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An investigation into the behaviour and population dynamics of the lemon shark (*Negaprion brevirostris*)

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Abstract

Coastal shark populations have been subject to increasing anthropogenic pressure over the past two decades. This study focused on two lemon shark (*Negaprion brevirostris*) populations, the site-attached maturing sub-adults at the Island of Bimini, Bahamas, threatened by a large-scale resort development, and adults forming winter aggregations off the coast of Jupiter, Florida, subject to direct fishing pressure. For the sub-adult population, analysis was carried out on the long-term temporal patterns in abundance and population structure, relative to potential driving factors, and the influence of variables affecting longline catch-rates used as the basis for stock assessment. For the aggregating adult population, life-history aspects of population structure and distribution were investigated for relative implications on the species' vulnerability status. The following analysis and methodologies were utilised to investigate the two populations: longline catch records from 1982 – 2008; monitoring of variables potentially affecting longline catch-rates; documentation of shark behavioural interactions with longline equipment using underwater video surveillance; aerial surveying for abundance estimates; comparison of spatial utilisation patterns with longline catch locations; external tagging; the utilisation of archival satellite tags; passive tracking with Vemco acoustic monitoring system and research collaborations with other scientific groups utilising the same acoustic monitoring system. The key findings of this study were that in the northwest Atlantic, *N. brevirostris* populations are experiencing considerable anthropogenic pressure at all life-stages. In Bimini, the effects of a large-scale resort development have resulted in a significant decline in abundance, to a level (~52 individuals) well below the temporal average (~158). On the U.S. east coast, seasonal aggregating behaviour has further increased vulnerability through increased catchability, beyond the highly vulnerable status already attributed to this species, and targeted *N. brevirostris* fisheries appear to be currently operating at unsustainable levels. Shark longline catchability was noted to be significantly influenced by multiple shark presence, resulting in greater susceptibility for *N. brevirostris* (and other similar species) that naturally exhibit group behaviour. Incidental encounterability and predation risk significantly influenced longline catch-rates.

Adult *N. brevirostris* exhibited large-scale seasonal migrations on the U.S. east coast, which, in addition to documented international transitions, supports existing evidence for genetic mixing across the distribution. Water temperature was found to be a significant driver of *N. brevirostris* behaviour at all life-stages, with an apparent adult temperature preference of ~24°C. This study represents the first long-term abundance assessment for sub-adult *N. brevirostris*, and the first in-depth study to focus on an adult *N. brevirostris* population. The results provide essential life-history information, revealing that at all life-stages *N. brevirostris* appear to be highly sensitive to anthropogenic activities, relative to other species, and therefore require enhanced management for species protection. It is therefore highly recommended that *N. brevirostris* be added to the U.S. prohibited species list.

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1. General Introduction

1.1. Chapter Introduction

This chapter provides a general background to the role of apex predators in marine ecosystems and general shark life-history relevant to the research focus of this study. The existing lemon shark (*Negaprion brevirostris* Poey 1868) life-history information relevant to this study is detailed along with the official current conservation status for this species. This is followed by the description of the study populations that form the research focus, the research motivation behind, and the overall aims and objectives of, this study.

1.1.2. Apex Predators

The work of Volterra (1928) long ago highlighted the importance of apex predators in the functioning of terrestrial ecosystems, with particular reference to population dynamics and energy exchanges between trophic levels. Apex predators are no less important in the marine environment than the terrestrial (Gruber, 1982). Smith and Mead (1974), Steele (1974) and Hassell (1976), among others, have demonstrated that apex predators can induce both oscillating and stabilising influences on ecosystem dynamics. Therefore the population dynamics of apex predators closely influence the ecosystems they inhabit. Many past population studies in the marine environment have focused solely on teleost species, yet, in the many marine environments, the influence of arguably the most important predators – the sharks – has often been overlooked (Gruber, 1982, Strasburg, 1958, Moss, 1972, Soucie, 1976, Gruber, 1977b, Myrberg, 1976).

Sharks, like all apex predators, have a very important influence over the equilibrium of the ecosystems they inhabit. Bascompte et al (2005) recently constructed a quantitative ecosystem model of a Caribbean coral reef food web, which suggested that sharks regulate the population size of large piscivorous fishes, in turn controlling herbivorous fish populations that graze algae, therefore maintaining the overall balance of the system (Pikitch et al., 2005). This suggests that, in this example, a decline in the shark population could ultimately lead to a shift from coral to algal dominated reefs (Pikitch et al., 2005, Bascompte et al., 2005). Additionally, due to predation of smaller sharks by larger sharks, declines in the abundance of larger sharks can lead to an increase in abundance of smaller sharks (Ulrich, 1995). Aside from their ecological importance, in many regions around the globe, living sharks are of more economic value to humans than the market value from harvest in fisheries (Info, 2000). Sharks are highly valued by some sports anglers, who usually now take only small numbers, but may contribute significantly to our knowledge by participating in tagging and research programmes, and are important contributors to the economy of coastal communities (Kohler and Turner, 2001, Trust, 2005). Sharks are also one of the main target species for observations by scuba-divers participating in a multi-million dollar industry, as well as drawing large attention from other members of the public at aquaria.

Chondrichthyes all diverged from a common ancestor, retaining the same major skeletal features for the duration of their 400 million year existence (Motta et al., 1997, Schaeffer and Williams, 1977, Long and Long, 1995), in which time they have evolved to exploit a wide variety of niches in the aquatic environment (Compagno, 1990). Despite a global distribution, much recent media attention and growing conservation concerns, relatively little is known of many biological and life-history aspects of elasmobranchs (Feldheim et al., 2001a). Sharks typically show *K*-selected life-history strategies, displaying slow growth rates, late maturity, long gestation periods and low fecundity (Musick et al., 2000). Sharks and other elasmobranchs account for low fecundity by maternally investing in larger offspring with relatively high survival rates (Frisk et al., 2001, Hussey et al., 2009b). Female sharks only produce enough offspring to sustain the population under low, natural levels of mortality, and communities are unable to sustain higher levels of mortality through increased fecundity to replace the large quantities lost through anthropogenic influences (NMFS, 1999). Therefore survival at the immature life-stage subsequently has considerable influence over total shark population dynamics (Frisk et al., 2001). Sharks clearly differ from long-lived teleost fish in their population biology, therefore management plans designed for teleost fish are inappropriate for application to shark stocks (Feldheim et al., 2001a, Musick et al., 2000).

Sharks have few natural predators, principally other larger sharks, such that anthropogenic impacts are of key importance in affecting shark species populations

(Musick et al., 2000, NOAA, 1995, Pratt et al., 1990). Globally, it has been estimated that some 100 million sharks have been harvested annually in recent years (Bonfil, 1997, Trust, 2005, Bonfil, 2000). The growth of many targeted shark fisheries has been driven by the recent expansion of demand in the international trade for shark products, particularly fins to supply the East Asian market (NMFS, 1999). Baum et al. (2003) and (2004) reported that long-line fisheries were responsible for declines of scalloped hammerheads (*Sphyrna lewini*) by 89%, threshers (*Alopias sp.*) by 80%, white sharks (*Carcharodon carcharias*) by 79%, oceanic whitetips (*Carcharhinus longimanus*) by 70%, tiger sharks (*Galeocerdo cuvier*) by 65% and blue sharks (*Prionace glauca*) by 60%. Though there is currently much debate over the validity of this data (Baum et al., 2005, Burgess et al., 2005a, Burgess et al., 2005b), even a fraction of these values would indicate a serious need for more effective shark management. However, effective management is only built upon sound life-history data and accuracy of stock assessments (Cortes, 2004).

In recent years, beginning in the early 1980s, U.S. shark resources have received a reasonable amount of attention in the form of many biological studies, encompassing several commercially important species, (Bonfil, 1997, Prince and Pulos, 1983, Pratt et al., 1990). Focused biological studies resulted in shark management plans to be initiated in the late 1980s that has helped to control the previously rapidly increasing exploitation (Bonfil, 1997, NOAA, 1995). A major advance in U.S. shark management occurred in 2002 with the complete ban of all shark finning (the removal and retention of a captured shark's fins only, with the body discarded), both commercial and recreational, whereby all harvested sharks have to be landed whole with the fins intact (NOAA/NMFS, 2006). A number of shark species have been added to the 'prohibited species list' (Appendix 1), which prohibits the landing of the listed species in U.S. state and federal waters (NOAA/NMFS, 2006). On a global scale, basking sharks (*Cetorhinus maxim's*), whale sharks (*Rhincodon typus*) and white sharks (*Carcharodon carcharias*) have all been added to the Convention of International Trade in Endangered Species (CITES) Appendix II, which has resulted in international trade of these species being heavily regulated (CITES, 2009). The importance of protecting shark stocks is increasing in global recognition and resultant management measures are progressively being implemented. The subsequently high demand for comprehensive shark species life-history, and accurate stock assessment data, is driving the feasibility in executing studies of this nature through the availability of funding resources.

1.1.3. Existing lemon shark (*Negaprion brevirostris*) life-history information and current conservation status

The lemon shark (*Negaprion brevirostris*; Poey 1868) is classed as a Large Coastal Shark (LCS) species (NOAA/NMFS, 2006). Belonging to the family Carcharhinidae, it is a large stocky, blunt nose shark, most easily identified by its similarly sized first and second dorsal fins (Compagno, 1988). *N. brevirostris* most commonly inhabit shallow sub-tropical waters around coral reefs, mangroves, seagrass beds, enclosed bays, sounds and river mouths (Morgan, 2005, Compagno, 1988), with a diet consisting mainly of bony fish and crustaceans (Wetherbee et al., 1990, Morrissey and Gruber, 1993a, Morrissey and Gruber, 1993b, Cortes and Gruber, 1990, Motta et al., 1997, Newman, 2003). *N. brevirostris* are active predators that use their eyes for hunting (Cohen, 1990), and all elasmobranchs, like most vertebrates, are able to see over a range of 10 log units of light intensity, from very bright to very dim (Cohen and Gruber, 1977, Gruber and Cohen, 1978). *N. brevirostris* are very well visually adapted for the near shore, coastal and even freshwater environments (Cohen, 1990). The visual pigment of the juvenile *N. brevirostris* was found to be better optimised for the shallow water environment than that of the adult (Cohen, 1990), which logically follows the ontogenetic shift from extremely shallow to deeper water through the *N. brevirostris* life-stages (Gruber, 1982). Like most shark species, *N. brevirostris* have the sensory ability for electroreception and can detect voltage gradients as low as 0.01 μV/cm, within the frequency range from DC up to 8Hz (Dawson et al., 1982, Fields, 2007, Lisney et al., 2007, Mello, 2009). It is commonly accepted that sharks use this sense for navigation and predation, and in relation to shark fishing the possible detection of the metal hook and leader.

N. brevirostris are one of the larger Carcharhinidae species, reaching a maximum length of ~260 cm Pre-Caudal Length (PCL), with both females and males reaching sexual maturity at around 12 years of age and ~166 cm PCL (Morgan, 2005, Brown and Gruber, 1988, Gruber et al., 1985). Three distinct life-stages are recognised for *N. brevirostris*: nursery bound juvenile (45 – 80 cm PCL) and sub-adult (81 – 165 cm PCL) both defined by home-range relative to age and size, and adult (166+ cm PCL) defined by the individual reaching sexual maturity (Gruber, 1982, Morgan, 2005, Sundström et al., 2001, Compagno, 1988). *N. brevirostris* are viviparous and therefore give birth to live free swimming pups, in litters of 4 – 17 individuals, therefore like many elasmobranch species, *N. brevirostris* depend on high maternal investment in a low number of large sized offspring (Feldheim et al., 2002a). *N. brevirostris* offer no physical post natal care to their offspring, and therefore rely on the suitability of the nursery site to ensure the relatively high level of survivorship for their litter (Feldheim et al., 2002a, Hussey et al., 2009b). At the nursery bound juvenile life stage *N. brevirostris* growth rate is largely governed by prey availability (Cortes and Gruber, 1994, Gruber, 1982) with a maintenance requirement of 20,600 calories or 16.5g of food per day, which is ~1.7% of their total body weight (Cortes and Gruber, 1990). Therefore at the nursery bound juvenile life-stage, *N. brevirostris* rely heavily for growth and survival on the prey availability within the nursery grounds they inhabit (Frisk et al., 2001).

