [4,]  293.4692   111.5088 1.393566e+02 6.180128e+02
 [5,] 1287.3687   499.3276 6.019273e+02 2.753353e+03
 [6,] 1206.4547  9920.6936 1.207648e-04 1.205262e+10
 [7,]  489.7801   205.8989 2.148609e+02 1.116464e+03
 [8,]  706.7867 32767.1824 2.433306e-37 2.052958e+42
 [9,] 2411.0266  1515.9235 7.030764e+02 8.268019e+03
[10,] 1116.7593   543.7913 4.300021e+02 2.900338e+03
[11,] 1507.2020   665.0129 6.347380e+02 3.578891e+03
[12,] 1147.3907   572.3261 4.316368e+02 3.050030e+03
[13,] 4535.6863  2129.0799 1.807492e+03 1.138177e+04
[14,] 2613.4270  1386.4334 9.239240e+02 7.392383e+03
[15,] 1613.3876   634.7523 7.461837e+02 3.488443e+03
[16,] 2023.6104  1735.5720 3.767654e+02 1.086883e+04
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se       mu.l95       mu.u95
 [1,] 1.025180e-12 9.414770e-20 1.025180e-12 1.025180e-12
 [2,] 3.101763e-11 1.910842e-16 3.101719e-11 3.101808e-11
 [3,] 7.105427e-15 3.497021e-23 7.105427e-15 7.105427e-15
 [4,] 8.129741e-11 3.689870e-14 8.122525e-11 8.136980e-11
 [5,] 4.929390e-14 3.282881e-18 4.929390e-14 4.929390e-14
 [6,] 1.503389e-01 1.350618e-01 2.405747e-02 7.327790e-01
 [7,] 1.572928e-08 1.144544e-11 1.570686e-08 1.575173e-08
 [8,] 3.016906e-01 8.704211e-01 5.031142e-04 5.511055e+00
 [9,] 0.000000e+00 9.958638e-15 0.000000e+00          Inf
[10,] 6.661338e-16 3.013157e-13 0.000000e+00          Inf
[11,] 0.000000e+00 6.991665e-17 0.000000e+00          Inf
[12,] 1.776357e-15 7.897508e-13 0.000000e+00          Inf
[13,] 0.000000e+00 4.796686e-16 0.000000e+00          Inf
[14,] 3.709938e-06 1.575944e-03 0.000000e+00          Inf
[15,] 3.597123e-13 1.527994e-10 0.000000e+00          Inf
[16,] 8.053014e-06 3.421097e-03 0.000000e+00          Inf
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q         q.se        q.l95        q.u95
 [1,] 0.021137190 0.010629360 0.007858544 0.056230667
 [2,] 0.023841466 0.008091477 0.012232413 0.046216308
 [3,] 0.025364676 0.008173884 0.013459244 0.047553666
 [4,] 0.017316198 0.004614861 0.010260403 0.029153848
 [5,] 0.014655718 0.004739865 0.007765835 0.027574635
 [6,] 0.016083848 0.005881341 0.007841713 0.032847869
 [7,] 0.024120257 0.008586814 0.011976342 0.048284288
 [8,] 0.018477831 0.011851183 0.005230293 0.064218101
 [9,] 0.006407073 0.003535705 0.002169376 0.018845111
[10,] 0.007233610 0.002901697 0.003292435 0.015855276
[11,] 0.007699849 0.002986855 0.003596704 0.016445557
[12,] 0.005241865 0.001782400 0.002690544 0.010200181
[13,] 0.004432380 0.001706185 0.002083321 0.009417691
[14,] 0.004866721 0.001806843 0.002349560 0.010067057
[15,] 0.007318908 0.002372432 0.003874904 0.013802883
```

```
[16,] 0.005595776 0.003233921 0.001800406 0.017323017
> detach(NSgatPgat)
>
> ##------------------------------------------------------------------------------
> ## Estimate Model Phi(group+time),P(group)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=9),rep(-2,times=2))
>
> ## Fit the model
> SgatPg<-FitCJS(p,
+           PhiDesign=gatDesign,PDesign=gDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRgat,NPphi=NPgat,NRp=NRg,NPp=NPg,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SgatPg)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -360.013
> np
[1] 11
> AIC
[1] 742.026
> AICc
[1] 742.3769
> detach(SgatPg)
>
> ## Estimate population size from catch
> NSgatPg<-EstimateN(C,Cvar,SgatPg)
> attach(NSgatPg)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N        N.se        N.l95        N.u95
 [1,]  761.8281   133.28897 5.406654e+02 1.073459e+03
 [2,]  597.9539   110.65205 4.160533e+02 8.593823e+02
 [3,]  700.0566   119.70557 5.007027e+02 9.787827e+02
 [4,]  267.6100    61.20781 1.709274e+02 4.189796e+02
 [5,]  996.5861   180.57957 6.986760e+02 1.421523e+03
 [6,]  965.6665  5146.76923 2.805725e-02 3.323604e+07
 [7,]  614.5630   112.13846 4.297798e+02 8.787935e+02
 [8,]  769.1286 22558.59782 8.312571e-23 7.116435e+27
 [9,] 2601.0723   618.34354 1.632284e+03 4.144854e+03
[10,] 1358.1802   344.51227 8.261140e+02 2.232928e+03
[11,] 1950.8042   463.75765 1.224213e+03 3.108640e+03
[12,] 1014.9888   309.96797 5.578374e+02 1.846779e+03
[13,] 3395.4505   861.28068 2.065285e+03 5.582321e+03
[14,] 2145.8846   510.13342 1.346634e+03 3.419504e+03
[15,] 1985.0326   503.51794 1.207397e+03 3.263511e+03
[16,] 1908.4400   424.57342 1.233977e+03 2.951549e+03
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se     mu.l95      mu.u95
 [1,] 2.436657e-06 7.983412e-04 0.00000000 629.2462254
 [2,] 2.072809e-06 7.910726e-04 0.00000000         Inf
 [3,] 8.045963e-07 2.889201e-04 0.00000000 689.7780156
 [4,] 4.857076e-06 1.641818e-03 0.00000000 650.2975837
 [5,] 1.699144e-07 1.352494e-04 0.00000000         Inf
 [6,] 1.100278e-01 1.042248e-01 0.01624006   0.6022619
 [7,] 1.435288e-06 4.459579e-04 0.00000000 595.5372634
 [8,] 4.339544e-01 5.678387e-01 0.02276087   2.6263911
 [9,] 0.000000e+00 3.615062e-43 0.00000000 538.6531476
[10,] 0.000000e+00 3.582147e-43 0.00000000 644.3407638
[11,] 0.000000e+00 1.308291e-43 0.00000000 599.1849378
```

```
[12,] 0.000000e+00 7.434528e-43 0.00000000 559.7045059
[13,] 0.000000e+00 6.124372e-44 0.00000000         Inf
[14,] 0.000000e+00 5.268436e-41 0.00000000   0.0000000
[15,] 0.000000e+00 2.019392e-43 0.00000000 504.9441856
[16,] 0.000000e+00 3.968398e-40 0.00000000   0.0000000
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q        q.se       q.l95       q.u95
 [1,] 0.019067178 0.002898302 0.014149164 0.025672799
 [2,] 0.019067178 0.002898302 0.014149164 0.025672799
 [3,] 0.019067178 0.002898302 0.014149164 0.025672799
 [4,] 0.019067178 0.002898302 0.014149164 0.025672799
 [5,] 0.019067178 0.002898302 0.014149164 0.025672799
 [6,] 0.019067178 0.002898302 0.014149164 0.025672799
 [7,] 0.019067178 0.002898302 0.014149164 0.025672799
 [8,] 0.019067178 0.002898302 0.014149164 0.025672799
 [9,] 0.005935297 0.001237614 0.003943251 0.008929199
[10,] 0.005935297 0.001237614 0.003943251 0.008929199
[11,] 0.005935297 0.001237614 0.003943251 0.008929199
[12,] 0.005935297 0.001237614 0.003943251 0.008929199
[13,] 0.005935297 0.001237614 0.003943251 0.008929199
[14,] 0.005935297 0.001237614 0.003943251 0.008929199
[15,] 0.005935297 0.001237614 0.003943251 0.008929199
[16,] 0.005935297 0.001237614 0.003943251 0.008929199
> detach(NSgatPg)
>
> ##-------------------------------------------------------------------------------------
> ## Estimate Model Phi(group+time),P(time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=9),rep(-2,times=8))
>
> ## Fit the model
> SgatPt<-FitCJS(p,
+           PhiDesign=gatDesign,PDesign=tDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRgat,NPphi=NPgat,NRp=NRt,NPp=NPt,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SgatPt)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -363.0495
> np
[1] 17
> AIC
[1] 760.0989
> AICc
[1] 760.9749
> detach(SgatPt)
>
> ## Estimate population size from catch
> NSgatPt<-EstimateN(C,Cvar,SgatPt)
> attach(NSgatPt)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N       N.se        N.l95        N.u95
 [1,]  837.9005   479.5091 2.729371e+02 2.572304e+03
 [2,]  602.8576   243.0118 2.735831e+02 1.328435e+03
 [3,]  667.6938   240.9786 3.291266e+02 1.354540e+03
 [4,]  377.9956   148.6295 1.748979e+02 8.169377e+02
 [5,] 1724.9858   677.2045 7.991163e+02 3.723583e+03
 [6,] 1597.6426   583.3291 7.810600e+02 3.267946e+03
 [7,]  754.5045   231.3335 4.136909e+02 1.376093e+03
```