N. brevirostris is one of, if not the, most intensively studied shark species (Ache de Freitas et al., 2009, Barker et al., 1997, Brown and Gruber, 1988, Chapman et al., 2009, Cohen and Gruber, 1977, Cortes and Gruber, 1994, Cortes and Gruber, 1992, Cortes and Gruber, 1990, de Freitas et al., 2009, Dibattista et al., 2007, Feldheim et al., 2001a, Feldheim et al., 2002a, Feldheim et al., 2004, Franks and Gruber, 2007, Freitas et al., 2006, Gruber, 1982, Gruber, 1984, Gruber et al., 1985, Gruber and Stout, 1983, Morrissey and Gruber, 1993a, Morrissey and Gruber, 1993b, Motta et al., 1997, Nixon and Gruber, 1988, Rasmussen and Gruber, 1993, Sundström et al., 2001, Watsky and Gruber, 1990, Wetherbee et al., 1990, Wetherbee et al., 2007). However, to date the vast majority of this research has focused on the juvenile life-stage and to a lesser extent the sub-adult life-stage (Kessel et al., 2009b). The majority of existing life-history data relating to the *N. brevirostris* adult life-stage had been reconstructed from the genetics obtained from juveniles (Dibattista et al., 2008, Feldheim et al., 2001a, Feldheim et al., 2002a, Feldheim et al., 2001b, Feldheim et al., 2004). Reconstruction to a satisfactory level of confidence was possible due to the extensive *N. brevirostris* genetic bank, that represents the second longest running fish genetic bank for any species, second only to salmon (Salmonidae; personal communications, Feldheim 2009).

From the genetic reconstructions, a number of discoveries were made relative to mature *N. brevirostris* life-history, some of which were the first examples of their kind for any shark species. Reconstruction revealed a biennial breeding cycle for mature *N. brevirostris*, with mature female *N. brevirostris* divided into two breeding groups, one group exhibiting parturition in even years and one group in odd (Feldheim et al., 2002a). *N. brevirostris* were the first shark species found to be polyandrous, with 86% of litters at Bimini found to have multiple (2 – 4) sires (Feldheim et al., 2001b, Feldheim et al., 2004, Dibattista et al., 2008). Female *N. brevirostris* were found initially to display a high level of philopatry (Feldheim et al., 2004), which more recently was confirmed as the first recorded case of specific natal homing for any shark species, through a combination of genetic and external tagging (Feldheim et al., 2009). Therefore the environmental health and state of all specific nursery sites is important for *N. brevirostris* breeding behaviour. Conversely, with the genetic markers of individual mature male *N. brevirostris* rarely replicated in separate breeding seasons, mature male *N. brevirostris* were assumed to be nomadic and wide roaming in their mature life-stage movements (Dibattista et al., 2008, Feldheim et al., 2002a, Feldheim et al., 2001b, Feldheim et al., 2004). Finally, through the analysis of DNA microsatellite variation, the western Atlantic distribution of *N. brevirostris* was found to represent a single stock unit (Feldheim et al., 2001a). Therefore the geographic regions addressed by this study (see below) represent *N. brevirostris* individuals from a single stock unit.

Many *N. brevirostris* life-history qualities make it the perfect species to form the focus of this study. Due to its large size and lack of natural predators in the adult stages, *N. brevirostris* is considered an 'apex predator' (Gruber 1982). *N. brevirostris* are commercially targeted, thus economically valuable and directly subject to fisheries pressure (NOAA/NMFS, 2006, Morgan et al., 2009). *N. brevirostris* size, abundance, generalised structure, ease of capture and adaptability to captivity (Gruber 1982) makes this species perfectly suited to systematic investigation. These characteristics have also allowed the collection of behavioural, bioenergetic and physiological data in both the field and laboratory (Gruber, 1982). Due to its unspecialised body shape and relatively average size of maturity in comparison to most other sharks, for *N. brevirostris*, many of the heretofore intractable elements of autecology of a tropical marine shark are soluble (Gruber, 1982). This will therefore allow the results of this study to be applied broadly to many other subtropical shark populations.

Currently *N. brevirostris* are classed as a Highly Migratory Species (HMS) by the National Marine Fisheries Service (NMFS; NOAA, 2009). *N. brevirostris* conservation status is currently listed as 'Near Threatened' by the International Union for Conservation of Nature (IUCN) Red List, largely due to habitat degradation of nursery areas (IUCN and SSC, 2000).

1.1.4. *N. brevirostris* study populations

This study focused on two populations of *N. brevirostris*, geographically separated by 160 km on opposing sides of the Gulf Stream, Bimini, Bahamas to the east and Jupiter, Florida to the west (Figure 1).

1.1.4.1. Bimini, Bahamas (25°44 N, 79°16 W)

The Bimini Islands are located on the far western edge of the Great Bahama Bank, approximately 80 km due east, across the Gulf Stream, from the Continental U.S. Considered a Mecca for big game fishing in the early 1900s, Bimini was frequented by the late author Ernest Hemmingway and provided the muse for his famous work 'The Island in the Stream' (Saunders, 2000). The current resident population of Bimini is ~1600 people, with development historically consisting of low-scale residential and small-scale tourists resorts with ~80 slip mariners (Saunders, 2000, Gruber, 2002). Bimini's economy revolves predominately around the marine environment through dive tours, and recreational and artisinal fisheries (Lutz et al., 2002), and it has been estimated that the tourism related annual value for each live shark in the Bahamas is around US$15,000 (Info, 2000). The Bimini Islands are surrounded by a wide range of marine habitats that have resulted in the presence of a high shark biodiversity and abundance (Chapman et al., 2009, Feldheim et al., 2002a).

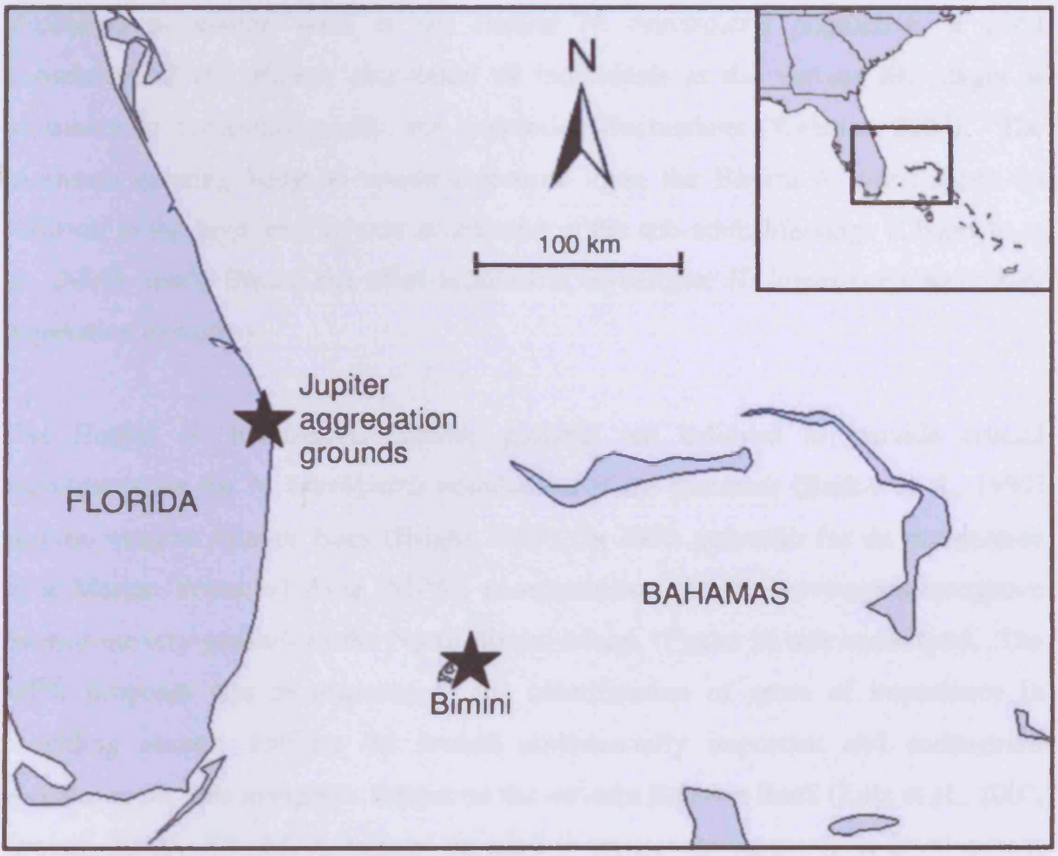


Figure 1. Geographical locations of *N. brevirostris* study populations

Bimini supports a relatively abundant *N. brevirostris* population containing all life-stages from neonate juveniles through to mature adults (Feldheim et al., 2002a) as a result of Bimini's habitat diversity, which includes a number of primary mangrove fringed nurseries, a large secondary sub-adult population in the central lagoon, the extensive shallow waters of the Great Bahama Bank to the east and the deep waters of the Gulf Stream to the west (Feldheim et al., 2002a, Chapman et al., 2009). For populations such as the Bimini *N. brevirostris*, with multiple age cohorts inhabiting the same areas, interactions can be an important source of density dependence, which in turn is essential for regulating population dynamics (Webster, 2004). For example, juvenile mortality increases as a function of adult density from inter-species predation and competition with adults, thus forcing them to overlap spatially with other predators (Webster, 2004). Therefore population growth rate is influenced inversely by population size, which can in turn stabilise population dynamics (Royama, 1977, Cappuccino and Price, 1995, Hixon and Webster, 2002). In a stage-structured population such as the Bimini *N. brevirostris* population, a good knowledge of the relative abundance of individuals at the various life stages is necessary to accurately predict the population fluctuations (Webster, 2004). The extensive existing body of research focused upon the Bimini *N. brevirostris*, in addition to the high level of site attachment at the sub-adult life-stage (Chapman et al., 2009), made Bimini the ideal location to investigate *N. brevirostris* secondary population dynamics.

The Bimini *N. brevirostris* nursery grounds are believed to provide crucial recruitment for the *N. brevirostris* populations of the Bahamas (Barker et al., 1997) and the western Atlantic Bank (Bright, 1999). In 2000, proposals for the designation of a Marine Protected Area (MPA), compromising the *N. brevirostris* mangrove fringed nursery grounds of the North Bimini Island, (Figure 2) was announced. The MPA proposal was in response to the identification of areas of importance in providing nursery habitats for several commercially important and endangered species, as the sole mangrove habitat on the western Bahama Bank (Lutz et al., 2002, Gruber, 2002). The MPA, largely intended to restrict the mega-resort development activities of the 'Bimini Bay Development', was initiated in 1997, with plans including mass seabed excavation and the complete removal of all North Sound nursery fringing mangroves (Appendix 2; Gruber, 2002, Jennings et al., 2007). However, a change of government in May 2002 resulted in a loss of support for the MPA proposal and the granting of planning permission to the Bimini Bay Development for the full extent of its site plans (Jennings et al., 2007, Lutz et al., 2002, Gruber, 2002). Subsequently, to date mass seabed excavation has been conducted in addition to the removal of 30% of total fringing mangroves from the North Sound nursery (Jennings et al., 2007). Results of a study by Jennings et al (2007) showed a decrease in nursery seagrass bed coverage and a reduction in nursery bound juvenile *N. brevirostris* survival rates, subsequent to the initiation the large-scale Bimini Bay Development.

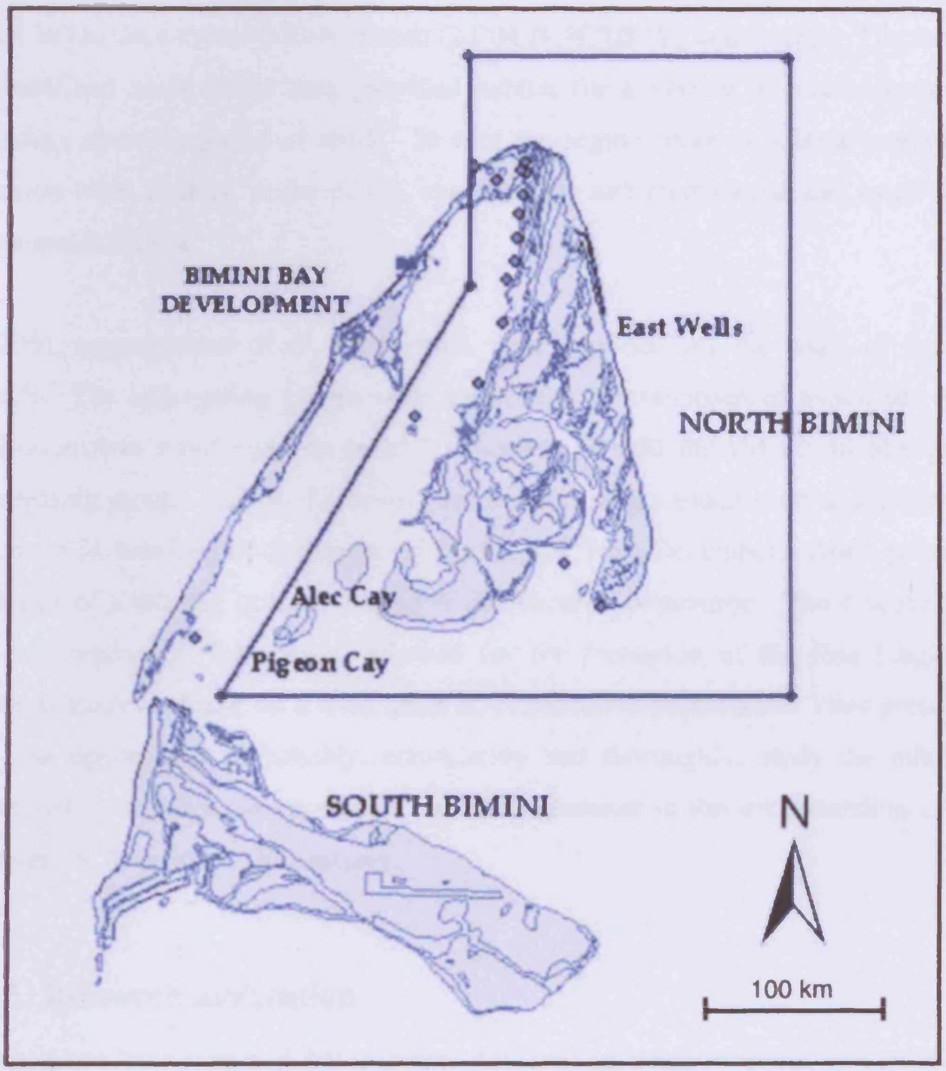


Figure 2. Designated area of North Bimini MPA (BBFS, 2009b)

1.1.4.2. Jupiter, Florida (26°55 N, 80°06 W)

Jupiter is a coastal community located on the southeast Atlantic coast of Florida, with a total resident population of ~39,328 people in 16,945 households (TOJ, 2009). Jupiter is centred on the Loxahatchee River and the Jupiter Inlet leading out to the Atlantic Ocean, with a long history of small scale local commercial fisheries. The marine environment is comprised of the relatively thin continental shelf (~6 km) dropping off steeply to the east into the deep waters of the Gulf Stream. The shelf contains reef-lines at 50 and 120 m depth contours, with an intermittent string of artificial reefs, running south to north established between Delray Beach (26°27 N, 80°04 W) to the south and Hobe Sound (27°04 N, 80°08 W) to the north. The natural and artificial reefs of the area provided habitat for a variety of marine creatures including several species of shark. In turn the region receives a large amount of attention from boaters, scuba divers, spearfishers, and recreational and small scale commercial fishing.

In 2001, aggregations of *N. brevirostris* were reported off the coast of Jupiter, Florida. The aggregating groups were reported to be comprised of mixed sex adult *N. brevirostris* numbering up to and in excess of 100 individuals in any given aggregating group. Repeated year-on-year reports and documentation of aggregating groups of *N. brevirostris* during the winter months, from December – April, provided evidence of a reliably occurring adult *N. brevirostris* population. The discovery of the aggregating *N. brevirostris* allowed for the formation of the first long-term research study to focus on a wild adult *N. brevirostris* population. Thus presented the first opportunity to reliably, consistently and thoroughly, study the adult *N. brevirostris* life-stage, in an attempt to fill the lacunae in the understanding of the complete *N. brevirostris* life-history.

1.1.5. Research motivation

Recent years have seen a global increase of interest in elasmobranchs, particularly in relation to the need for management advice (IMM, 1997, ICES, 1997) and conservation (STECF, 2002). However, the biggest hurdle in achieving this is a basic lack of species life-history data to be used in assessment (Rodriguez-Cabello et al., 2004, Feldheim et al., 2001a, Cortes, 2002, NMFS, 1999, NOAA, 1995, Musick et al., 2000). The lack of species life-history data, in addition to limited understanding over the effects of variables affecting catch rates, can lead to considerable errors in the stock assessments that form the basis for management decisions (Cortes, 2004, Gruber and Hoenig, 1990, Pratt et al., 1990, Musick et al., 2000). For example, populations can often be underestimated from mark-recapture data. Otway et al. (2004) found that population estimates of Australian grey nurses (*Carcharias taurus*), based on mark-recaptures, were around 300 individuals of an actual population of closer to 1000. Also, as part of stock assessment of the whiskery shark (*Furgaleus macki*) in south-western Australia Simpfendorfer et al. (2000) found raw catch and effort data to produce unrealistic estimates of true current biomass. The identified inaccuracies highlight the need to improve the understanding of assessment techniques, in order to improve the accuracy of results.

The recent publication of high profile articles, suggesting the collapse and possible extirpation of the northwest Atlantic and Gulf of Mexico shark stocks (Baum et al., 2003, Baum and Myers, 2004), may have greatly influenced a number of subsequent conservation decisions, despite much scepticism from the scientific community over the validity of the results (Burgess et al., 2005a, Burgess et al., 2005b, Baum et al., 2005). Many questions were raised in relation to shortfalls in accounting for influencing variables in the analysis catch records (Burgess et al., 2005a), however the true influence of many of the driving variables over shark catch rates are currently poorly understood (Ward, 2008). Additionally, the lack of life-history data such as habitat utilisation patterns, for many shark species is restricting the ability for effective stock assessments, as an essential requirement of which is the definition of the area of distribution and its geographical limits (Rodriguez-Cabello et al., 2004). Booke (1981) gave the general definition of a stock as: "a species group or population of fish that maintains and sustains itself over time in a definable area". Therefore, stock assessment for elasmobranchs is entirely dependent on accurate estimations of population size, dispersal capability and annual survival (Otway et al., 2004).

For *N. brevirostris*, despite an extensive existing Bimini longline catch database, no in-depth population assessment has ever been conducted for the secondary sub-adult life-stage lagoon based population. The Bimini *N. brevirostris* longlines catch database spans from 1982 – 2008, but to date had never been critically analysed for temporal variations in catches. Additionally for the juvenile and sub-adult *N. brevirostris* life-stages, a comprehensive understanding, relative to other shark species, is provided by the extensive body of past *N. brevirostris* focused studies (see section 1.1.3), thus provided a good platform for the critical analysis of the Bimini longline catch dataset. At the *N. brevirostris* adult life-stage the western Atlantic distribution had previously been genetically demonstrated to represent a single stock unit (Feldheim et al., 2001a). However, a lack of focused study on mature *N. brevirostris* has resulted in a poor understanding of adult life-history, for this species, on which to base effective stock assessments (Otway et al., 2004). The discovery of the seasonal Jupiter adult *N. brevirostris* winter aggregations subsequently provided the research opportunity to greatly increase the understanding of the *N. brevirostris* adult life-history, to in turn facilitate more effective stock assessment on which to base future management decisions.

In Bimini, Bahamas, the mega-resort activities of the Bimini Bay Development had been documented to have reduce *N. brevirostris* nursery survival rates (Jennings et al., 2007). Survival rates at the juvenile life-stage often has great influence on the population abundance growth rate of long-lived species such as *N. brevirostris* (Frisk et al., 2001), thus the long-term existing Bimini longline dataset, with results prior and post development activities, provided the opportunity to assess the secondary effects of the Bimini Bay Development activities to the lagoon sub-adult population.

In a recent Environmental Risk Assessment (ERA) conducted by the National Marine Fisheries Service (NMFS), *N. brevirostris* was found to be the Large Coastal Shark (LCS) species most vulnerable to the direct pressure imposed by the U.S. east and Gulf coast commercial fisheries (Cortes et al., 2008). The results of the ERA highlighted the urgent need to provide mature life-history data for *N. brevirostris* inhabiting U.S. east and Gulf coast waters, to allow for effective management regulations to be devised in response to the newly attributed highly vulnerable status for this species.

Driven by the identified research motivations, the overall aims of this study were to a) assess the long-term temporal patterns of the Bimini lagoon *N. brevirostris* population, in relation to potential driving factors; b) assess the life-history structure, distribution and vulnerability of the Jupiter aggregating *N. brevirostris* population;

and c) assess the influence of variables affecting longline catch rates used for the basis of stock assessments. The stated aims were achieved by the critical analysis of the Bimini longline database from 1982 – 2008, the incorporation of existing *N. brevirostris* life-history data in the analysis of results, the monitoring of variables potentially affecting longline catch-rates, the documentation of shark behavioural interactions with longline equipment using underwater video surveillance, aerial surveying of the Bimini lagoon *N. brevirostris* population, the comparison of Bimini sub-adult *N. brevirostris* spatial utilisation patterns with longline catches, the establishment of a representative Jupiter *N. brevirostris* aggregation study population through polyball capture, processing and release, external tagging under the National Marine Fisheries Service (NMFS) Cooperative Shark Tagging Program (CSTP), the utilisation of pop-off archival satellite tags, the passive tracking of mature *N. brevirostris* using the Vemco® acoustic monitoring system, and research collaborations with other scientific groups utilising the Vemco® acoustic monitoring system. Between the two study sites, it was possible to assess the implications of the contrasting pressures – mega-resort development driven habitat loss/alteration to a secondary sub-adult dominated *N. brevirostris* population in Bimini, Bahamas, and direct commercial fisheries pressure to the mature aggregating population of Jupiter, Florida.

1.1.6. Thesis structure

This thesis has been structured so that the chapters are presented in a logical order. Following on from this introduction:

Chapter 2 focuses on the historical section of the Bimini longline dataset from 1982 – 2003, divided into two research periods. The first period considers records from the longlining activities, conducted during the Bimini research cruises, from 1982 – 1989, and the second period considers records from longlining activities conducted, out of the island based Bimini Biological Field Station (BBFS), from 1992 – 2003. Temporal analysis of the longline catch records was conducted for both periods and comparisons between the two were made. The effects of potential influencing variables were assessed throughout.

Chapter 3 considers the results of the most recent research section of the longline dataset from 2003 – 2008, following the initiation of a more comprehensive longline regime design. Temporal analysis of the longline catch records was conducted for the research period and comparisons with the two prior research periods, considered in Chapter 2, were made. Additionally all longline catch records from 1982 – 2008 were considered as a single continuous dataset and temporal analysis was conducted. Again the effects of potential influencing variables were assessed throughout, with a greater level of detail provided by the additional monitoring of driving influences during the new longline regime design. The temporal affects of the Bimini Bay Development activities to the lagoon sub-adult *N. brevirostris* population, based on the results of this study, are discussed in Chapters 2 and 3.

Chapter 4 focuses on the assessment of the effects of potential driving variables over the Bimini longline catches. The implications of the results towards the analysis of results in Chapters 2 and 3 are discussed, along with the broader potential implications over longline based stock assessments.

Chapter 5 assesses the life-history, structure and distribution of the Jupiter aggregating adult *N. brevirostris* population. The implications of the results relative to identified anthropogenic pressures, and subsequently the overall *N. brevirostris* vulnerability status in the U.S. east and Gulf coast commercial fisheries, are discussed. Finally recommendations of alterations to shark management regulations, at both a state and federal level for the U.S., based on the results of this study, are given.

Chapter 6 details the key finding of this study. The collective implications of the assessed variables for future shark stock assessment based on longline catch records are discussed. Chapter 6 then draws together and discusses how the cross-chapter results have advanced the understanding of *N. brevirostris* life-history and the implications to the vulnerability of both the secondary *N. brevirostris* sub-adult site-attached population in Bimini and the broader north-western Atlantic *N. brevirostris* stock unit. The current progress in regard to protection for both populations is detailed, followed by the overall conclusions based on the research described in Chapters 1 – 5.

1.1.7. Data sources

Chapter 2 – 1982 – 1989 research campaign data was collected was collected entirely By Dr. Gruber and his various research team members. The author had no active role in field data collection. All data was transcribe from the field data books and organised by the author. **1992 – 2003 research campaign** data was collected by the various staff and volunteers of the Bimini Biological Field Station (BBFS) including the author from 2002 onwards. All data was transcribe from the field data books and organised by the author.

Chapter 3 – the **longline** regime was designed by the author, based on past longlining activities conducted by the BBFS research teams and during the 1980s research cruises. All longline activities were conducted by the staff and volunteers of the BBFS, led by and under the supervision of the author.

Chapter 4 – the **baited hook video surveillance** experiments were conceived and designed by the author in conjunction with Dr. Nigel Hussey of the University of Bangor, and data was collected in the field by the author in conjunction with Mark Bond (an undergraduate industry placement student from Cardiff University) and field teams comprised of BBFS volunteers. **Acoustic tracking** data was collected from 1990 onwards by various project students of the BBFS (including the author from 2002 onwards) and field teams comprised of BBFS volunteers. The **aerial surveys** program was conceived and designed entirely by the author. Aerial surveys were conducted by a field team comprised of BBFS staff, led by the author.

Chapter 5 – The Jupiter lemon shark project pilot studies were initiated by Dr. Gruber and various volunteers that comprised a field research team in 2002. The author joined the project and took over as principal investigator in 2007, shortly after the focused research project was initiated. Following this time, all field data was collected by a field research team led by the author. Data processing was conducted in conjunction with Dr. Todd Gedamke of the National Marine Fisheries Service (NMFS).