```
 [8,]  881.0217   356.1553 3.989145e+02 1.945778e+03
 [9,] 1431.6558 13832.4215 8.541198e-06 2.399708e+11
[10,]  435.3973   175.6536 1.974589e+02 9.600518e+02
[11,]  638.1762  3447.2026 1.610519e-02 2.528806e+07
[12,]  460.1712   183.0319 2.110328e+02 1.003434e+03
[13,] 1869.7626  4396.3837 1.863436e+01 1.876111e+05
[14,] 1318.0624   481.4659 6.441703e+02 2.696940e+03
[15,] 1185.2117 12942.8696 6.001332e-07 2.340692e+12
[16,] 1027.8844   729.7475 2.556359e+02 4.133013e+03
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se       mu.l95       mu.u95
 [1,] 3.762951e-05 1.523370e-03 0.000000e+00 6.916120e+01
 [2,] 1.925193e-11 3.084613e-08 0.000000e+00          Inf
 [3,] 5.287816e-06 2.142923e-04 0.000000e+00 6.728041e+01
 [4,] 1.561984e-10 7.902434e-08 0.000000e+00          Inf
 [5,] 2.610915e-08 2.659922e-06 0.000000e+00 1.822179e+02
 [6,] 3.466143e-10 6.311566e-11 2.425755e-10 4.952749e-10
 [7,] 2.467286e-05 9.992422e-04 0.000000e+00 6.877050e+01
 [8,] 2.370009e-09 6.257155e-07 0.000000e+00 4.976071e+02
 [9,] 3.355909e-01 1.703317e-01 1.165674e-01 8.268832e-01
[10,] 2.040112e-07 3.267712e-04 0.000000e+00          Inf
[11,] 5.452136e-02 1.111525e-01 9.228849e-04 1.481769e+00
[12,] 1.655230e-06 8.347321e-04 0.000000e+00          Inf
[13,] 2.766399e-04 2.586393e-02 0.000000e+00 1.750792e+02
[14,] 3.673058e-06 1.487817e-04 0.000000e+00 6.687786e+01
[15,] 2.322706e-01 1.723034e-01 4.999017e-02 8.474163e-01
[16,] 2.511462e-05 6.552088e-03 0.000000e+00 5.007537e+02
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q         q.se       q.l95      q.u95
 [1,] 0.017297292 0.008740059 0.006404870 0.04628996
 [2,] 0.018907130 0.006399271 0.009722797 0.03660979
 [3,] 0.020016056 0.006455414 0.010620372 0.03756927
 [4,] 0.013319473 0.003638897 0.007790833 0.02272709
 [5,] 0.010870928 0.003536793 0.005740314 0.02054036
 [6,] 0.009710656 0.003125320 0.005163515 0.01822582
 [7,] 0.015440828 0.003890638 0.009415419 0.02527378
 [8,] 0.011072911 0.004215687 0.005243916 0.02330619
 [9,] 0.017297292 0.008740059 0.006404870 0.04628996
[10,] 0.018907130 0.006399271 0.009722797 0.03660979
[11,] 0.020016056 0.006455414 0.010620372 0.03756927
[12,] 0.013319473 0.003638897 0.007790833 0.02272709
[13,] 0.010870928 0.003536793 0.005740314 0.02054036
[14,] 0.009710656 0.003125320 0.005163515 0.01822582
[15,] 0.015440828 0.003890638 0.009415419 0.02527378
[16,] 0.011072911 0.004215687 0.005243916 0.02330619
> detach(NSgatPt)
>
> ##-----------------------------------------------------------------------------
> ## Estimate Model Phi(group+time),P(constant)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=9),rep(-2,times=1))
>
> ## Fit the model
> SgatP<-FitCJS(p,
+           PhiDesign=gatDesign,PDesign=cDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRgat,NPphi=NPgat,NRp=NRc,NPp=NPc,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SgatP)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
```

```
> CJS$maximum ## = log-likelihood kernel
[1] -365.3167
> np
[1] 10
> AIC
[1] 750.6334
> AICc
[1] 750.92
> detach(SgatP)
>
> ## Estimate population size from catch
> NSgatP<-EstimateN(C,Cvar,SgatP)
> attach(NSgatP)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N        N.se        N.l95        N.u95
 [1,] 1041.5892   236.57803 6.673566e+02 1.625680e+03
 [2,]  816.0081   120.61938 6.107600e+02 1.090230e+03
 [3,]  956.9586   133.91578 7.274024e+02 1.258959e+03
 [4,]  363.8464    64.26226 2.573811e+02 5.143507e+02
 [5,] 1360.0564   201.84125 1.016789e+03 1.819211e+03
 [6,] 1125.8022   155.91392 8.581750e+02 1.476891e+03
 [7,]  838.8271   154.84055 5.841775e+02 1.204481e+03
 [8,]  705.9477    93.40497 5.446866e+02 9.149520e+02
 [9,] 1688.8376 20332.13772 9.542718e-08 2.988847e+13
[10,]  589.4291   192.92859 3.103245e+02 1.119559e+03
[11,]  905.0559  9418.49378 1.254457e-06 6.529725e+11
[12,]  460.0421  2555.04439 8.613746e-03 2.456988e+07
[13,] 1583.7399 15441.84913 7.945278e-06 3.156884e+11
[14,]  934.4706  9856.87541 9.814183e-07 8.897687e+11
[15,] 1237.0840 20628.24581 7.914832e-12 1.933556e+17
[16,]  855.5756 45139.80016 1.052951e-42 6.951983e+47
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
               mu        mu.se       mu.l95     mu.u95
 [1,] 1.447801e-04 2.615039e-03 0.000000e+00 26.5641486
 [2,] 3.266516e-08 1.858822e-06 0.000000e+00 94.2975136
 [3,] 2.048110e-05 3.750745e-04 0.000000e+00 25.0982453
 [4,] 4.702006e-06 9.190508e-05 0.000000e+00 26.0425925
 [5,] 1.593500e-05 2.937312e-04 0.000000e+00 25.0821439
 [6,] 1.742906e-06 7.125569e-05 0.000000e+00 66.8713211
 [7,] 9.142722e-05 1.654786e-03 0.000000e+00 26.1767087
 [8,] 1.666514e-05 4.472267e-04 0.000000e+00 41.5969170
 [9,] 2.935102e-01 1.694043e-01 8.844102e-02  0.8146736
[10,] 7.695622e-05 4.152032e-03 0.000000e+00 96.2800410
[11,] 4.712593e-02 1.467985e-01 9.310669e-05  3.2583749
[12,] 1.101705e-02 7.957099e-02 7.287688e-09  9.7315440
[13,] 3.685561e-02 1.381131e-01 2.116037e-05  4.2137451
[14,] 4.097886e-03 1.489334e-01 0.000000e+00 65.8849639
[15,] 1.950836e-01 2.356228e-01 1.578315e-02  1.3652920
[16,] 3.851224e-02 7.404003e-01 0.000000e+00 35.1739202
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
              q         q.se      q.l95      q.u95
 [1,] 0.01385495 0.001704784 0.01088394 0.01762984
 [2,] 0.01385495 0.001704784 0.01088394 0.01762984
 [3,] 0.01385495 0.001704784 0.01088394 0.01762984
 [4,] 0.01385495 0.001704784 0.01088394 0.01762984
 [5,] 0.01385495 0.001704784 0.01088394 0.01762984
 [6,] 0.01385495 0.001704784 0.01088394 0.01762984
 [7,] 0.01385495 0.001704784 0.01088394 0.01762984
 [8,] 0.01385495 0.001704784 0.01088394 0.01762984
 [9,] 0.01385495 0.001704784 0.01088394 0.01762984
[10,] 0.01385495 0.001704784 0.01088394 0.01762984
[11,] 0.01385495 0.001704784 0.01088394 0.01762984
[12,] 0.01385495 0.001704784 0.01088394 0.01762984
[13,] 0.01385495 0.001704784 0.01088394 0.01762984
```

```
[14,] 0.01385495 0.001704784 0.01088394 0.01762984
[15,] 0.01385495 0.001704784 0.01088394 0.01762984
[16,] 0.01385495 0.001704784 0.01088394 0.01762984
> detach(NSgatP)
>
> ##------------------------------------------------------------------------------
> ## Estimate Model Phi(group),P(group*time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=2),rep(-2,times=16))
>
> ## Fit the model
> SgPgxt<-FitCJS(p,
+           PhiDesign=gDesign,PDesign=gxtDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRg,NPphi=NPg,NRp=NRgxt,NPp=NPgxt,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SgPgxt)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -356.8031
> np
[1] 18
> AIC
[1] 749.6062
> AICc
[1] 750.5933
> detach(SgPgxt)
>
> ## Estimate population size from catch
> NSgPgxt<-EstimateN(C,Cvar,SgPgxt)
> attach(NSgPgxt)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N      N.se    N.l95      N.u95
 [1,]  727.6787  470.2837 205.0291  2582.6392
 [2,]  418.4982  173.7855 185.4460   944.4301
 [3,]  514.2498  201.9003 238.2191  1110.1244
 [4,]  281.7534  115.7887 125.9085   630.4975
 [5,] 1222.4792  517.7168 533.0319  2803.6886
 [6,] 1711.9995  869.3405 632.7934  4631.7523
 [7,]  705.8198  234.0867 368.4561  1352.0785
 [8,]  982.7989  467.2020 387.0917  2495.2583
 [9,] 1999.9968 2277.0339 214.7349 18627.5627
[10,] 2313.9237 2842.7148 208.2604 25709.3602
[11,] 1695.0006 1369.4631 347.8846  8258.5618
[12,] 1334.6841 1140.1662 250.1603  7120.9614
[13,] 5459.8396 4765.0345 986.9301 30204.6191
[14,] 1511.3131  772.0535 555.2782  4113.3749
[15,] 1627.5342  812.5458 611.7307  4330.1205
[16,] 2022.9672 1257.6934 598.1098  6842.2152
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se mu.l95   mu.u95
 [1,] 6.108101e-08 3.354724e-05      0      Inf
 [2,] 6.108101e-08 3.354724e-05      0      Inf
 [3,] 6.108101e-08 3.354724e-05      0      Inf
 [4,] 6.108101e-08 3.354724e-05      0      Inf
 [5,] 6.108101e-08 3.354724e-05      0      Inf
 [6,] 6.108101e-08 3.354724e-05      0      Inf
 [7,] 6.108101e-08 3.354724e-05      0      Inf
 [8,] 6.108101e-08 3.354724e-05      0      Inf
 [9,] 5.391561e-06 5.412598e-04      0 184.6346
```

```
[10,] 5.391561e-06 5.412598e-04      0 184.6346
[11,] 5.391561e-06 5.412598e-04      0 184.6346
[12,] 5.391561e-06 5.412598e-04      0 184.6346
[13,] 5.391561e-06 5.412598e-04      0 184.6346
[14,] 5.391561e-06 5.412598e-04      0 184.6346
[15,] 5.391561e-06 5.412598e-04      0 184.6346
[16,] 5.391561e-06 5.412598e-04      0 184.6346
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q        q.se        q.l95      q.u95
 [1,] 0.019985664 0.011540135 0.0064155438 0.06139102
 [2,] 0.027620447 0.009768575 0.0137727220 0.05501355
 [3,] 0.026196759 0.009263760 0.0130658857 0.05218396
 [4,] 0.018067766 0.005217328 0.0102465668 0.03176481
 [5,] 0.015453548 0.005464190 0.0077161341 0.03083103
 [6,] 0.009054281 0.004049295 0.0037635095 0.02170258
 [7,] 0.016534226 0.004586245 0.0095902077 0.02843524
 [8,] 0.009915550 0.004434435 0.0041210181 0.02376150
 [9,] 0.007737270 0.007737399 0.0010851868 0.05407574
[10,] 0.003469896 0.003469880 0.0004878354 0.02445902
[11,] 0.006839130 0.004836169 0.0017066027 0.02719888
[12,] 0.004498513 0.002597425 0.0014492237 0.01391926
[13,] 0.003677666 0.002600682 0.0009185889 0.01466336
[14,] 0.008455166 0.003781775 0.0035144477 0.02027165
[15,] 0.007254613 0.002962275 0.0032556948 0.01612590
[16,] 0.005597550 0.003232205 0.0018027083 0.01731197
> detach(NSgPgxt)
>
> ##-------------------------------------------------------------------------------------
> ## Estimate Model Phi(group),P(group+time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=2),rep(-2,times=9))
>
> ## Fit the model
> SgPgat<-FitCJS(p,
+           PhiDesign=gDesign,PDesign=gatDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRg,NPphi=NPg,NRp=NRgat,NPp=NPgat,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SgPgat)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -359.2198
> np
[1] 11
> AIC
[1] 740.4396
> AICc
[1] 740.7905
> detach(SgPgat)
>
> ## Estimate population size from catch
> NSgPgat<-EstimateN(C,Cvar,SgPgat)
> attach(NSgPgat)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N      N.se     N.l95     N.u95
 [1,]  717.1410  403.3438  238.1507 2159.5200
 [2,]  503.6124  202.0872  229.3634 1105.7801
 [3,]  553.9564  198.5142  274.4328 1118.1891
 [4,]  306.7664  116.5965  145.6382  646.1605
 [5,] 1348.7318  523.1104  630.6349 2884.5174
```