2. Historical longline catches

(1982 – 2003)

2.2. Chapter Introduction

This chapter reports the historical Bimini longlining dataset and is divided into two sections. The first section covers the research cruises from 1982 – 1989, and the second comprises research conducted at the Bimini Biological Field Station (BBFS) from 1992 – 2003. The aims of this chapter were to a) assess the shark population dynamics, with specific focus upon lemon shark (*Negaprion brevirostris*), for temporal patterns in catch proportions, Catch Per Unit Effort (CPUE), catch related mortality, mark-recapture and mean Pre-Caudal Length (PCL); and b) to assess the effects of external driving variables, including lunar, temperature, inter/intra-species relationships, and anthropogenic influences, that have influenced the local shark population dynamics. The aims were achieved by the compilation, organisation and analysis of the historical Bimini longline database, the explanation of identified patterns and relationships using existing species life-history information, and the incorporation of influencing historical information, both anthropogenic and environmental.

2.3. 1982 – 1989 research campaign

2.3.1. Background

Since the closure of the Learner Marine Laboratory in 1973, populations of shark species present at the start of the research campaign in 1982 had not been subject to any great anthropogenic pressures or disturbance, with terrestrial development predominantly at a small-scale residential level (Lutz et al., 2002). A number of marinas were built on the western side of the inner lagoon, but all were small scale at around ~30 slips, and had been in place since the early 1900s. In the 1980s the entire Bimini population totalled 1,450 people (Halberstein, 1980), a population size that would unlikely have caused habitat alteration as the result of waste disposal into the marine environment. In addition, the presence of the adjacent Gulf Stream meant that waste, such as sewage, was not localised around the island but transported away from it.

No large-scale commercial fisheries have been present around the islands, and locally, the only artisanal fisheries that have been in operation were for queen conch (*Strobus gigas*) and spiny lobster (*Panulirus argus*; Lutz et al., 2002). Although it does appear that these fisheries, even on a small scale, have resulted in the local depletion of both of the aforementioned species (personal observations 2002 – 2008), neither contribute significantly to the diet of *N. brevirostris* (Newman, 2003, Wetherbee et al., 1990, Cortes and Gruber, 1990), therefore no direct effects on *N. brevirostris* feeding and in turn abundance would have been likely.

The Bimini islands have historically been a popular destination for recreational sport fishermen; however shark fishing has not typically been the focus of their efforts and therefore *N. brevirostris* would have been caught only as by-catch (Saunders, 2000). At the time of the first research cruise in March 1982, the *N. brevirostris* population could be considered relatively uninfluenced by anthropogenic activities.

The research cruises of the 1980s were undertaken and led by Dr. Samuel H. Gruber of the University of Miami. They were funded by the National Science Foundation (NSF) under the long term research project entitled 'Role of the lemon shark *Negaprion brevirostris* in the Marine Ecosystem: A Multidisciplinary Study'. The main purpose of the Bimini research cruises within this project was to collect field data to validate laboratory experiments in bioenergetics (personal communications Gruber 2008). Prior to 1982, fieldwork was conducted off the coast of Miami and also in the Florida Keys. Following severe fishing pressure on the South Florida juvenile *N. brevirostris* population, used primarily as bait in the lobster and stone crab fisheries, *N. brevirostris* specimens became hard to obtain, therefore, forcing a switch of research location to the Bahamas (personal communications Gruber 2008). Bimini was chosen for its high abundance of *N. brevirostris*, the pre-chosen model species, and for the variety of life-stages (neonate, juvenile, sub-adult, and adult; Chapman et al., 2009, Jennings et al., 2007, Feldheim et al., 2001a, Feldheim et al., 2002a, Feldheim et al., 2004, Brown and Gruber, 1988, Barker et al., 1997) that could be sampled there. A population assessment was not conducted as part of the initial research programme. However, fortunately, the analysis of certain research techniques that were utilised to obtain specimens has allowed the study reported here on to be conducted more than 20 years later.

A number of research methods were employed to obtain specimens, including gillnets for juveniles, block rigs, rod and reel, pursuit and netting with an airboat and in a few cases even a crossbow. Many of these techniques were utilised intermittently, but relatively standard longlining was conducted on all 17 research cruises and it is the resultant temporal data set that has been used as the basis for this population assessment. Data from other methods were not considered in this population study.

2.3.2. Methodologies

2.3.2.1. Research cruises

No island-based operations were conducted. Research cruises were conducted from two different research vessels, and were intermittent. Between 1982 – 1986 the main research vessel was the R.V. Cape Florida, a 41 m long, single hulled boat owned by the University of Miami. The R.V. Columbus Iselin, a 19 m long, single hulled boat, also owned by the University of Miami, was utilised between 1986 – 1989. These were used as a floating base of operations for the duration of each cruise. Due to the high vessel drafts (the maximum depth of the vessel below the water), three and two meters respectively, of these larger R.V.s and the very shallow water depths around the islands, they were forced to anchor in deeper waters on the edge of the Gulf Stream. A number of smaller tenders were used to conduct the fieldwork around the shallow waters of the island. These included a 7 m centre counsel Aquasport®, a number of small flat-bottom skiffs and an airboat.

2.3.2.2. Longlines

The majority of the longline gear was obtained from the National Marine Fisheries Service (NMFS), and were originally designed to be floating pelagic longlines. They were adapted into bottom-set longlines by Dr. Gruber, tested and utilised from the 1960s onwards in the similarly shallow waters of Bear and Government Cut off Virginia Key, Miami, Florida (personal communications Gruber 2008). In order to work as bottom-set longlines the usual end floats were replaced with concrete blocks and fluke anchors (Figure 3). This provided the weight to keep the mainline on the bottom, the tension in the line to allow for self-hooking of specimens, and stability to stop the larger sharks from dragging the line out of position. The main bottom line was 3/16 twisted nylon tarred rope of 500 m length. For each of the four bottom-set mainlines 15 gangions were attached with tuna clips. From the tuna clip upwards gangions consisted of 2 m length of twisted nylon 3/16 tarred rope, attached to a heavy duty swivel. On the other side of the gangion was a 2 m length of 3/32 stainless steel aircraft cable attached to the swivel with a copper crimp. In the centre of the length a small foam net float was held in position by two loops in the line held by crimps. Floatation was in response to crab related base loss, noted during the

Miami based survey work, but was also found to eliminate the by-catch of southern stingrays (*Dasyatis americana*). Gangions were tipped with Mustad® 9/0 J hooks secured to the aircraft cable by another copper crimp.

Gangions were attached to the mainline at 30 m intervals and separated by overhand knots in the mainline. Separation reduced the possibility of gangions becoming tangled together. When a shark becomes captured, the knot eliminated the possibility of a shark dragging one gangion, movement provided by the tuna clip, into the neighbouring section. This setup meant that once a shark was captured it could swim within a circle, of radius 4 m, and linearly 30 m by dragging the tuna clip along the mainline. The increased freedom of movement, relative to commercial longlines, was designed to reduce shark mortalities resulting from movement restriction, and therefore suffocation for ram ventilating species. Marker floats were attached to the overhand knots with tuna clips and a 2 m section of 3/16 twisted nylon rope. Floats were white, with the exception of the two end floats that were larger and painted bright orange to signify the start and end points of the set line. This float system allowed the line to be checked by tender without having to haul it in. As the tender drove alongside the line, the small gangion float was registered at the surface between the two larger section marker floats. If one of the smaller gangion floats was not at the surface then that section of line was pulled up by the marker float and checked for the presence of a shark.

The four lines were set, each 500 m in length and containing 15 gangions running north to south in shallow water (1 – 3 m deep depending on tidal state) to the east and south of the main lagoon (Figure 4). Each was set in as straight a line as possible, achieved by a tender driving forwards and the line spooling out of the back of the vessel. The main lines were marked with spray paint for gangion placement. As the line spooled out, the floats were clipped to the overhand knots, the gangions to the main line and then thrown over the side. Once all gangions and floats were deployed, the line was tightened using the power of the boat before the final anchor was set. The gangions were baited with a random mix of Atlantic mackerel (*Scomber scombrus*) and great barracuda (*Sphyraena barracuda*).

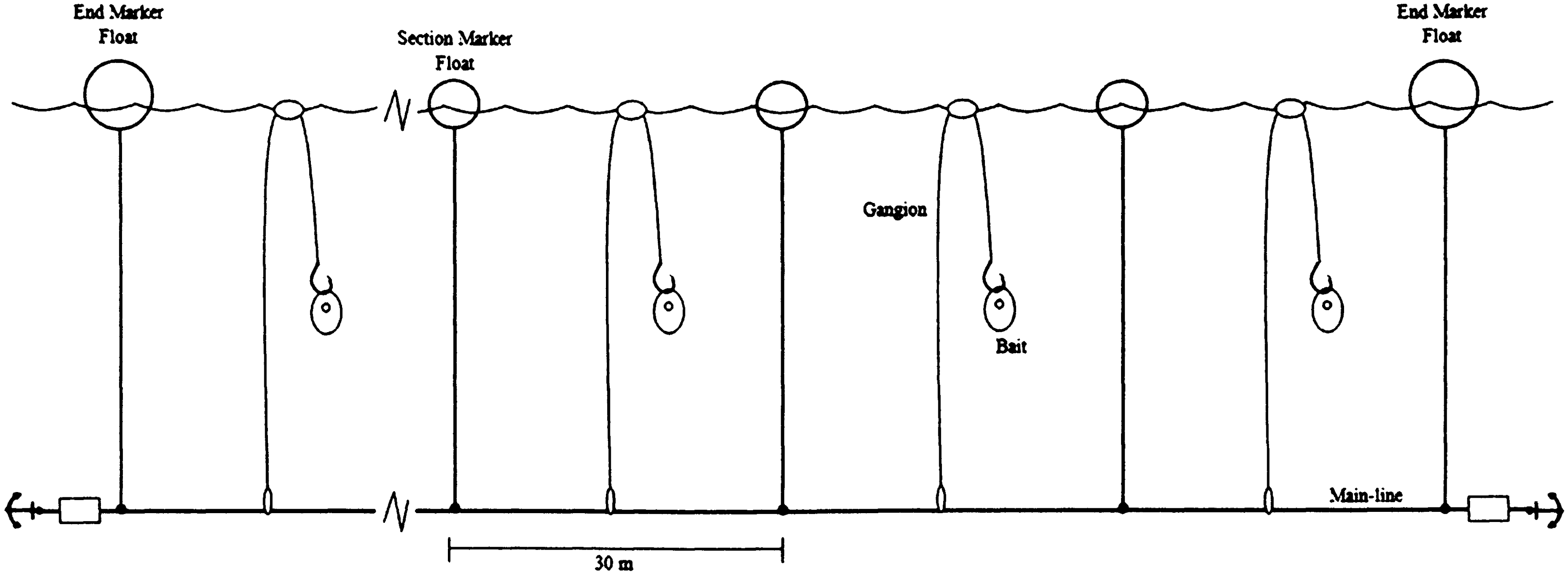


Figure 3. Depiction of bottom set longline gear setup representing either end of the 500 m long rig. Break in the middle is fictional and represents ongoing replicates of depicted set up (not to scale)

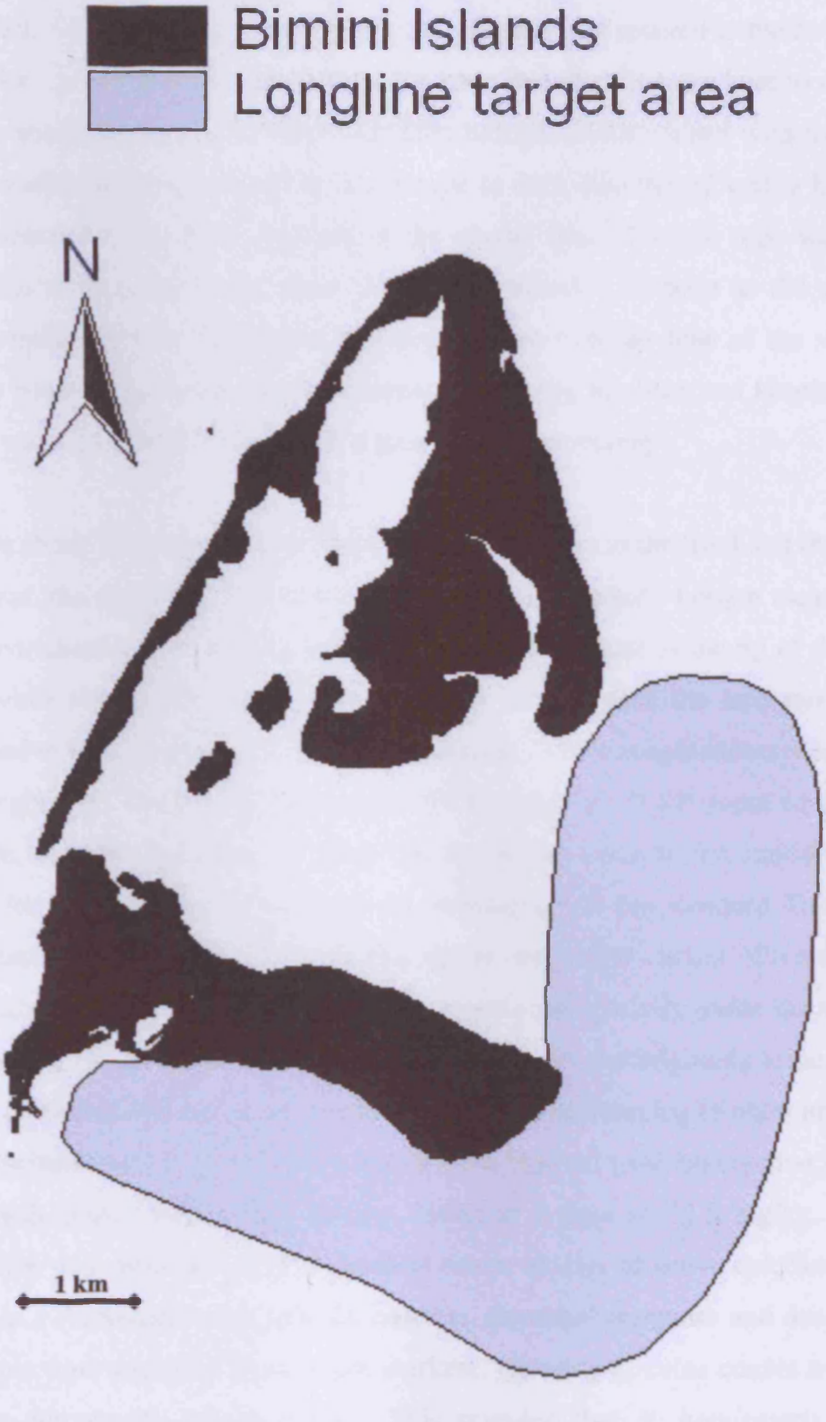


Figure 4. Bimini longline target area (~30 km^2)

2.3.2.3. Shark processing

The lines were checked twice a day, with times dependent on other activities being conducted. When a shark was captured, the gangion was secured to the bow cleat of the tender. It was then detached from the main line allowing the boat to drift away with the shark attached. The shark was then brought under control with the use of a tailer, which was then replaced by a tail rope (a dock line tipped with a hangman's noose) secured to the shark forward of the caudal fins. The tail rope was used to secure the shark's tail to the stern cleat of the vessel. As soon as the shark was brought under control, the anchor was deployed to turn the bow of the vessel and thus the head of the shark into the current, stabilizing the boat and keeping a good flow of water passing over the shark's gills during processing.

Once the shark was secured to the boat, with the gangion to the front and the tail rope to the rear, the species and sex were identified and recorded. Length measurements were then taken using a tape measure, one end held in place at the tip of the shark's snout, while the measurements were taken by the tail once the tape measure was confirmed to be tight and the shark's body straight. Three length measurements were taken (Figure 5), the Pre-Caudal Length (PCL) from tip of the snout to the caudal peduncle, the Fork Length (FL) from the tip of the snout to the caudal fork (not present for nurse sharks *Ginglymostoma cirratum*), and the standard Total Length (TL) from the tip of the snout to the tip of the upper caudal (Francis, 2006). Measurements were made as the shark was positioned naturally under the support of the seawater. If the shark was a first time capture, or the originally issued tag was missing or damaged, it was issued with a NMFS M-type dart tag (Kohler and Turner, 2001). Suitable host *N. brevirostris* sharks were injected with tetracycline for an age and growth study (Brown and Gruber, 1988) at a dose of 12.5 mg/kg. Injected tetracycline was deposited on the vertebral centra at sites of active calcification thus serving as a fluorescent time specific marker. Repeated recapture and dose resulted in multiple time-separated fluorescent markers, allowing circulus counts to be fitted to a von Bertalanffy growth curve. This revealed that *N. brevirostris* are slow growing and long lived (Brown and Gruber, 1988). General comments were recorded, usually in reference to any distinctive markings the specimen had. The hook was then completely removed, if possible, and the shark was released with condition on release recorded. Should the shark be dead on arrival, as many samples as could be utilized were taken, such as vertebrae, eyes, organs and muscle tissues.

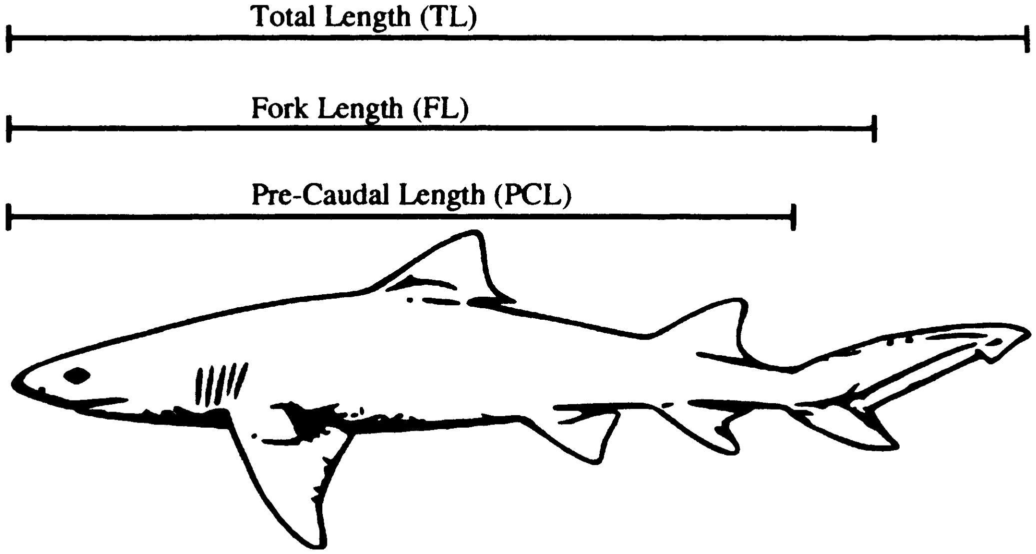


Figure 5. Length measurements taken during shark processing
Example shark = *N. brevirostris*

2.3.2.4. Data set

The workable Bimini longline dataset was compiled from a number of sources. Firstly, the longline logbooks provided catch records for all shark species between December 1984 and May 1989. These were transcribed onto an excel spreadsheet then double checked by a third party for accuracy. All *N. brevirostris* catches between March 1982 and May 1989, for all gear types were recorded additionally in a separate data book. The records from the *N. brevirostris* exclusive data book were also transcribed onto an excel spreadsheet then double checked by a third party for accuracy. Once the data was entered records were examined individually to deduce gear type and isolate the longline catches. Most commonly this was possible from the direct recording of gear type in the individual catch records. When gear type was absent, data were cross-referenced with the cruise logs, hook books, and personal communications with the scientists that operated the longlines on the 1980s cruises. To confirm the accuracy of the data, records for *N. brevirostris* between December 1984 and May 1989 were then cross-checked between the two data books, all longline catches and *N. brevirostris* specimens only. The two data sets were then organized and combined onto a single spreadsheet ready for analysis. The final data set represented a total of 117 *N. brevirostris* captured between March 1982 and May 1989, and an additional 234 sharks of other species captured between December 1984 and May 1989.

2.3.2.5. Analytical methodologies

2.3.2.5.1. Deduction of Unit Effort (UE)

As the main purpose of the longlining activities during the 1980s cruises was not a standardized population assessment, records of fishing effort were not as thorough as would be ideal for this study. Unit Effort (UE) therefore had to be deduced from a range of available information to form the basis for further Catch Per Unit Effort (CPUE) analysis. Deduction of the number of hooks per fishing day was relatively easy as a standard four longlines were set on each research cruise, each with 15 hooks. Thus in a given fishing day, 60 hooks were being fished. The number of days of baited longlines per research cruise, however, varied and were therefore harder to deduce. A number of factors were considered for each research cruise in order to calculate the fishing days (Table 1). UE was then determined from the following:-

$$UE = Fishing\ Days\ \times No.Hooks$$

Subsequently CPUE was calculated as:-

$$CPUE = \frac{No.sharks\ caught}{UE}$$

Where available, cruise start and end date was used to determine the duration of effort. Under usual operating procedure, the longlines were set the day after leaving port in Miami and hauled the day of departure from the islands. The dates of the first and last catch records were also taken into account. It was, and is, unusual not to catch at least one shark within the first 12 hrs of the lines being set, thus the first catch record acted as an indicator for set time (see section 3.3.3). Last catch records can also be a good indication of haul time as with only two checks a day, sharks

Table 1. Research cruise information for shark study expeditions to the Bimini islands, Bahamas, between 1982 – 1989. Records highlighted in grey represent summer month cruises

Cruise	Reserch Vessel	# Hooks	Cruise Start	Criuse Finish	First Catch Record	Last Catch Record	Extra Factors	Fishing days
Mar-82	Cape Florida	60	N/A	N/A	23 March 1982	01 April 1982	N/A	9
Jun-82	Cape Florida	60	N/A	N/A	06 June 1982	19 June 1982	N/A	13
Mar-83	Cape Florida	60	N/A	N/A	07 March 1983	16 March 2007	Storm, no fishing 11 -13th March	7
Jun-83	Cape Florida	60	N/A	N/A	25 June 1983	06 July 1983	N/A	11
Oct-83	Cape Florida	60	22 October 1983	04 November 1983	23 October 1980	04 November 1983	N/A	11
Mar-84	Cape Florida	60	N/A	N/A	02 March 1984	10 March 1984	N/A	7
Jun-84	Cape Florida	60	N/A	N/A	27 May 1984	09 June 1984	N/A	13
Oct-84	Cape Florida	60	N/A	N/A	02 December 1984	08 December 1984	N/A	6
Mar-85	Cape Florida	60	N/A	N/A	27 February 1985	06 March 1985	N/A	7
May-85	Cape Florida	60	06 May 1985	20 May 1985	07 May 1985	18 May 1985	N/A	11
Nov-85	Cape Florida	60	13 November 1985	26 November 1985	14 November 1985	25 November 1985	N/A	11
Jan-86	Cape Florida	60	16 January 1986	28 January 1986	18 January 1986	28 January 1986	Boat capsized, fishing time lost	9
May-86	Columbus Iselin	60	07 May 1986	16 May 1986	09 May 1986	13 May 2006	N/A	7
May-87	Columbus Iselin	60	28 April 1987	12 May 1987	30 April 1987	10 May 1987	N/A	11
May-88	Columbus Iselin	60	12 May 1988	26 May 1988	12 May 1988	24 May 1988	N/A	13
May-89	Columbus Iselin	60	18 May 1989	26 May 1989	19 May 1989	25 May 1989	N/A	7

would have been regularly encountered on the lines during the hauling process (personal communications Gruber 2008). These dates were also compared to the cruise dates, where available, to truth one with the other. Available cruise logs were then examined for continuity with the devised number of days and any relevant entries to the logs, for example circumstances resulting in the interruption of fishing activities were taken into account. Once fishing effort had been devised from the combination of this available data, it was cross-referenced for accuracy with the available hook books for each period. Finally the devised fishing effort was presented to the scientists that operated the longlines during 1980s cruises to verify they were a true and complete representation of fishing effort.