```
 [6,] 1194.2290  436.1099  583.7664 2443.0710
 [7,]  668.7053  190.7684  382.2956 1169.6884
 [8,]  852.3014  325.4753  403.2106 1801.5837
 [9,] 2093.1166 1275.7505  633.8378 6912.0784
[10,]  974.7095  448.6949  395.3924 2402.8244
[11,] 1313.6928  545.5801  582.0779 2964.8762
[12,] 1001.5783  461.7883  405.7161 2472.5642
[13,] 3961.8959 1752.7132 1664.6806 9429.2074
[14,] 2681.9506 1110.2293 1191.4561 6037.0323
[15,] 1853.5023  653.5431  928.6559 3699.4016
[16,] 2719.0485 1150.3076 1186.6021 6230.5847
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se       mu.l95       mu.u95
 [1,] 1.053841e-07 5.818067e-05 0.000000e+00          Inf
 [2,] 1.053841e-07 5.818067e-05 0.000000e+00          Inf
 [3,] 1.053841e-07 5.818067e-05 0.000000e+00          Inf
 [4,] 1.053841e-07 5.818067e-05 0.000000e+00          Inf
 [5,] 1.053841e-07 5.818067e-05 0.000000e+00          Inf
 [6,] 1.053841e-07 5.818067e-05 0.000000e+00          Inf
 [7,] 1.053841e-07 5.818067e-05 0.000000e+00          Inf
 [8,] 1.053841e-07 5.818067e-05 0.000000e+00          Inf
 [9,] 3.178115e-09 4.854191e-13 3.177163e-09 3.179066e-09
[10,] 3.178115e-09 4.854191e-13 3.177163e-09 3.179066e-09
[11,] 3.178115e-09 4.854191e-13 3.177163e-09 3.179066e-09
[12,] 3.178115e-09 4.854191e-13 3.177163e-09 3.179066e-09
[13,] 3.178115e-09 4.854191e-13 3.177163e-09 3.179066e-09
[14,] 3.178115e-09 4.854191e-13 3.177163e-09 3.179066e-09
[15,] 3.178115e-09 4.854191e-13 3.177163e-09 3.179066e-09
[16,] 3.178115e-09 4.854191e-13 3.177163e-09 3.179066e-09
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q         q.se       q.l95       q.u95
 [1,] 0.020287252 0.010198386 0.007546314 0.053966716
 [2,] 0.022774449 0.007721858 0.011693648 0.044126194
 [3,] 0.024258227 0.007809724 0.012881248 0.045457773
 [4,] 0.016535563 0.004399982 0.009806263 0.027818886
 [5,] 0.013973521 0.004513957 0.007410265 0.026273971
 [6,] 0.013047377 0.004218139 0.006916146 0.024547697
 [7,] 0.017478519 0.004176423 0.010933307 0.027887748
 [8,] 0.011450051 0.004119247 0.005650409 0.023134051
 [9,] 0.007389647 0.003958180 0.002582480 0.021051425
[10,] 0.008302176 0.003153906 0.003939381 0.017454707
[11,] 0.008847245 0.003235170 0.004316678 0.018090051
[12,] 0.006015904 0.001894258 0.003243913 0.011143459
[13,] 0.005079647 0.001844759 0.002491588 0.010342105
[14,] 0.004741577 0.001719013 0.002328704 0.009642509
[15,] 0.006360876 0.001845018 0.003601048 0.011223987
[16,] 0.004158973 0.001646403 0.001913389 0.009028139
> detach(NSgPgat)
>
> ##-----------------------------------------------------------------------------
> ## Estimate Model Phi(group),P(group)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=2),rep(-2,times=2))
>
> ## Fit the model
> SgPg<-FitCJS(p,
+           PhiDesign=gDesign,PDesign=gDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRg,NPphi=NPg,NRp=NRg,NPp=NPg,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SgPg)
The following object is masked _by_ .GlobalEnv:
```

```
    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -361.4371
> np
[1] 4
> AIC
[1] 730.8742
> AICc
[1] 730.9121
> detach(SgPg)
>
> ## Estimate population size from catch
> NSgPg<-EstimateN(C,Cvar,SgPg)
> attach(NSgPg)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N      N.se     N.l95    N.u95
 [1,]  851.5592  553.6416  238.1199 3045.328
 [2,]  669.0739  428.4136  190.7360 2347.013
 [3,]  782.5139  508.7517  218.8129 2798.409
 [4,]  300.4990  184.5303   90.1837 1001.286
 [5,] 1115.1232  714.0227  317.8933 3911.689
 [6,]  920.6046  598.5314  257.4269 3292.246
 [7,]  687.6593  440.3140  196.0342 2412.208
 [8,]  575.6188  380.2871  157.6782 2101.350
 [9,] 2597.7571 1045.5545 1180.3142 5717.412
[10,] 1356.5286  555.5257  607.9087 3027.049
[11,] 1948.3178  784.1659  885.2357 4288.059
[12,] 1013.9302  441.7371  431.6779 2381.531
[13,] 3391.3214 1388.8143 1519.7719 7567.623
[14,] 2143.1496  862.5825  973.7592 4716.865
[15,] 1982.6187  811.9222  888.4820 4424.149
[16,] 1905.8951  755.2788  876.5443 4144.042
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu       mu.se       mu.l95    mu.u95
 [1,] 0.0033701869 0.013652041 1.186969e-06  2.360982
 [2,] 0.0033701869 0.013652041 1.186969e-06  2.360982
 [3,] 0.0033701869 0.013652041 1.186969e-06  2.360982
 [4,] 0.0033701869 0.013652041 1.186969e-06  2.360982
 [5,] 0.0033701869 0.013652041 1.186969e-06  2.360982
 [6,] 0.0033701869 0.013652041 1.186969e-06  2.360982
 [7,] 0.0033701869 0.013652041 1.186969e-06  2.360982
 [8,] 0.0033701869 0.013652041 1.186969e-06  2.360982
 [9,] 0.0001121045 0.002128261 0.000000e+00 28.115911
[10,] 0.0001121045 0.002128261 0.000000e+00 28.115911
[11,] 0.0001121045 0.002128261 0.000000e+00 28.115911
[12,] 0.0001121045 0.002128261 0.000000e+00 28.115911
[13,] 0.0001121045 0.002128261 0.000000e+00 28.115911
[14,] 0.0001121045 0.002128261 0.000000e+00 28.115911
[15,] 0.0001121045 0.002128261 0.000000e+00 28.115911
[16,] 0.0001121045 0.002128261 0.000000e+00 28.115911
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
               q        q.se       q.l95      q.u95
 [1,] 0.017100062 0.003429495 0.011535321 0.02531551
 [2,] 0.017100062 0.003429495 0.011535321 0.02531551
 [3,] 0.017100062 0.003429495 0.011535321 0.02531551
 [4,] 0.017100062 0.003429495 0.011535321 0.02531551
 [5,] 0.017100062 0.003429495 0.011535321 0.02531551
 [6,] 0.017100062 0.003429495 0.011535321 0.02531551
 [7,] 0.017100062 0.003429495 0.011535321 0.02531551
 [8,] 0.017100062 0.003429495 0.011535321 0.02531551
 [9,] 0.005943935 0.001247586 0.003938352 0.00896628
[10,] 0.005943935 0.001247586 0.003938352 0.00896628
[11,] 0.005943935 0.001247586 0.003938352 0.00896628
```

```
[12,] 0.005943935 0.001247586 0.003938352 0.00896628
[13,] 0.005943935 0.001247586 0.003938352 0.00896628
[14,] 0.005943935 0.001247586 0.003938352 0.00896628
[15,] 0.005943935 0.001247586 0.003938352 0.00896628
[16,] 0.005943935 0.001247586 0.003938352 0.00896628
> detach(NSgPg)
>
> ##------------------------------------------------------------------------------
> ## Estimate Model Phi(group),P(time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=2),rep(-2,times=8))
>
> ## Fit the model
> SgPt<-FitCJS(p,
+           PhiDesign=gDesign,PDesign=tDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRg,NPphi=NPg,NRp=NRt,NPp=NPt,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SgPt)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -365.5586
> np
[1] 10
> AIC
[1] 751.1172
> AICc
[1] 751.4038
> detach(SgPt)
>
> ## Estimate population size from catch
> NSgPt<-EstimateN(C,Cvar,SgPt)
> attach(NSgPt)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N      N.se     N.l95      N.u95
 [1,]  978.3494  551.6445 323.99120  2954.3008
 [2,]  676.6235  270.8893 308.71549  1482.9814
 [3,]  712.3229  255.1316 353.01865  1437.3287
 [4,]  376.4731  143.8413 178.03463   796.0924
 [5,] 1590.3511  623.0973 737.88268  3427.6677
 [6,] 1439.6674  527.2514 702.29525  2951.2405
 [7,]  779.5111  225.4289 442.23848  1374.0041
 [8,]  986.6187  379.5100 464.21855  2096.8925
 [9,] 1124.3308 1329.6680 110.71811 11417.4618
[10,]  529.8907  543.3393  71.01749  3953.7326
[11,]  668.0586  612.8929 110.63373  4034.0521
[12,]  527.1936  672.5255  43.26106  6424.5557
[13,] 1868.6187 2729.3527 106.71141 32721.2969
[14,] 1262.7130 2032.5644  53.84148 29613.6738
[15,]  868.1780  992.8000  92.30052  8166.0749
[16,] 1199.2596 2119.0941  37.56737 38283.8543
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se     mu.l95       mu.u95
 [1,] 1.267607e-06 9.471112e-05 0.00000000 132.86601143
 [2,] 1.267607e-06 9.471112e-05 0.00000000 132.86601143
 [3,] 1.267607e-06 9.471112e-05 0.00000000 132.86601143
 [4,] 1.267607e-06 9.471112e-05 0.00000000 132.86601143
 [5,] 1.267607e-06 9.471112e-05 0.00000000 132.86601143
 [6,] 1.267607e-06 9.471112e-05 0.00000000 132.86601143
 [7,] 1.267607e-06 9.471112e-05 0.00000000 132.86601143
```