2.3.2.5.2. Assumptions

For data relating to longline fishing, especially historical data, there are a number of necessary assumptions that needed to be made in order to enable temporal records to be comparable (Stoner, 2004). Often it was not possible to monitor all variables whilst the lines were set. Historically these variables, such as temperature and time of day, were frequently not considered in the first place. Ward (2008) identified the following variables that have been justified in relation to their potential influence on shark catchability during the 1980s research campaign:

A. **Encounterability** – variability in movements and migrations can lead to variable rates of species presence in the target area and therefore variable encounter rates with the longline gear;
B. **Fishing location** – though locations were relatively standard within a 30 km^2 target area, there was some discontinuity in specific line placement around the islands. Habitat type remained virtually the same throughout (Hussey, 2003), but it is possible that minor geographic variations may have influenced catch rates;
C. **Fishing-master experience** – as more fishing experience was gained in a given location, the relative skill of the fishing-master in that area could have resulted in increased fishing efficiency;
D. **Operation time** – longer periods of back to back fishing efforts could have affected the number of sharks available for capture, both from a

temporal reduction in near-by individuals and also an increase in dispersion of the odour corridor bringing in sharks from further afield (Lokkeborg and Pina, 1997, Ward et al., 2004);

E. **Bait loss** – unintended bait loss reduced the number of hooks fished, thus reducing fishing effort;

F. **Gear saturation** – once a hook had caught a shark it was then occupied and therefore effort decreased, unless a larger shark becomes captured in a predation attempt of the already captured shark, which would have also altered the fishing power from the presence of a live bait;

G. **Detection of gear** – visual and metallic cues may have alerted sharks to the fishing gear, causing variable rates of gear avoidance, dependant on each individual shark's experience, acuteness and awareness of these said cues;

H. **Hunger** – variable rates of hunger between individuals affect the likelihood of each shark seeking out and taking the bait;

I. **Competition among gears** – a number of other research techniques were used to obtain specimens, and their involvement with other gears could have affected their ability/motivation to interact with the longline gear;

J. **Bait type** – two types of bait were utilized with no complete records relative to each catch record for the period. Each may have been more or less affective at attracting sharks than the other;

K. **Bite-off** – or any form of unsuccessful hooking attempts, and variations between individuals to successfully steal bait, leading to variability in catch rates;

L. **Activity** – the activity caused by the presence of other sharks on or around the long lines may have acted as an attractant catalyst for bait taking or deterrent (see section 4.4.1.2);

M. **Environmental factors** – these may have included water temperature, salinity and turbidity. Variations in all of which may have influenced catch rates;

N. **Diel** - it is possible that time of day could have influenced catch rates, for example it has been documented for various species of elasmobranchs that feeding activity increases during crepuscular hours. Fortunately fishing efforts were most commonly conducted for 24 h periods from set to haul/re-bait; therefore diel influences would have been largely eliminated;

O. **Lunar** - the effects of lunar phase on the behaviour and activities (Dewar et al., 2008, Graham et al., 2006, Hernandez-Leon, 2008, Kraus and Rooker, 2007, Kuparinen et al., 2009, Nanami and Yamada, 2009, Oliveira et al., 2009, Whitty et al., 2009), and CPUE (Bigelow et al., 1999, Lowry et al., 2007), are well documented for many teleost and elasmobranch species. Therefore, the lunar phase under which fishing effort was conducted could have influenced the catch rates;

P. **Hook type** - hooking success can relate directly to hook type (Bolten et al., 2002, Cooke et al., 2003a, Cooke and Suski, 2004, Cooke et al., 2003b, Falterman and Graves, 2002, Galeana-Villasenor et al., 2008, Hand, 2001, Huse and Ferno, 1990, Malchoff et al., 2002, McEachron et al., 1985, Prince et al., 2002, Skomal et al., 2002). During the 1980s campaign all hooks used were standardised as Mustad® 9/0 J hooks, therefore there was no influence from variability of hook type.

It is assumed for the subsequent results and analysis that this list of variables had no effect upon the catch records included in the data set. In a given section, should a variable be accounted for, or additional variable assumed to have no further effect, this will be stated at the beginning of the specific analytical methodology section.

2.3.2.5.3. Seasonal variation

Seasonal patterns exist in CPUE for total catch of all species and *N. brevirostris* specimens at the Bimini Islands (see section 3.3.4). The most consistent cruise time over the entire survey was the summer months between April – July, with at least one cruise taking place during these months every year. It was therefore possible that during years with additional out of season cruises, the influence of data collected outside of the summer months could be skewing the identification of temporal trends. Two data sets were therefore compiled, one comprising the data from all research cruises and one for data from summer month research cruises only. Where seasonal and non-seasonal dataset represented equal record numbers, they were checked for normality and a t-test for significant difference between the two catch data sets was conducted. Only when the two datasets were found by the t-test to be significantly different, were results from both data sets considered for further analysis and comparison.

2.3.2.5.4. Species catch proportions

Proportions were calculated for each species from all cruises where multiple species records existed, December 1984 to May 1989. Proportions of total CPUE and were analysed by cruise for *N. brevirostris*. Total proportions for all cruises were analysed to assess the community structure of the sharks present from the years 1982 – 1989.

2.3.2.5.5. Catch Per Unit Effort (CPUE)

Due to variability of fishing effort between cruises, it was necessary to conduct all analysis of catch rates as a normalised value of CPUE as described above. A Spearman rank correlation test was conducted for species CPUE against cruise CPUE. Multivariate analysis (MVA) was then conducted using a cluster analysis to identify groups of species and cruises showing similar properties and dissimilar outliers. The cluster analyses were followed by Principal Component Analysis (PCA) using score and loading plots to identify which cruises were responsible for the species groupings and which species were responsible for the cruise groupings. Software used was Minitab 1.5®.

2.3.2.5.6. Catch related mortality

Scientific sacrifices contributed to total catch related mortalities for several of the captured species, most prominently *N. brevirostris*. However should a shark have suffered death as a direct result of its interaction with the longline gear and been recorded as Dead On Arrival (DOA), samples similar to the sacrificed individual were almost always taken. As it is not known for each of these individuals what its fate would have been decided to be, i.e. sacrificed or released, if it was not recorded as DOA, it was impossible to separate the two causes of catch related mortality. Thus no definition for analytical purposes was made. For *N. brevirostris*, catch related mortalities were analysed by cruise as: the total number caught, total number killed, and proportion of the total number caught that were killed. For all species catch related mortality is reported for the entire research period where multi-species records exist, December 1984 to May 1989. Mortalities were also analysed as: total number caught, total number killed, and proportion of the total number caught that were killed.

*2.3.2.5.7. **Mark-recapture rates***

In addition to the assumption that all variables A – P had no effect upon catchability for the analysis of mark-recapture rates, zero incidences of tag loss by individuals was assumed. This was a justified assumption as the tag loss study conducted by Gruber (personal communications) during the 1980s yielded a result of 97% retention for this type of tag. Sharks were tagged with a multitude of different tag styles over the research period. The most consistent tag used was the NMFS issue stainless steel dart tags (Kohler and Turner, 2001). Therefore, only recaptures indentified through the presence of a previously applied NMFS dart tags captures were considered as a mark-recapture. Sharks caught by other gears and techniques were also issued tags and when subsequently recorded on the longline gear, were recorded as a recapture of the total research efforts. These however did not constitute a mark-recapture for the longlining efforts, thus only mark-recaptures that were originally caught and tagged under the previous longlining efforts were considered for this data set. For species with mark-recaptures recorded, rates were analysed by cruise as: total number caught, total number of mark-recaptures, and proportion of the total number caught that were mark-recaptures.

*2.3.2.5.8. **Temporal Pre-Caudal Length (PCL) variation of N. brevirostris***

Of the three length measurements taken during the processing of sharks, Pre-Caudal Length (PCL) was used for length-based analysis. PCL is the most accurate and representative of all the length measurements (Francis, 2006). Fork Length (FL) measurements have a relatively low potential of measurement errors, however certain species such as *G. cirratum* do not have a caudal fork, thus preventing the potential for cross species comparisons to be made. Total Length (TL) is the most unreliable and unrepresentative of the three length measurements. Firstly there is an ongoing dispute over which TL length measurement, stretch or standard, should be employed (Francis, 2006). Secondly, as it involves the absolute extremities of the shark being measured, it is the longest of the three distances point to point and therefore subject to the largest possible error. Thirdly, as many species reach the upper limits of their size range, it is a common occurrence for a proportion of their upper caudal to be missing, whether through mating, predation attempts or many other possible causes (personal observations 2002 – 2008). For many species the upper caudal can represent a large proportion of their TL, these occurrences can cause individual sharks to fall into unrepresentative size classes. PCL is the measurement with the least margin for measurement error and subject to no potential externally influenced morphometric changes over time (Francis, 2006). If the tail was removed beyond the caudal peduncle the absence of a caudal fin would result in the loss of mobility required for survival. For all these reasons, size based analysis is conducted on PCL measurement.

In a few cases only TL was measured. PCL was plotted against TL from 615 available *N. brevirostris* records. A linear trend line ($r^2 = 0.996$, $n = 615$, $P < 0.0001$) was fitted to generate the equation for PCL from TL:

$$PCL = (0.7589 \times TL) + 1.6861$$

Missing PCLs were then generated from TL to fill in the missing records. For all cruises, minimum, maximum and mean PCL were calculated.

2.3.2.5.9. *National Marine Fisheries Service (NMFS) landing records*

Large Coastal Shark (LCS) landings of the U.S. east coast and Gulf fisheries must be considered to have the potential to effect the Bimini *N. brevirostris* population for two reasons. Firstly, the results of a genetic study by Feldheim et al. (2001a) showed the east coast distribution of *N. brevirostris* to represent a single stock. Secondly, *N. brevirostris* tagged under the NMFS Cooperative Shark Tagging Program (CSTP) in Bimini have been shown to cross the Gulf Stream (Kohler et al., 1998) and therefore directly expose themselves to the U.S. coastal fisheries. Thus on a broader scale, the effects of *N. brevirostris* catches in the US fishery could influence *N. brevirostris* population dynamics in the nearby waters of the Bimini Islands. Results from the 'SEDAR 11 Stock Assessment Report' (NOAA/NMFS, 2006) were utilised for comparative analysis. Three variations of catch records were presented in the report: the baseline scenario including all LCS species, the baseline-prohibited scenario excluding prohibited species, and the 'baseline-prohib-SB-BT' scenario excluding prohibited species plus sandbar sharks (*Carcharhinus plumbeus*) and *Carcharhinus limbatus*. Of the three datasets the baseline scenario was selected, as many of the excluded species in the other two scenarios were Carcharhinidae species with similar life-history patterns to *N. brevirostris* (NOAA/NMFS, 2006). Therefore their removal from the dataset would have increased the ratio of *N. brevirostris* relative to other non-Carcharhinidae species, thus making them less representative to proportional *N. brevirostris* catches.

In addition to the previously stated assumptions A – P, total annual LCS species landing records were assumed to be proportionally representative of *N. brevirostris* catches contained within. Annual catch records were extracted from the report then plotted against annual *N. brevirostris* Bimini CPUE records for the same period. Results were examined for pattern and then a Spearman rank correlation test was conducted on the Bimini *N. brevirostris* CPUE and the NMFS 'baseline-prohib-SB-BT' scenario for the same time period.

2.3.3. Results

2.3.3.1. Unit Effort (UE)

UE varied between cruises from 420 – 780 with a mean of 573.75 (± 37.13 s.e.; Figure 6).

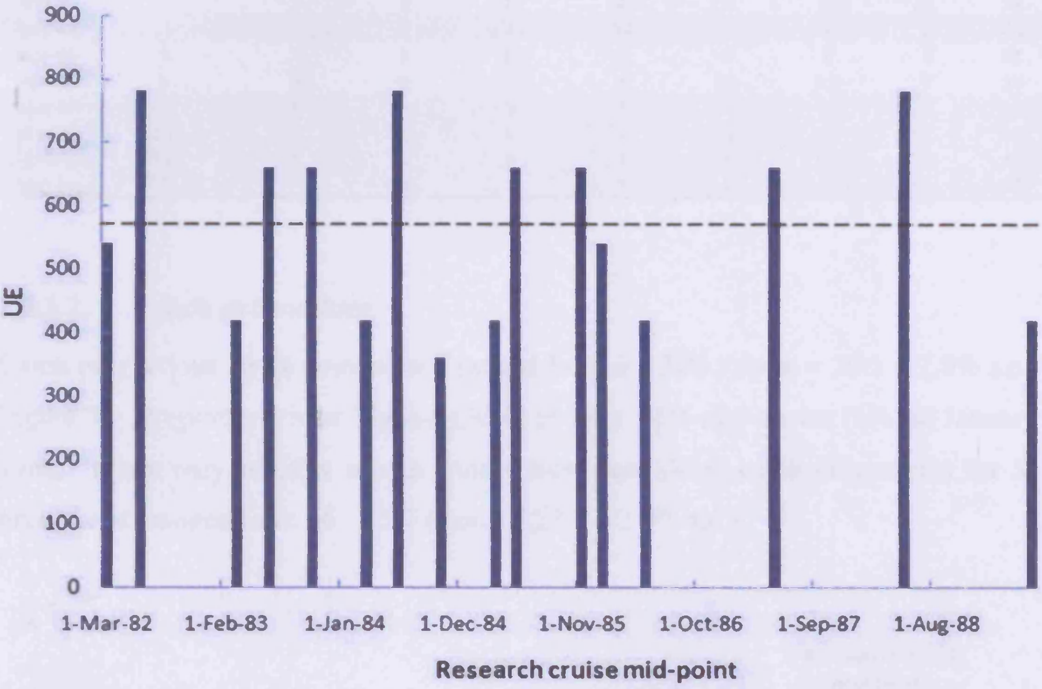


Figure 6. . UE for each 1980s research cruise as a product of number of hooks × number of fishing days. Cruises plotted by mid-point date. Dashed line represents mean UE (mean = 573.75 ± 37.13 s.e.)

A total of 351 sharks were captured (Table 2), which represented eight different species: lemon shark (*Negaprion brevirostris*), blacknose shark (*Carcharhinus acronotus*), bull shark (*Carcharhinus leucas*), blacktip shark (*Carcharhinus limbatus*), nurse shark (*Ginglymostoma cirratum*), tiger shark (*Galeocerdo cuvier*), Caribbean sharpnose shark (*Rhizoprionodon porosus*) and bonnethead shark (*Sphyrna tiburo*).

Table 2. Number of sharks caught by species and total for 1980 cruises - rows highlighted in grey represent summer month cruises

Cruise	*N. brevirostris*	*C. acronotus*	*C. leucas*	*C. limbatus*	*G. cirratum*	*G. cuvier*	*R. porosus*	*S. tiburo*	Total
Mar-82	12	N/A	N/A	N/A	N/A	N/A	N/A	N/A	12
Jun-82	15	N/A	N/A	N/A	N/A	N/A	N/A	N/A	15
Mar-83	5	N/A	N/A	N/A	N/A	N/A	N/A	N/A	5
Jun-83	2	N/A	N/A	N/A	N/A	N/A	N/A	N/A	2
Oct-83	3	N/A	N/A	N/A	N/A	N/A	N/A	N/A	3
Mar-84	12	N/A	N/A	N/A	N/A	N/A	N/A	N/A	12
Jun-84	7	N/A	N/A	N/A	N/A	N/A	N/A	N/A	7
Oct-84	4	2	0	5	3	10	6	0	30
Mar-85	4	2	2	1	2	5	13	0	29
May-85	14	3	0	0	13	4	8	2	44
Nov-85	6	2	1	2	4	4	2	0	21
Jan-86	2	2	0	0	3	14	11	0	32
May-86	3	1	0	1	2	6	6	0	19
May-87	10	3	3	2	5	11	15	1	50
May-88	11	6	1	0	3	6	14	1	42
May-89	7	5	0	4	7	4	1	0	28

2.3.3.2. Catch proportions

Catch proportions for *N. brevirostris* ranged from 6 - 32% (mean = 20.1 ± 2.9% s.e.; Figure 7). Proportions were highest (36%) in May 1985 and lowest (6%) in January 1986. When only summer month cruises were considered catch proportions for *N. brevirostris* ranged from 16 - 32% (mean = 23.8 ± 2.7% s.e.).

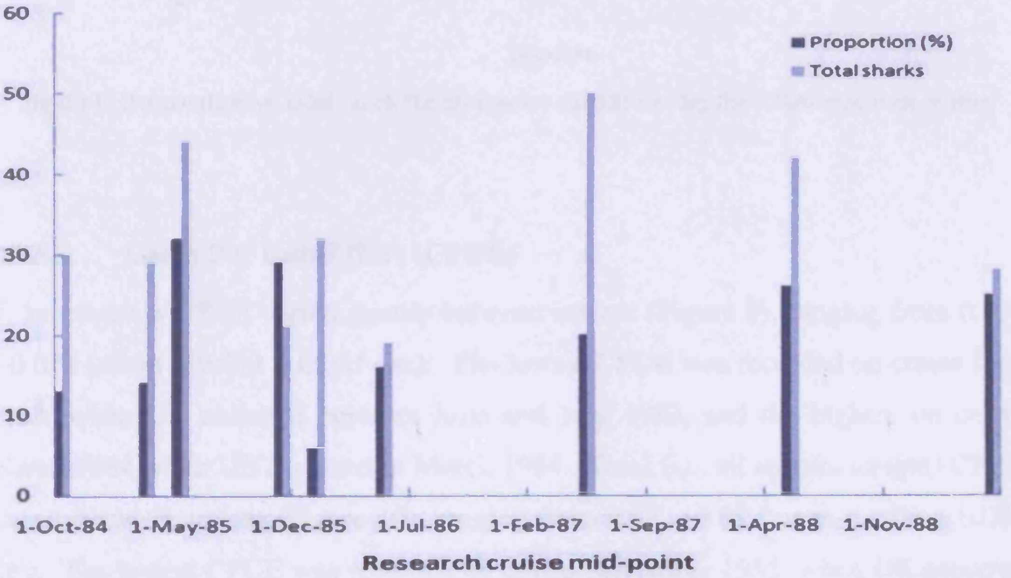


Figure 7. Proportion of *N. brevirostris* caught on longlines, during 1980s research cruises, relative to the total of all sharks captured

Proportions of *N. brevirostris* for the entire 1980s research period were 21% of total catch for all species (Figure 8). Overall the four species with the highest catch proportions were: *R. porosus* (26%), *G. cuvier* (22%), *N. brevirostris* (21%) and *G. cirratum* (14%). These four species represented the most abundant shark species present in the waters around the Bimini Islands that were susceptible to capture by longline tackle.

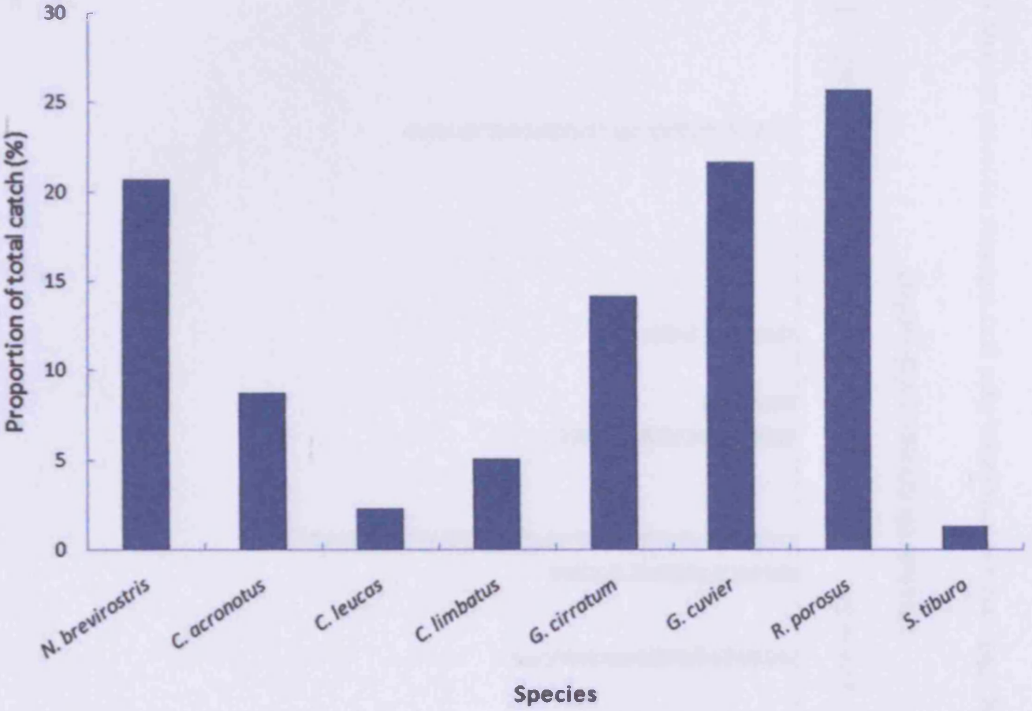


Figure 8. Proportions of total catch for all species caught during the 1980s research cruises

2.3.3.3. Catch Per Unit Effort (CPUE)

N. brevirostris CPUE varied greatly between cruises (Figure 9), ranging from 0.003 – 0.029 (mean = 0.013 ± 0.001 s.e.). The lowest CPUE was recorded on cruise June 1983, when UE occurred between June and July 1983, and the highest on cruise March 1984 when UE occurred in March 1984. Total (i.e. all species caught) CPUE varied between cruises (Figure 10), ranging from 0.03 – 0.08 (mean = 0.06 ± 0.005 s.e.). The lowest CPUE was recorded on cruise November 1985, when UE occurred in November 1985, and the highest on cruise October 1984 when UE occurred in December 1984.

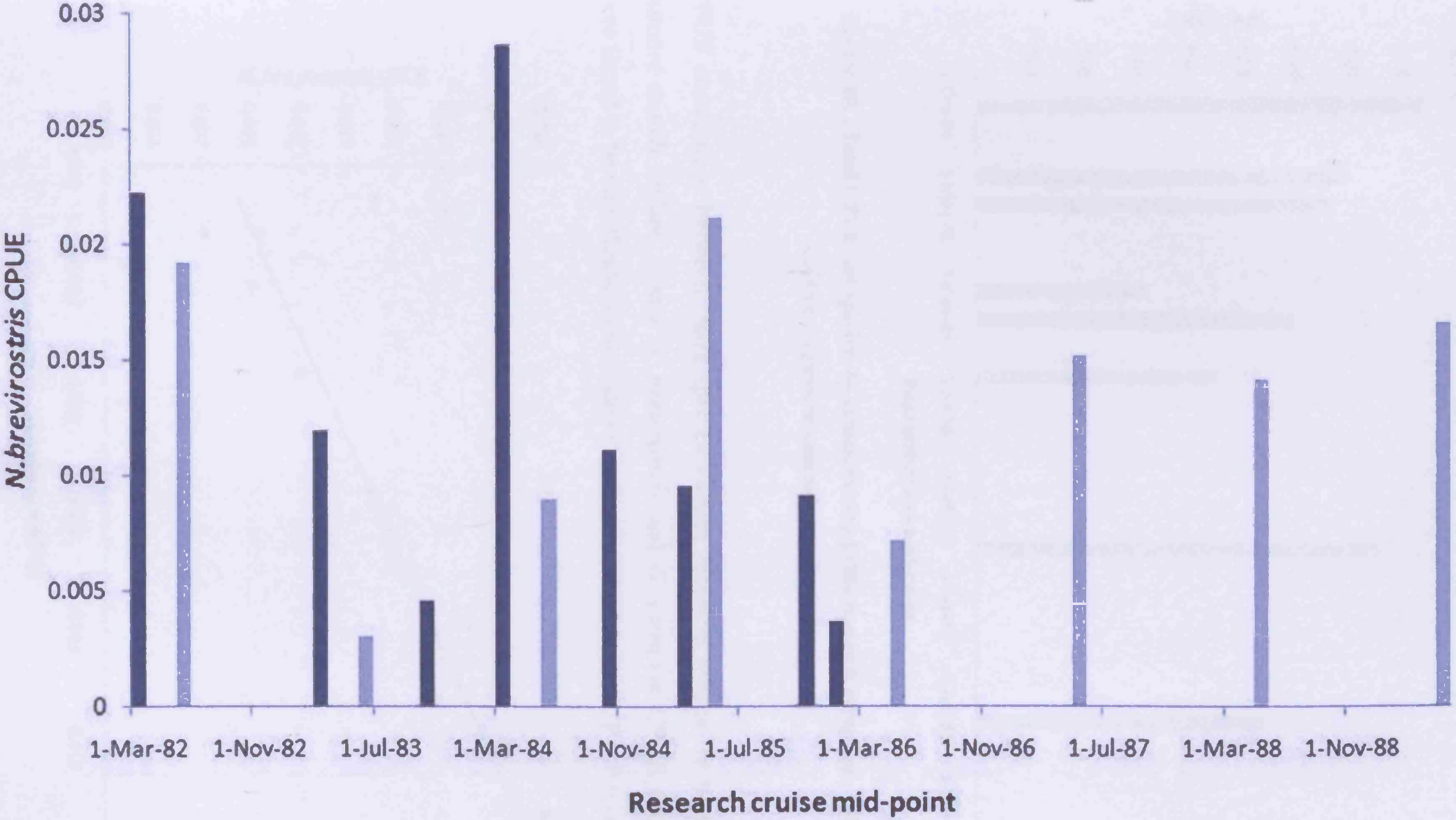


Figure 9. ***N. brevirostris*** **CPUE by cruise, during 1980s research campaign, light grey columns represent summer month cruises**

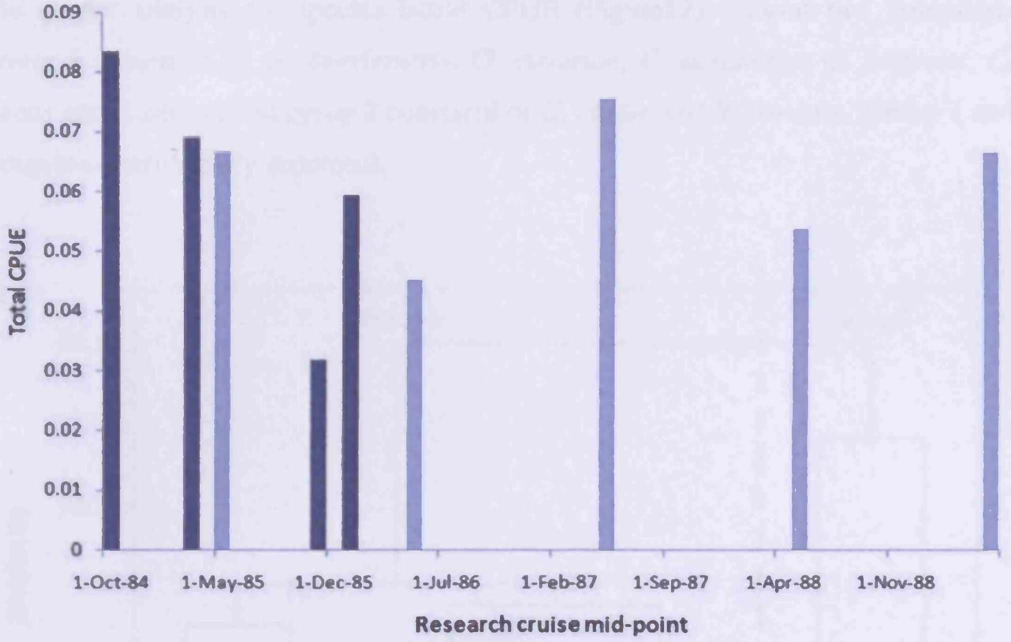


Figure 10. . Total CPUE (all species) by cruise, during 1980s research campaign, light grey columns represent summer month cruises

CPUE correlations between shark species yielded identical results for both all and summer month cruises. Only *N. brevirostris* and *G. cirratum* CPUE (Figure 11) were found to be significantly correlated together ($r = 0.774$, $n = 9$, $P < 0.05$).