```
 [8,] 1.267607e-06 9.471112e-05 0.00000000 132.86601143
 [9,] 4.143998e-02 1.773780e-02 0.01780833   0.09497629
[10,] 4.143998e-02 1.773780e-02 0.01780833   0.09497629
[11,] 4.143998e-02 1.773780e-02 0.01780833   0.09497629
[12,] 4.143998e-02 1.773780e-02 0.01780833   0.09497629
[13,] 4.143998e-02 1.773780e-02 0.01780833   0.09497629
[14,] 4.143998e-02 1.773780e-02 0.01780833   0.09497629
[15,] 4.143998e-02 1.773780e-02 0.01780833   0.09497629
[16,] 4.143998e-02 1.773780e-02 0.01780833   0.09497629
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q        q.se       q.l95      q.u95
 [1,] 0.014764788 0.007387601 0.005523021 0.03917098
 [2,] 0.016788451 0.005624070 0.008693948 0.03229861
 [3,] 0.018730689 0.005983714 0.009999296 0.03495425
 [4,] 0.013375131 0.003551241 0.007942509 0.02248209
 [5,] 0.011809176 0.003840088 0.006237297 0.02230331
 [6,] 0.010791378 0.003488395 0.005721758 0.02030743
 [7,] 0.014932534 0.003602095 0.009300100 0.02393556
 [8,] 0.009876818 0.003573733 0.004854998 0.02004122
 [9,] 0.014764788 0.007387601 0.005523021 0.03917098
[10,] 0.016788451 0.005624070 0.008693948 0.03229861
[11,] 0.018730689 0.005983714 0.009999296 0.03495425
[12,] 0.013375131 0.003551241 0.007942509 0.02248209
[13,] 0.011809176 0.003840088 0.006237297 0.02230331
[14,] 0.010791378 0.003488395 0.005721758 0.02030743
[15,] 0.014932534 0.003602095 0.009300100 0.02393556
[16,] 0.009876818 0.003573733 0.004854998 0.02004122
> detach(NSgPt)
>
> ##-------------------------------------------------------------------------------------
> ## Estimate Model Phi(group),P(constant)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=2),rep(-2,times=1))
>
> ## Fit the model
> SgP<-FitCJS(p,
+           PhiDesign=gDesign,PDesign=cDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRg,NPphi=NPg,NRp=NRc,NPp=NPc,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SgP)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -367.1302
> np
[1] 3
> AIC
[1] 740.2604
> AICc
[1] 740.2793
> detach(SgP)
>
> ## Estimate population size from catch
> NSgP<-EstimateN(C,Cvar,SgP)
> attach(NSgP)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
             N       N.se      N.l95      N.u95
 [1,] 1061.3087  149.41214  805.39045  1398.5466
 [2,]  831.5724  124.35387  620.30962  1114.7864
 [3,]  975.2566  137.29764  740.08852  1285.1510
```

```
 [4,]  370.7184   66.06857  261.42209   525.7098
 [5,] 1385.9540  207.25646 1033.84937  1857.9773
 [6,] 1147.3607  161.52663  870.69238  1511.9423
 [7,]  854.6717  127.80815  637.54044  1145.7526
 [8,]  719.5211   95.29269  555.02064   932.7772
 [9,] 1224.9563 1520.21316  107.57977 13947.9562
[10,]  655.0376  809.69018   58.08702  7386.7505
[11,]  918.7172 1140.15987   80.68483 10460.9671
[12,]  524.1697  642.56298   47.42330  5793.6469
[13,] 1637.5941 2024.22545  145.21754 18466.8762
[14,] 1010.5890 1254.17585   88.75331 11507.0639
[15,]  957.3627 1183.39334   84.89641 10796.0199
[16,]  877.0842 1093.68535   76.13966 10103.4946
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se     mu.l95      mu.u95
 [1,] 1.523158e-05 0.0003777263 0.00000000 37.51408084
 [2,] 1.523158e-05 0.0003777263 0.00000000 37.51408084
 [3,] 1.523158e-05 0.0003777263 0.00000000 37.51408084
 [4,] 1.523158e-05 0.0003777263 0.00000000 37.51408084
 [5,] 1.523158e-05 0.0003777263 0.00000000 37.51408084
 [6,] 1.523158e-05 0.0003777263 0.00000000 37.51408084
 [7,] 1.523158e-05 0.0003777263 0.00000000 37.51408084
 [8,] 1.523158e-05 0.0003777263 0.00000000 37.51408084
 [9,] 4.439758e-02 0.0173300863 0.02055284  0.09462783
[10,] 4.439758e-02 0.0173300863 0.02055284  0.09462783
[11,] 4.439758e-02 0.0173300863 0.02055284  0.09462783
[12,] 4.439758e-02 0.0173300863 0.02055284  0.09462783
[13,] 4.439758e-02 0.0173300863 0.02055284  0.09462783
[14,] 4.439758e-02 0.0173300863 0.02055284  0.09462783
[15,] 4.439758e-02 0.0173300863 0.02055284  0.09462783
[16,] 4.439758e-02 0.0173300863 0.02055284  0.09462783
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
               q         q.se      q.l95      q.u95
 [1,] 0.01359022 0.001673409 0.01067417 0.01729605
 [2,] 0.01359022 0.001673409 0.01067417 0.01729605
 [3,] 0.01359022 0.001673409 0.01067417 0.01729605
 [4,] 0.01359022 0.001673409 0.01067417 0.01729605
 [5,] 0.01359022 0.001673409 0.01067417 0.01729605
 [6,] 0.01359022 0.001673409 0.01067417 0.01729605
 [7,] 0.01359022 0.001673409 0.01067417 0.01729605
 [8,] 0.01359022 0.001673409 0.01067417 0.01729605
 [9,] 0.01359022 0.001673409 0.01067417 0.01729605
[10,] 0.01359022 0.001673409 0.01067417 0.01729605
[11,] 0.01359022 0.001673409 0.01067417 0.01729605
[12,] 0.01359022 0.001673409 0.01067417 0.01729605
[13,] 0.01359022 0.001673409 0.01067417 0.01729605
[14,] 0.01359022 0.001673409 0.01067417 0.01729605
[15,] 0.01359022 0.001673409 0.01067417 0.01729605
[16,] 0.01359022 0.001673409 0.01067417 0.01729605
> detach(NSgP)
>
> ##-----------------------------------------------------------------------------
> ## Estimate Model Phi(time),P(group*time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=8),rep(-2,times=16))
>
> ## Fit the model
> StPgxt<-FitCJS(p,
+           PhiDesign=tDesign,PDesign=gxtDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRt,NPphi=NPt,NRp=NRgxt,NPp=NPgxt,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
```

```
> attach(StPgxt)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -356.6047
> np
[1] 24
> AIC
[1] 761.2094
> AICc
[1] 763.0074
> detach(StPgxt)
>
> ## Estimate population size from catch
> NStPgxt<-EstimateN(C,Cvar,StPgxt)
> attach(NStPgxt)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N       N.se        N.l95        N.u95
 [1,]  728.2460  2440.7520 1.021838e+00 5.190079e+05
 [2,]  401.8746   177.7445 1.688912e+02 9.562560e+02
 [3,]  498.5619   203.0656 2.243965e+02 1.107700e+03
 [4,]  274.6680   117.1888 1.190230e+02 6.338478e+02
 [5,] 1194.7525   516.1326 5.123331e+02 2.786143e+03
 [6,] 1682.6682 23931.4186 1.317434e-09 2.149157e+15
 [7,]  573.4184   317.4128 1.937692e+02 1.696909e+03
 [8,]  815.2757   478.4876 2.580612e+02 2.575647e+03
 [9,] 1998.2108 17713.3216 5.687864e-05 7.019940e+10
[10,] 2227.1313  2739.8769 1.997816e+02 2.482768e+04
[11,] 1644.9021  1336.0414 3.347762e+02 8.082124e+03
[12,] 1303.5223  1114.9447 2.438063e+02 6.969346e+03
[13,] 5351.4556  4637.9526 9.789184e+02 2.925482e+04
[14,] 1489.2287 22766.3084 1.445894e-10 1.533862e+16
[15,] 1314.6815   892.6266 3.474333e+02 4.974732e+03
[16,] 1677.0342  1189.1602 4.177884e+02 6.731742e+03
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se       mu.l95       mu.u95
 [1,] 2.268573e-02 7.196657e-02 4.261809e-05 2.591743e+00
 [2,] 1.084806e-07 8.613287e-05 0.000000e+00          Inf
 [3,] 0.000000e+00 1.011595e-25 0.000000e+00 0.000000e+00
 [4,] 3.102623e-08 2.686994e-05 0.000000e+00          Inf
 [5,] 0.000000e+00 1.108316e-23 0.000000e+00 0.000000e+00
 [6,] 7.711288e-02 1.490738e-01 1.562476e-03 1.631133e+00
 [7,] 8.881784e-16 6.004407e-19 8.881784e-16 8.881784e-16
 [8,] 1.372152e-06 3.277919e-09 1.365743e-06 1.378592e-06
 [9,] 2.268573e-02 7.196657e-02 4.261809e-05 2.591743e+00
[10,] 1.084806e-07 8.613287e-05 0.000000e+00          Inf
[11,] 0.000000e+00 1.011595e-25 0.000000e+00 0.000000e+00
[12,] 3.102623e-08 2.686994e-05 0.000000e+00          Inf
[13,] 0.000000e+00 1.108316e-23 0.000000e+00 0.000000e+00
[14,] 7.711288e-02 1.490738e-01 1.562476e-03 1.631133e+00
[15,] 8.881784e-16 6.004407e-19 8.881784e-16 8.881784e-16
[16,] 1.372152e-06 3.277919e-09 1.365743e-06 1.378592e-06
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q         q.se         q.l95      q.u95
 [1,] 0.020669310 0.012133358 0.0065094145 0.06465073
 [2,] 0.028818268 0.010877068 0.0137097077 0.06008421
 [3,] 0.027050869 0.009934959 0.0131322806 0.05531900
 [4,] 0.018554825 0.005569138 0.0102893950 0.03335004
 [5,] 0.015821576 0.005710086 0.0077866867 0.03201580
 [6,] 0.010330482 0.005135568 0.0038919496 0.02727611
 [7,] 0.020481869 0.009544634 0.0081902707 0.05075783
 [8,] 0.011975917 0.006626003 0.0040387757 0.03523889
 [9,] 0.008012552 0.008062691 0.0011099184 0.05664143
```

```
[10,] 0.003605879 0.003632354 0.0004996569 0.02577504
[11,] 0.007049299 0.005029590 0.0017370967 0.02837770
[12,] 0.004607143 0.002682257 0.0014702662 0.01438870
[13,] 0.003752567 0.002664052 0.0009321884 0.01504217
[14,] 0.009621142 0.004782587 0.0036254218 0.02540740
[15,] 0.009006427 0.005052266 0.0029936786 0.02693409
[16,] 0.006759469 0.004496903 0.0018313624 0.02478547
> detach(NStPgxt)
>
> ##------------------------------------------------------------------------------
> ## Estimate Model Phi(time),P(group+time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=8),rep(-2,times=9))
>
> ## Fit the model
> StPgat<-FitCJS(p,
+           PhiDesign=tDesign,PDesign=gatDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRt,NPphi=NPt,NRp=NRgat,NPp=NPgat,
+           Ngroups=Ngroups,Nocc=Nocc)
Warning message:
In sqrt(diag(var)) : NaNs produced
>
> ## Model selection criteria
> attach(StPgat)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -359.0185
> np
[1] 17
> AIC
[1] 752.037
> AICc
[1] 752.913
> detach(StPgat)
>
> ## Estimate population size from catch
> NStPgat<-EstimateN(C,Cvar,StPgat)
Warning messages:
1: In sqrt(var2$cov.qmu[i, i]) : NaNs produced
2: In sqrt(var2$cov.logistic[i, i]) : NaNs produced
3: In sqrt(var2$cov.qmu[i, i]) : NaNs produced
4: In sqrt(var2$cov.logistic[i, i]) : NaNs produced
5: In sqrt(var2$cov.qmu[CJS$NRphi + i, CJS$NRphi + i]) : NaNs produced
6: In sqrt(var2$cov.logistic[CJS$NRphi + i, CJS$NRphi + i]) :
  NaNs produced
7: In sqrt(var2$cov.qmu[CJS$NRphi + i, CJS$NRphi + i]) : NaNs produced
8: In sqrt(var2$cov.logistic[CJS$NRphi + i, CJS$NRphi + i]) :
  NaNs produced
9: In sqrt(d %*% v %*% d) : NaNs produced
10: In sqrt(d %*% v %*% d) : NaNs produced
> attach(NStPgat)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N       N.se        N.l95        N.u95
 [1,]  717.2189  2352.5804 1.157545e+00 4.443913e+05
 [2,]  483.6627   207.1076 2.089516e+02 1.119540e+03
 [3,]  536.8671   200.8244 2.579018e+02 1.117582e+03
 [4,]  299.0145   118.5526 1.374686e+02 6.504008e+02
 [5,] 1318.1901   522.8827 6.057984e+02 2.868322e+03
 [6,] 1173.3989 11340.3070 6.964056e-06 1.977102e+11
 [7,]  540.6115   368.4058 1.421719e+02 2.055686e+03
 [8,]  704.1760        NaN          NaN          NaN
 [9,] 2098.6059 19478.5876 2.637580e-05 1.669768e+11
```

```
[10,]  937.7912   454.4517 3.627505e+02 2.424400e+03
[11,] 1275.9822   547.3470 5.504342e+02 2.957903e+03
[12,]  978.5284   464.3777 3.860233e+02 2.480466e+03
[13,] 3882.5904  1746.5813 1.607689e+03 9.376509e+03
[14,] 2639.0684 71396.5034 2.471132e-20 2.818417e+26
[15,] 1494.5297  2066.3214 9.945357e+01 2.245891e+04
[16,] 2244.5965        NaN          NaN          NaN
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se       mu.l95       mu.u95
 [1,] 2.284214e-02 7.168068e-02 4.590682e-05 2.535960e+00
 [2,] 3.308885e-07 1.512788e-04 0.000000e+00          Inf
 [3,] 2.853859e-08 3.555496e-05 0.000000e+00          Inf
 [4,] 3.931802e-08 3.042870e-05 0.000000e+00          Inf
 [5,] 8.207359e-09 2.566555e-12 8.202331e-09 8.212391e-09
 [6,] 7.833366e-02 1.474283e-01 1.758262e-03 1.562951e+00
 [7,] 1.418209e-04 1.025290e-02 0.000000e+00 1.328469e+02
 [8,] 1.734935e-01          NaN          NaN          NaN
 [9,] 2.284214e-02 7.168068e-02 4.590682e-05 2.535960e+00
[10,] 3.308885e-07 1.512788e-04 0.000000e+00          Inf
[11,] 2.853859e-08 3.555496e-05 0.000000e+00          Inf
[12,] 3.931802e-08 3.042870e-05 0.000000e+00          Inf
[13,] 8.207359e-09 2.566555e-12 8.202331e-09 8.212391e-09
[14,] 7.833366e-02 1.474283e-01 1.758262e-03 1.562951e+00
[15,] 1.418209e-04 1.025290e-02 0.000000e+00 1.328469e+02
[16,] 1.734935e-01          NaN          NaN          NaN
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q         q.se        q.l95       q.u95
 [1,] 0.021000822 0.010790615 0.007641248 0.05706043
 [2,] 0.023751108 0.008606754 0.011646211 0.04813844
 [3,] 0.025056212 0.008429185 0.012929914 0.04828387
 [4,] 0.016981858 0.004718746 0.009840064 0.02923186
 [5,] 0.014304935 0.004728698 0.007474335 0.02729323
 [6,] 0.014925305 0.005804598 0.006952393 0.03189679
 [7,] 0.021776219 0.009676520 0.009085807 0.05173900
 [8,] 0.016463657          NaN          NaN         NaN
 [9,] 0.007627223 0.004162126 0.002613237 0.02215548
[10,] 0.008633654 0.003452555 0.003938639 0.01887275
[11,] 0.009111854 0.003442580 0.004340855 0.01907684
[12,] 0.006159691 0.001996951 0.003261192 0.01161941
[13,] 0.005184284 0.001914825 0.002512205 0.01068335
[14,] 0.005410185 0.002280742 0.002366240 0.01234578
[15,] 0.007910792 0.003754176 0.003116772 0.02000527
[16,] 0.005970741          NaN          NaN         NaN
> detach(NStPgat)
>
> ##-------------------------------------------------------------------------------------
> ## Estimate Model Phi(time),P(group)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=8),rep(-2,times=2))
>
> ## Fit the model
> StPg<-FitCJS(p,
+           PhiDesign=tDesign,PDesign=gDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRt,NPphi=NPt,NRp=NRg,NPp=NPg,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(StPg)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -360.5755
```

```
> np
[1] 10
> AIC
[1] 741.1511
> AICc
[1] 741.4377
> detach(StPg)
>
> ## Estimate population size from catch
> NStPg<-EstimateN(C,Cvar,StPg)
> attach(NStPg)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N         N.se        N.l95        N.u95
 [1,]  806.9107   2968.37335 5.962968e-01 1.091914e+06
 [2,]  623.5645    133.30111 4.101232e+02 9.480875e+02
 [3,]  730.2041    141.70205 4.991817e+02 1.068144e+03
 [4,]  278.8955     67.10896 1.740277e+02 4.469561e+02
 [5,] 1039.2261    209.79916 6.996264e+02 1.543668e+03
 [6,]  932.2854   4323.58933 1.051777e-01 8.263694e+06
 [7,]  640.8673    136.99869 4.215050e+02 9.743914e+02
 [8,]  744.6728  17747.60982 3.846886e-18 1.441523e+23
 [9,] 2378.0696  24856.56486 3.012668e-06 1.877145e+12
[10,] 1223.0499    429.93124 6.140744e+02 2.435944e+03
[11,] 1756.2780    513.89880 9.897405e+02 3.116486e+03
[12,]  914.3988    314.97183 4.655081e+02 1.796156e+03
[13,] 3057.4825    879.08465 1.740295e+03 5.371619e+03
[14,] 2097.4600  27408.24827 1.579570e-08 2.785150e+14
[15,] 1787.4826    624.69440 9.010649e+02 3.545909e+03
[16,] 2381.4140 158593.40240 4.885444e-54 1.160822e+60
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se       mu.l95      mu.u95
 [1,] 1.033868e-02 6.975639e-02 1.752669e-08   8.7263243
 [2,] 2.374661e-05 1.386086e-03 0.000000e+00 103.7582523
 [3,] 8.817290e-06 7.918491e-04 0.000000e+00 164.3825244
 [4,] 9.426766e-08 8.660668e-05 0.000000e+00         Inf
 [5,] 4.080250e-07 1.952881e-04 0.000000e+00         Inf
 [6,] 5.575932e-02 8.700069e-02 2.468471e-03   0.8460623
 [7,] 9.194044e-06 1.343955e-03 0.000000e+00 274.9106147
 [8,] 3.474605e-01 4.418351e-01 2.150428e-02   2.1906433
 [9,] 1.033868e-02 6.975639e-02 1.752669e-08   8.7263243
[10,] 2.374661e-05 1.386086e-03 0.000000e+00 103.7582523
[11,] 8.817290e-06 7.918491e-04 0.000000e+00 164.3825244
[12,] 9.426766e-08 8.660668e-05 0.000000e+00         Inf
[13,] 4.080250e-07 1.952881e-04 0.000000e+00         Inf
[14,] 5.575932e-02 8.700069e-02 2.468471e-03   0.8460623
[15,] 9.194044e-06 1.343955e-03 0.000000e+00 274.9106147
[16,] 3.474605e-01 4.418351e-01 2.150428e-02   2.1906433
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
               q        q.se       q.l95      q.u95
 [1,] 0.018261108 0.003087197 0.013104675 0.02542086
 [2,] 0.018261108 0.003087197 0.013104675 0.02542086
 [3,] 0.018261108 0.003087197 0.013104675 0.02542086
 [4,] 0.018261108 0.003087197 0.013104675 0.02542086
 [5,] 0.018261108 0.003087197 0.013104675 0.02542086
 [6,] 0.018261108 0.003087197 0.013104675 0.02542086
 [7,] 0.018261108 0.003087197 0.013104675 0.02542086
 [8,] 0.018261108 0.003087197 0.013104675 0.02542086
 [9,] 0.006598476 0.001553339 0.004158418 0.01046283
[10,] 0.006598476 0.001553339 0.004158418 0.01046283
[11,] 0.006598476 0.001553339 0.004158418 0.01046283
[12,] 0.006598476 0.001553339 0.004158418 0.01046283
[13,] 0.006598476 0.001553339 0.004158418 0.01046283
[14,] 0.006598476 0.001553339 0.004158418 0.01046283
[15,] 0.006598476 0.001553339 0.004158418 0.01046283
```

```
[16,] 0.006598476 0.001553339 0.004158418 0.01046283
> detach(NStPg)
>
> ##-----------------------------------------------------------------------------
> ## Estimate Model Phi(time),P(time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=7),rep(-2,times=8))
>
> ## Fit the model
> StPt<-FitCJS(p,
+           PhiDesign=tcDesign,PDesign=tDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRtc,NPphi=NPtc,NRp=NRt,NPp=NPt,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(StPt)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -368.621
> np
[1] 15
> AIC
[1] 767.242
> AICc
[1] 767.9161
> detach(StPt)
>
> ## Estimate population size from catch
> NStPt<-EstimateN(C,Cvar,StPt)
> attach(NStPt)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N       N.se        N.l95        N.u95
 [1,] 1008.5542  4942.3103 6.798325e-02 1.496224e+07
 [2,]  693.8315   297.5954 2.993321e+02 1.608254e+03
 [3,]  766.5328   285.5032 3.693907e+02 1.590653e+03
 [4,]  431.5121   168.6353 2.006026e+02 9.282166e+02
 [5,] 1934.6241   757.2700 8.982652e+02 4.166665e+03
 [6,] 1737.7274 25162.6639 8.206818e-10 3.679497e+15
 [7,]  771.8664   670.9676 1.404742e+02 4.241190e+03
 [8,] 1019.7364  1231.9213 9.553248e+01 1.088491e+04
 [9,] 1090.3289  5343.0381 7.349541e-02 1.617539e+07
[10,]  501.1005   214.9300 2.161843e+02 1.161517e+03
[11,]  676.3525   251.9146 3.259329e+02 1.403518e+03
[12,]  525.3190   205.2951 2.442119e+02 1.130003e+03
[13,] 2095.8427   820.3759 9.731207e+02 4.513887e+03
[14,] 1433.6251 20759.1977 6.770625e-10 3.035585e+15
[15,]  792.7277   689.1019 1.442708e+02 4.355817e+03
[16,] 1189.6925  1437.2415 1.114546e+02 1.269906e+04
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se       mu.l95       mu.u95
 [1,] 2.785372e-02 7.511189e-02 1.328496e-04 1.946602e+00
 [2,] 3.019140e-06 4.956561e-04 0.000000e+00 3.090657e+02
 [3,] 9.610914e-09 9.203604e-11 9.432206e-09 9.793008e-09
 [4,] 3.235054e-07 8.721397e-05 0.000000e+00 5.134533e+02
 [5,] 1.684507e-08 2.858586e-05 0.000000e+00          Inf
 [6,] 8.857949e-02 1.492904e-01 2.930685e-03 1.366832e+00
 [7,] 1.759481e-04 1.102727e-02 0.000000e+00 1.142054e+02
 [8,] 1.759481e-04 1.102727e-02 0.000000e+00 1.142054e+02
 [9,] 2.785372e-02 7.511189e-02 1.328496e-04 1.946602e+00
[10,] 3.019140e-06 4.956561e-04 0.000000e+00 3.090657e+02
[11,] 9.610914e-09 9.203604e-11 9.432206e-09 9.793008e-09
```

```
[12,] 3.235054e-07 8.721397e-05 0.000000e+00 5.134533e+02
[13,] 1.684507e-08 2.858586e-05 0.000000e+00          Inf
[14,] 8.857949e-02 1.492904e-01 2.930685e-03 1.366832e+00
[15,] 1.759481e-04 1.102727e-02 0.000000e+00 1.142054e+02
[16,] 1.759481e-04 1.102727e-02 0.000000e+00 1.142054e+02
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q        q.se       q.l95      q.u95
 [1,] 0.014928431 0.007650469 0.005452334 0.04054331
 [2,] 0.016360837 0.005855527 0.008099429 0.03291134
 [3,] 0.017375476 0.005762075 0.009057447 0.03320669
 [4,] 0.011621454 0.003142597 0.006835663 0.01972499
 [5,] 0.009674176 0.003131891 0.005125039 0.01822463
 [6,] 0.010166613 0.003892135 0.004795226 0.02149047
 [7,] 0.015089477 0.006666263 0.006334054 0.03573300
 [8,] 0.009554856 0.004604501 0.003709616 0.02449829
 [9,] 0.014928431 0.007650469 0.005452334 0.04054331
[10,] 0.016360837 0.005855527 0.008099429 0.03291134
[11,] 0.017375476 0.005762075 0.009057447 0.03320669
[12,] 0.011621454 0.003142597 0.006835663 0.01972499
[13,] 0.009674176 0.003131891 0.005125039 0.01822463
[14,] 0.010166613 0.003892135 0.004795226 0.02149047
[15,] 0.015089477 0.006666263 0.006334054 0.03573300
[16,] 0.009554856 0.004604501 0.003709616 0.02449829
> detach(NStPt)
>
> ##-------------------------------------------------------------------------------------
> ## Estimate Model Phi(time),P(constant)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=8),rep(-2,times=1))
>
> ## Fit the model
> StP<-FitCJS(p,
+           PhiDesign=gatDesign,PDesign=cDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRt,NPphi=NPt,NRp=NRc,NPp=NPc,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(StP)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -370.315
> np
[1] 9
> AIC
[1] 758.6301
> AICc
[1] 758.859
> detach(StP)
>
> ## Estimate population size from catch
> NStP<-EstimateN(C,Cvar,StP)
> attach(NStP)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N        N.se        N.l95        N.u95
 [1,] 1176.9832  6688.45164 1.712189e-02 8.090749e+07
 [2,]  903.0910   172.94014 6.204762e+02 1.314431e+03
 [3,] 1059.5189   197.29087 7.355383e+02 1.526202e+03
 [4,]  402.2829    92.93178 2.557944e+02 6.326626e+02
 [5,] 1505.1728   305.03422 1.011768e+03 2.239194e+03
 [6,] 1368.9800  9440.28499 1.847262e-03 1.014532e+09
 [7,]  928.1721   173.92566 6.428699e+02 1.340090e+03
```

```
 [8,] 1084.6667 37974.65241 1.713220e-27 6.867197e+32
 [9,] 1272.4143  7230.75853 1.851016e-02 8.746756e+07
[10,]  652.2324   124.90121 4.481217e+02 9.493116e+02
[11,]  934.8696   174.08018 6.490043e+02 1.346649e+03
[12,]  489.7358   113.13434 3.114019e+02 7.701979e+02
[13,] 1630.6038   330.45374 1.096082e+03 2.425793e+03
[14,] 1129.4085  7788.23511 1.523991e-03 8.369887e+08
[15,]  953.2578   178.62635 6.602447e+02 1.376309e+03
[16,] 1265.4445 44303.76115 1.998757e-27 8.011730e+32
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
               mu        mu.se       mu.l95       mu.u95
 [1,] 1.385298e-02 7.262904e-02 4.474787e-07 6.077293e+00
 [2,] 2.670699e-06 5.145154e-04 0.000000e+00 3.647652e+02
 [3,] 8.232295e-06 7.897086e-04 0.000000e+00 1.763125e+02
 [4,] 6.360945e-06 7.402293e-04 0.000000e+00 2.161225e+02
 [5,] 9.716096e-06 9.978303e-04 0.000000e+00 1.897487e+02
 [6,] 6.386245e-02 8.765749e-02 4.094619e-03 7.226646e-01
 [7,] 7.610714e-08 2.296028e-12 7.610264e-08 7.611164e-08
 [8,] 3.486964e-01 4.418670e-01 2.177694e-02 2.186800e+00
 [9,] 1.385298e-02 7.262904e-02 4.474787e-07 6.077293e+00
[10,] 2.670699e-06 5.145154e-04 0.000000e+00 3.647652e+02
[11,] 8.232295e-06 7.897086e-04 0.000000e+00 1.763125e+02
[12,] 6.360945e-06 7.402293e-04 0.000000e+00 2.161225e+02
[13,] 9.716096e-06 9.978303e-04 0.000000e+00 1.897487e+02
[14,] 6.386245e-02 8.765749e-02 4.094619e-03 7.226646e-01
[15,] 7.610714e-08 2.296028e-12 7.610264e-08 7.611164e-08
[16,] 3.486964e-01 4.418670e-01 2.177694e-02 2.186800e+00
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
              q        q.se       q.l95      q.u95
 [1,] 0.01249145 0.001944538 0.009204285 0.01694267
 [2,] 0.01249145 0.001944538 0.009204285 0.01694267
 [3,] 0.01249145 0.001944538 0.009204285 0.01694267
 [4,] 0.01249145 0.001944538 0.009204285 0.01694267
 [5,] 0.01249145 0.001944538 0.009204285 0.01694267
 [6,] 0.01249145 0.001944538 0.009204285 0.01694267
 [7,] 0.01249145 0.001944538 0.009204285 0.01694267
 [8,] 0.01249145 0.001944538 0.009204285 0.01694267
 [9,] 0.01249145 0.001944538 0.009204285 0.01694267
[10,] 0.01249145 0.001944538 0.009204285 0.01694267
[11,] 0.01249145 0.001944538 0.009204285 0.01694267
[12,] 0.01249145 0.001944538 0.009204285 0.01694267
[13,] 0.01249145 0.001944538 0.009204285 0.01694267
[14,] 0.01249145 0.001944538 0.009204285 0.01694267
[15,] 0.01249145 0.001944538 0.009204285 0.01694267
[16,] 0.01249145 0.001944538 0.009204285 0.01694267
> detach(NStP)
>
> ##-------------------------------------------------------------------------------
> ## Estimate Model Phi(constant),P(group*time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=1),rep(-2,times=16))
>
> ## Fit the model
> SPgxt<-FitCJS(p,
+           PhiDesign=cDesign,PDesign=gxtDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRc,NPphi=NPc,NRp=NRgxt,NPp=NPgxt,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SPgxt)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
```

```
> CJS$maximum ## = log-likelihood kernel
[1] -356.8031
> np
[1] 17
> AIC
[1] 747.6062
> AICc
[1] 748.4822
> detach(SPgxt)
>
> ## Estimate population size from catch
> NSPgxt<-EstimateN(C,Cvar,SPgxt)
> attach(NSPgxt)
>
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N      N.se     N.l95      N.u95
 [1,]  727.5886  470.1784  205.0298  2581.9919
 [2,]  418.5234  173.7992  185.4543   944.5013
 [3,]  514.2827  201.9194  238.2287  1110.2216
 [4,]  281.8189  115.8272  125.9276   630.6950
 [5,] 1222.5494  517.7683  533.0438  2803.9475
 [6,] 1711.9682  869.4585  632.6848  4632.3779
 [7,]  705.9844  234.1826  368.4998  1352.5487
 [8,]  982.7763  467.2578  387.0315  2495.5318
 [9,] 2000.0107 2274.5679  215.2593 18582.4418
[10,] 2313.7154 2825.7463  211.2109 25345.6586
[11,] 1695.1417 1365.0593  349.7358  8216.2180
[12,] 1334.4396 1132.2211  252.9726  7039.2157
[13,] 5458.8487 4714.2589 1004.5934 29662.7747
[14,] 1511.3746  768.2252  558.0872  4093.0037
[15,] 1627.6470  806.8742  616.0074  4300.6539
[16,] 2022.9328 1247.0073  604.3118  6771.7643
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                 mu        mu.se mu.l95   mu.u95
 [1,] 1.533056e-06 0.0001451589      0 172.1963
 [2,] 1.533056e-06 0.0001451589      0 172.1963
 [3,] 1.533056e-06 0.0001451589      0 172.1963
 [4,] 1.533056e-06 0.0001451589      0 172.1963
 [5,] 1.533056e-06 0.0001451589      0 172.1963
 [6,] 1.533056e-06 0.0001451589      0 172.1963
 [7,] 1.533056e-06 0.0001451589      0 172.1963
 [8,] 1.533056e-06 0.0001451589      0 172.1963
 [9,] 1.533056e-06 0.0001451589      0 172.1963
[10,] 1.533056e-06 0.0001451589      0 172.1963
[11,] 1.533056e-06 0.0001451589      0 172.1963
[12,] 1.533056e-06 0.0001451589      0 172.1963
[13,] 1.533056e-06 0.0001451589      0 172.1963
[14,] 1.533056e-06 0.0001451589      0 172.1963
[15,] 1.533056e-06 0.0001451589      0 172.1963
[16,] 1.533056e-06 0.0001451589      0 172.1963
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                 q        q.se        q.l95      q.u95
 [1,] 0.019988248 0.011540902 0.0064168283 0.06139461
 [2,] 0.027618792 0.009768321 0.0137715725 0.05501155
 [3,] 0.026195085 0.009263529 0.0130646970 0.05218203
 [4,] 0.018063479 0.005216800 0.0102433454 0.03175972
 [5,] 0.015452684 0.005464172 0.0077154215 0.03083042
 [6,] 0.009054469 0.004049411 0.0037635609 0.02170318
 [7,] 0.016530317 0.004585881 0.0095871216 0.02843094
 [8,] 0.009915795 0.004434599 0.0041210752 0.02376234
 [9,] 0.007737170 0.007737324 0.0010851664 0.05407537
[10,] 0.003470184 0.003469993 0.0004879240 0.02445864
[11,] 0.006838515 0.004835848 0.0017063938 0.02719733
[12,] 0.004499285 0.002597508 0.0014497013 0.01391946
```

```
[13,] 0.003678309 0.002600728 0.0009189495 0.01466275
[14,] 0.008454769 0.003781196 0.0035146107 0.02026882
[15,] 0.007254048 0.002961572 0.0032558585 0.01612259
[16,] 0.005597624 0.003231811 0.0018030081 0.01730957
> detach(NSPgxt)
>
> ##------------------------------------------------------------------------------
> ## Estimate Model Phi(constant),P(group+time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=1),rep(-2,times=9))
>
> ## Fit the model
> SPgat<-FitCJS(p,
+           PhiDesign=cDesign,PDesign=gatDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRc,NPphi=NPc,NRp=NRgat,NPp=NPgat,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SPgat)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -359.2209
> np
[1] 10
> AIC
[1] 738.4418
> AICc
[1] 738.7284
> detach(SPgat)
>
> ## Estimate population size from catch
> NSPgat<-EstimateN(C,Cvar,SPgat)
> attach(NSPgat)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N      N.se     N.l95     N.u95
 [1,]  717.0373  403.1755  238.1879 2158.5585
 [2,]  503.6438  202.1194  229.3602 1105.9334
 [3,]  553.9497  198.5444  274.3977 1118.3048
 [4,]  306.8608  116.6561  145.6609  646.4572
 [5,] 1348.5646  523.3857  630.2451 2885.5861
 [6,] 1194.0055  436.6748  583.0382 2445.2072
 [7,]  668.7914  190.9623  382.1552 1170.4197
 [8,]  852.1668  326.0801  402.5389 1804.0199
 [9,] 2092.3576 1278.5174  631.6942 6930.5064
[10,]  974.5636  450.5387  393.8168 2411.7157
[11,] 1313.3952  548.0636  579.6862 2975.7597
[12,] 1001.6809  465.3163  403.0036 2489.7167
[13,] 3960.5431 1775.8952 1644.6428 9537.5733
[14,] 2680.8632 1131.4751 1172.2308 6131.0688
[15,] 1853.3488  662.1258  920.1361 3733.0367
[16,] 2718.0274 1178.7030 1161.7535 6359.0712
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se mu.l95   mu.u95
 [1,] 1.515677e-05 0.0004595384      0 48.32869
 [2,] 1.515677e-05 0.0004595384      0 48.32869
 [3,] 1.515677e-05 0.0004595384      0 48.32869
 [4,] 1.515677e-05 0.0004595384      0 48.32869
 [5,] 1.515677e-05 0.0004595384      0 48.32869
 [6,] 1.515677e-05 0.0004595384      0 48.32869
 [7,] 1.515677e-05 0.0004595384      0 48.32869
 [8,] 1.515677e-05 0.0004595384      0 48.32869
```

```
 [9,] 1.515677e-05 0.0004595384      0 48.32869
[10,] 1.515677e-05 0.0004595384      0 48.32869
[11,] 1.515677e-05 0.0004595384      0 48.32869
[12,] 1.515677e-05 0.0004595384      0 48.32869
[13,] 1.515677e-05 0.0004595384      0 48.32869
[14,] 1.515677e-05 0.0004595384      0 48.32869
[15,] 1.515677e-05 0.0004595384      0 48.32869
[16,] 1.515677e-05 0.0004595384      0 48.32869
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q        q.se       q.l95       q.u95
 [1,] 0.020290730 0.010199170 0.007548311 0.053970958
 [2,] 0.022773679 0.007721898 0.011692950 0.044125838
 [3,] 0.024259088 0.007810351 0.012881338 0.045460652
 [4,] 0.016531171 0.004400208 0.009802033 0.027816082
 [5,] 0.013975720 0.004515497 0.007410564 0.026281141
 [6,] 0.013050159 0.004219645 0.006916988 0.024555144
 [7,] 0.017476739 0.004178266 0.010929406 0.027891967
 [8,] 0.011452052 0.004120860 0.005650529 0.023141603
 [9,] 0.007392522 0.003959355 0.002583734 0.021057567
[10,] 0.008303691 0.003154518 0.003940065 0.017458035
[11,] 0.008849476 0.003236027 0.004317725 0.018094774
[12,] 0.006015601 0.001894531 0.003243360 0.011144232
[13,] 0.005081551 0.001845668 0.002492313 0.010346843
[14,] 0.004743620 0.001719902 0.002329564 0.009647250
[15,] 0.006361602 0.001845832 0.003600789 0.011227348
[16,] 0.004160604 0.001647305 0.001913909 0.009032762
> detach(NSPgat)
>
> ##-------------------------------------------------------------------------------------
> ## Estimate Model Phi(constant),P(group)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=1),rep(-2,times=2))
>
> ## Fit the model
> SPg<-FitCJS(p,
+           PhiDesign=cDesign,PDesign=gDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRc,NPphi=NPc,NRp=NRg,NPp=NPg,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SPg)
The following object is masked _by_ .GlobalEnv:

    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -361.4641
> np
[1] 3
> AIC
[1] 728.9282
> AICc
[1] 728.9471
> detach(SPg)
>
> ## Estimate population size from catch
> NSPg<-EstimateN(C,Cvar,SPg)
> attach(NSPg)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
             N       N.se    N.l95      N.u95
 [1,]  877.0166  243.54302 508.8961  1511.4245
 [2,]  687.9052  190.75847 399.4690  1184.6063
 [3,]  805.9071  223.79629 467.6343  1388.8766
 [4,]  307.4355   86.07458 177.5962   532.1995
```

```
 [5,] 1146.5086  317.93078 665.7817  1974.3438
 [6,]  948.1260  263.28976 550.1580  1633.9725
 [7,]  707.0137  196.05732 410.5654  1217.5120
 [8,]  593.8570  165.52494 343.8930  1025.5114
 [9,] 2592.7625 2149.37520 510.6365 13164.7799
[10,] 1354.0449 1120.56081 267.4207  6856.0035
[11,] 1944.5719 1612.03140 382.9774  9873.5849
[12,] 1012.3493  836.56395 200.4100  5113.7720
[13,] 3385.1122 2801.40204 668.5518 17140.0087
[14,] 2139.0291 1773.23454 421.2751 10860.9434
[15,] 1978.9886 1637.74273 390.8457 10020.3128
[16,] 1902.0544 1580.49170 373.1755  9694.6631
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
               mu       mu.se mu.l95   mu.u95
 [1,] 0.000288466 0.005168155      0 26.96962
 [2,] 0.000288466 0.005168155      0 26.96962
 [3,] 0.000288466 0.005168155      0 26.96962
 [4,] 0.000288466 0.005168155      0 26.96962
 [5,] 0.000288466 0.005168155      0 26.96962
 [6,] 0.000288466 0.005168155      0 26.96962
 [7,] 0.000288466 0.005168155      0 26.96962
 [8,] 0.000288466 0.005168155      0 26.96962
 [9,] 0.000288466 0.005168155      0 26.96962
[10,] 0.000288466 0.005168155      0 26.96962
[11,] 0.000288466 0.005168155      0 26.96962
[12,] 0.000288466 0.005168155      0 26.96962
[13,] 0.000288466 0.005168155      0 26.96962
[14,] 0.000288466 0.005168155      0 26.96962
[15,] 0.000288466 0.005168155      0 26.96962
[16,] 0.000288466 0.005168155      0 26.96962
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
                q        q.se       q.l95       q.u95
 [1,] 0.016515238 0.002321918 0.012533888 0.021747569
 [2,] 0.016515238 0.002321918 0.012533888 0.021747569
 [3,] 0.016515238 0.002321918 0.012533888 0.021747569
 [4,] 0.016515238 0.002321918 0.012533888 0.021747569
 [5,] 0.016515238 0.002321918 0.012533888 0.021747569
 [6,] 0.016515238 0.002321918 0.012533888 0.021747569
 [7,] 0.016515238 0.002321918 0.012533888 0.021747569
 [8,] 0.016515238 0.002321918 0.012533888 0.021747569
 [9,] 0.005957058 0.001289791 0.003896092 0.009103289
[10,] 0.005957058 0.001289791 0.003896092 0.009103289
[11,] 0.005957058 0.001289791 0.003896092 0.009103289
[12,] 0.005957058 0.001289791 0.003896092 0.009103289
[13,] 0.005957058 0.001289791 0.003896092 0.009103289
[14,] 0.005957058 0.001289791 0.003896092 0.009103289
[15,] 0.005957058 0.001289791 0.003896092 0.009103289
[16,] 0.005957058 0.001289791 0.003896092 0.009103289
> detach(NSPg)
>
> ##-----------------------------------------------------------------------------
> ## Estimate Model Phi(constant),P(time)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=1),rep(-2,times=8))
>
> ## Fit the model
> SPt<-FitCJS(p,
+           PhiDesign=cDesign,PDesign=tDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRc,NPphi=NPc,NRp=NRt,NPp=NPt,
+           Ngroups=Ngroups,Nocc=Nocc)
>
> ## Model selection criteria
> attach(SPt)
```

```
The following object is masked _by_ .GlobalEnv:
    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -368.8824
> np
[1] 9
> AIC
[1] 755.7647
> AICc
[1] 755.9937
> detach(SPt)
> ## Estimate population size from catch
> NSPt<-EstimateN(C,Cvar,SPt)
> attach(NSPt)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N     N.se     N.l95     N.u95
 [1,] 1008.2639 568.5224  333.8910 3044.6952
 [2,]  728.0036 290.6536  332.8796 1592.1349
 [3,]  795.6090 282.8766  396.3252 1597.1571
 [4,]  444.6649 166.0985  213.8318  924.6839
 [5,] 1985.9785 759.9291  938.1206 4204.2679
 [6,] 1771.9970 636.8678  876.0516 3584.2331
 [7,]  983.4104 271.9843  571.8887 1691.0562
 [8,] 1264.5018 476.5290  604.1395 2646.6815
 [9,] 1090.0151 614.6188  360.9632 3291.5624
[10,]  525.7803 209.9165  240.4130 1149.8752
[11,]  702.0079 249.5970  349.6987 1409.2563
[12,]  541.3312 202.2068  260.3170 1125.7022
[13,] 2151.4767 823.2565 1016.2973 4554.6236
[14,] 1461.8975 525.4159  722.7426 2956.9923
[15,] 1009.9890 279.3352  587.3452 1736.7604
[16,] 1475.2521 555.9505  704.8294 3087.7950
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu        mu.se mu.l95   mu.u95
 [1,] 1.224394e-06 0.0001373558      0 206.2651
 [2,] 1.224394e-06 0.0001373558      0 206.2651
 [3,] 1.224394e-06 0.0001373558      0 206.2651
 [4,] 1.224394e-06 0.0001373558      0 206.2651
 [5,] 1.224394e-06 0.0001373558      0 206.2651
 [6,] 1.224394e-06 0.0001373558      0 206.2651
 [7,] 1.224394e-06 0.0001373558      0 206.2651
 [8,] 1.224394e-06 0.0001373558      0 206.2651
 [9,] 1.224394e-06 0.0001373558      0 206.2651
[10,] 1.224394e-06 0.0001373558      0 206.2651
[11,] 1.224394e-06 0.0001373558      0 206.2651
[12,] 1.224394e-06 0.0001373558      0 206.2651
[13,] 1.224394e-06 0.0001373558      0 206.2651
[14,] 1.224394e-06 0.0001373558      0 206.2651
[15,] 1.224394e-06 0.0001373558      0 206.2651
[16,] 1.224394e-06 0.0001373558      0 206.2651
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
               q        q.se       q.l95      q.u95
 [1,] 0.014318431 0.007159683 0.005359855 0.03796893
 [2,] 0.015572996 0.005191581 0.008091217 0.02987046
 [3,] 0.016726431 0.005289846 0.008987246 0.03102747
 [4,] 0.011268443 0.002909884 0.006788674 0.01867688
 [5,] 0.009420162 0.002979087 0.005064558 0.01748905
 [6,] 0.008744203 0.002765280 0.004701434 0.01623525
 [7,] 0.011776198 0.002701921 0.007507214 0.01845045
 [8,] 0.007690673 0.002719164 0.003843085 0.01536089
 [9,] 0.014318431 0.007159683 0.005359855 0.03796893
[10,] 0.015572996 0.005191581 0.008091217 0.02987046
[11,] 0.016726431 0.005289846 0.008987246 0.03102747
[12,] 0.011268443 0.002909884 0.006788674 0.01867688
```

```
[13,] 0.009420162 0.002979087 0.005064558 0.01748905
[14,] 0.008744203 0.002765280 0.004701434 0.01623525
[15,] 0.011776198 0.002701921 0.007507214 0.01845045
[16,] 0.007690673 0.002719164 0.003843085 0.01536089
> detach(NSPt)
>
> ##------------------------------------------------------------------------------
>
## Estimate Model Phi(constant),P(constant)
>
> ## Starting values for the parameters
> p<-c(rep(2,times=1),rep(-2,times=1))
> ## Fit the model
> SP<-FitCJS(p,
+           PhiDesign=cDesign,PDesign=cDesign,
+           marray=m,effort=effort,dt=dt,
+           NRphi=NRc,NPphi=NPc,NRp=NRc,NPp=NPc,
+           Ngroups=Ngroups,Nocc=Nocc)
> ## Model selection criteria
> attach(SP)
The following object is masked _by_ .GlobalEnv:
    dt, effort, Ngroups, Nocc
> CJS$maximum ## = log-likelihood kernel
[1] -371.2971
> np
[1] 2
> AIC
[1] 746.5942
> AICc
[1] 746.6005
> detach(SP)
> ## Estimate population size from catch
> NSP<-EstimateN(C,Cvar,SP)
> attach(NSP)
> ## Population summary
> cbind(N,N.se,N.l95,N.u95)
              N      N.se    N.l95    N.u95
 [1,] 1284.1381  924.5768 313.1389 5266.067
 [2,] 1005.7526  715.6055 249.3673 4056.419
 [3,] 1180.0188  849.6111 287.7493 4839.089
 [4,]  448.0696  308.2179 116.3619 1725.363
 [5,] 1676.2543 1192.6759 415.6122 6760.699
 [6,] 1388.2574  999.5425 338.5286 5693.045
 [7,] 1033.6902  735.4835 256.2942 4169.098
 [8,]  871.0539  634.8729 208.7518 3634.627
 [9,] 1388.2574  999.5425 338.5286 5693.045
[10,]  726.3769  516.8262 180.0986 2929.636
[11,] 1041.1930  749.6569 253.8964 4269.784
[12,]  545.4761  375.2218 141.6579 2100.442
[13,] 1815.9422 1292.0656 450.2465 7324.090
[14,] 1145.3124  824.6226 279.2861 4696.762
[15,] 1061.6277  755.3614 263.2210 4281.776
[16,] 1016.2296  740.6851 243.5438 4240.398
> ## mu summary
> cbind(mu,mu.se,mu.l95,mu.u95)
                mu       mu.se       mu.l95   mu.u95
 [1,] 0.0007166745 0.009371691 5.329071e-15 18.39886
 [2,] 0.0007166745 0.009371691 5.329071e-15 18.39886
 [3,] 0.0007166745 0.009371691 5.329071e-15 18.39886
 [4,] 0.0007166745 0.009371691 5.329071e-15 18.39886
 [5,] 0.0007166745 0.009371691 5.329071e-15 18.39886
 [6,] 0.0007166745 0.009371691 5.329071e-15 18.39886
 [7,] 0.0007166745 0.009371691 5.329071e-15 18.39886
 [8,] 0.0007166745 0.009371691 5.329071e-15 18.39886
 [9,] 0.0007166745 0.009371691 5.329071e-15 18.39886
[10,] 0.0007166745 0.009371691 5.329071e-15 18.39886
[11,] 0.0007166745 0.009371691 5.329071e-15 18.39886
```

```
[12,] 0.0007166745 0.009371691 5.329071e-15 18.39886
[13,] 0.0007166745 0.009371691 5.329071e-15 18.39886
[14,] 0.0007166745 0.009371691 5.329071e-15 18.39886
[15,] 0.0007166745 0.009371691 5.329071e-15 18.39886
[16,] 0.0007166745 0.009371691 5.329071e-15 18.39886
> ## q summary
> cbind(q,q.se,q.l95,q.u95)
               q        q.se       q.l95      q.u95
 [1,] 0.01120904 0.001710885 0.008308922 0.01511378
 [2,] 0.01120904 0.001710885 0.008308922 0.01511378
 [3,] 0.01120904 0.001710885 0.008308922 0.01511378
 [4,] 0.01120904 0.001710885 0.008308922 0.01511378
 [5,] 0.01120904 0.001710885 0.008308922 0.01511378
 [6,] 0.01120904 0.001710885 0.008308922 0.01511378
 [7,] 0.01120904 0.001710885 0.008308922 0.01511378
 [8,] 0.01120904 0.001710885 0.008308922 0.01511378
 [9,] 0.01120904 0.001710885 0.008308922 0.01511378
[10,] 0.01120904 0.001710885 0.008308922 0.01511378
[11,] 0.01120904 0.001710885 0.008308922 0.01511378
[12,] 0.01120904 0.001710885 0.008308922 0.01511378
[13,] 0.01120904 0.001710885 0.008308922 0.01511378
[14,] 0.01120904 0.001710885 0.008308922 0.01511378
[15,] 0.01120904 0.001710885 0.008308922 0.01511378
[16,] 0.01120904 0.001710885 0.008308922 0.01511378
> detach(NSP)
```

Mark Output

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
{Phi(.)p(s)}	708.1105	0.0000	0.69370	1.0000	3	156.8043
{Phi(s)p(s)}	710.1126	2.0021	0.25493	0.3675	4	156.7809
{Phi(t)p(s)}	714.1626	6.0521	0.03365	0.0485	10	148.5413
{Phi(s)p(.)}	715.8483	7.7378	0.01449	0.0209	3	164.5421
{Phi(s)p(t)}	720.6119	12.5014	0.00134	0.0019	10	154.9906
{Phi(.)p(s*t)}	721.7588	13.6483	0.00075	0.0011	17	141.4972
{Phi(.)p(.)}	721.9928	13.8823	0.00067	0.0010	2	172.7056
{Phi(s)p(s*t)}	723.8775	15.7670	0.00026	0.0004	18	141.4972
{Phi(.)p(t)}	724.9848	16.8743	0.00015	0.0002	9	161.4282
{Phi(t)p(.)}	727.6531	19.5426	0.00004	0.0001	9	164.0965
{Phi(s*t)p(s)}	728.5990	20.4885	0.00002	0.0000	18	146.2187
{Phi(t)p(s*t)}	734.2798	26.1693	0.00000	0.0000	23	141.2018
{Phi(s*t)p(.)}	734.6125	26.5020	0.00000	0.0000	17	154.3509
{Phi(t)p(t)}	737.0894	28.9789	0.00000	0.0000	15	161.0446
{Phi(s*t)p(t)}	743.0941	34.9836	0.00000	0.0000	23	150.0161
{Phi(s*t)p(s*t)}	748.3240	40.2135	0.00000	0.0000	30	139.9712

LR Test on the top two models, as they are nested:

Reduced Model	General Model	Chi-sq.	df	Prob.
(Phi(.)p(s))	(Phi(s)p(s))	0.023	1	0.8784

No statistical significant difference between the two models. But use S()p(s) as it is less complex.

BOOTSTRAPPING

First: General Model **Phi(s*t)p(s*t):**

Original deviance 139.9712

Number 870/1000 iterations has deviance 140.372 therefore;

(1000-870)/1000 = p = 0.13

Parsimonious model Phi(.) p(s)

Original deviance 156.8043