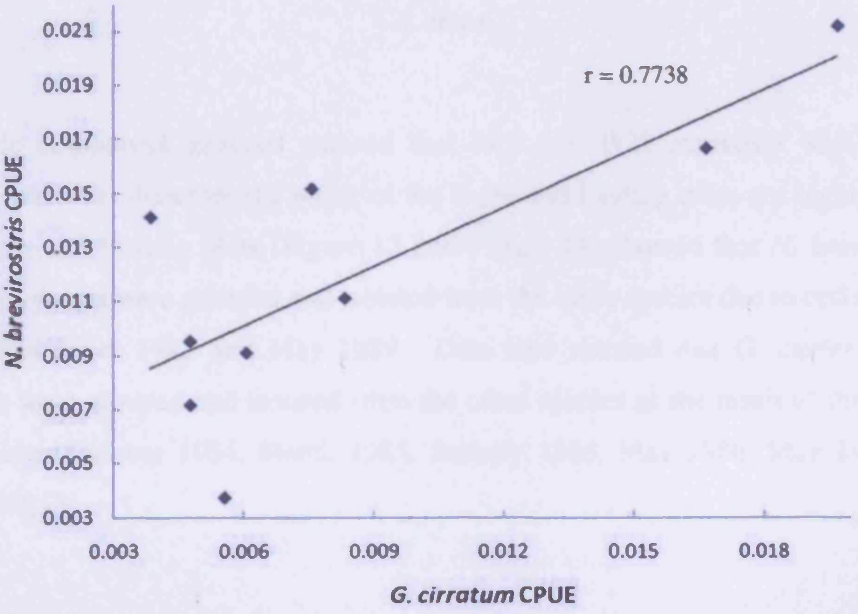


Figure 11. Relationship between *N. brevirostris* CPUE and *G. cirratum* CPUE

The cluster analysis for species based CPUE (Figure12) showed two groupings. Group 1 consisted of: *N. brevirostris*, *G. cirratum*, *C. acronotus*, *C. limbatus*, *C. leucas* and *S. tiburo*, and group 2 consisted of *G. cuvier* and *R. porosus*. Group 1 and group two were clearly separated.

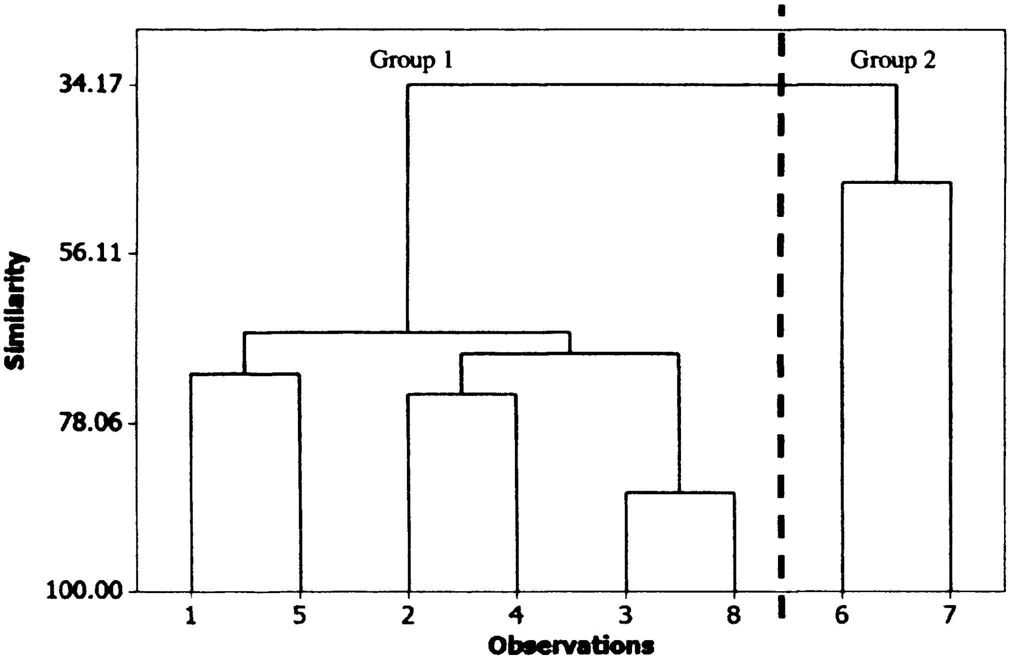


Figure 12. Similarity between species CPUE during 1980s research cruises; 1 = *N. brevirostris*, 2 = *C. acronotus*, 3 = *C. leucas*, 4 = *C. limbatus*, 5 = *G. cirratum*, 6 = *G. cuvier*, 7 = *R. porosus* and 8 = *S. tiburo*

Principle component analysis showed that PC1 and PC2 explained 85% of the dataset variance, therefore the result of the score and loading plots are highly valid. The score and loading plots (Figure 13 and Figure 14) showed that *N. brevirostris* and *G. cirratum* were grouped and isolated from the other species due to cruises May 1985, November 1985 and May 1989. Data also showed that *G. cuvier* and *R. porosus* were grouped and isolated from the other species as the result of the rest of the cruises; October 1984, March 1985, January 1986, May 1986, May 1987 and May 1988.

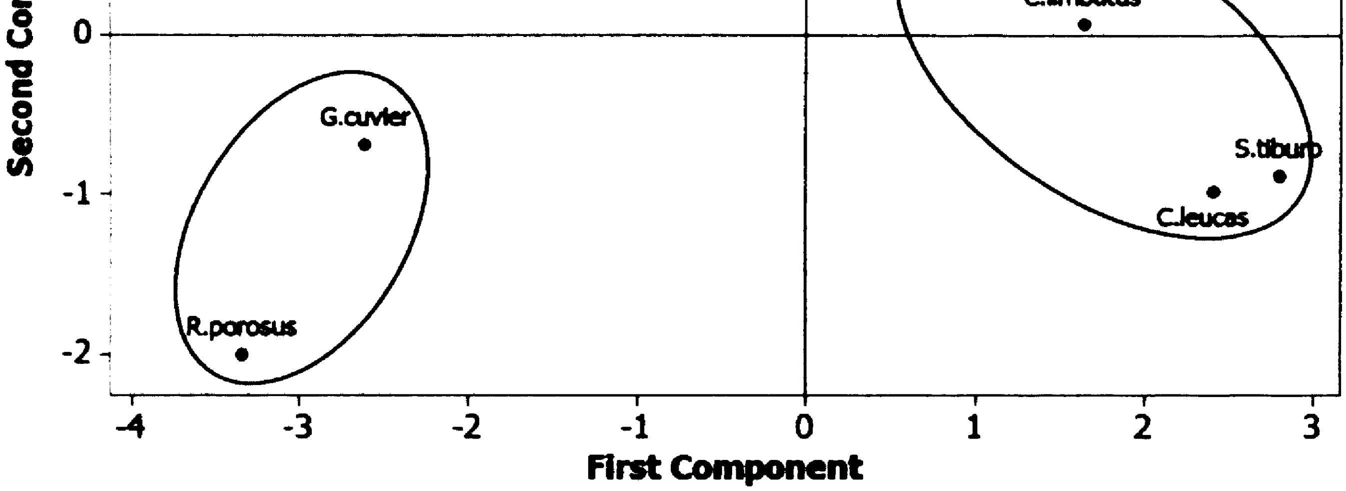


Figure 13. Score plot of research cruises' October 1984 – May 1989 species CPUE, groups encircled to show distribution

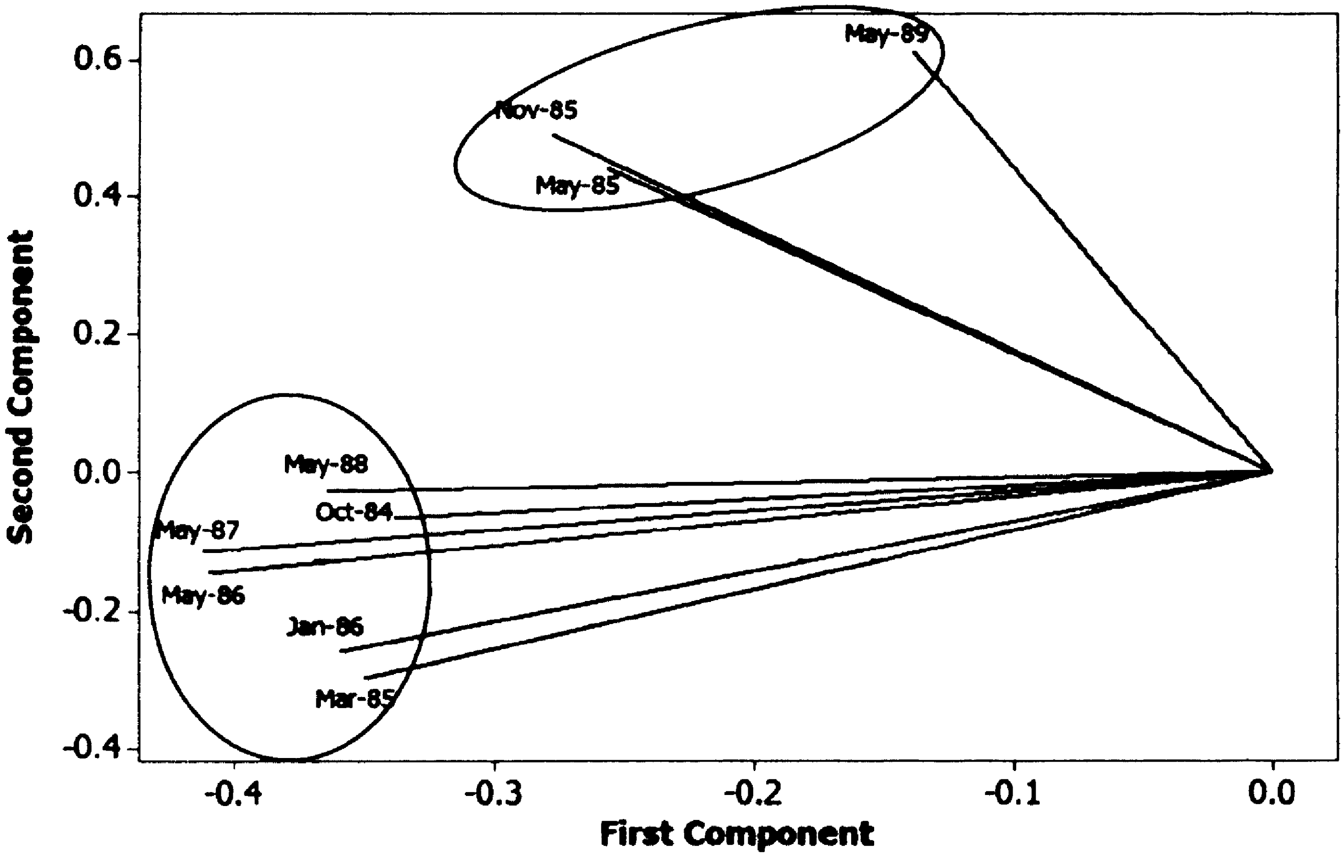


Figure 14. Loading plot of research cruises' October 1984 – May 1989 species CPUE, groups encircled to show distribution

The cluster analysis for cruise based CPUE (Figure 15) showed little similarity between cruises. The closest similarity between two cruises, March 1985 (2) and May 1987 (6), separated by two years, was 65%. There was a clustered group of all cruises in the centre, except three outliers, October 1984 (1), May 1985 (3) and May 1989 (9).

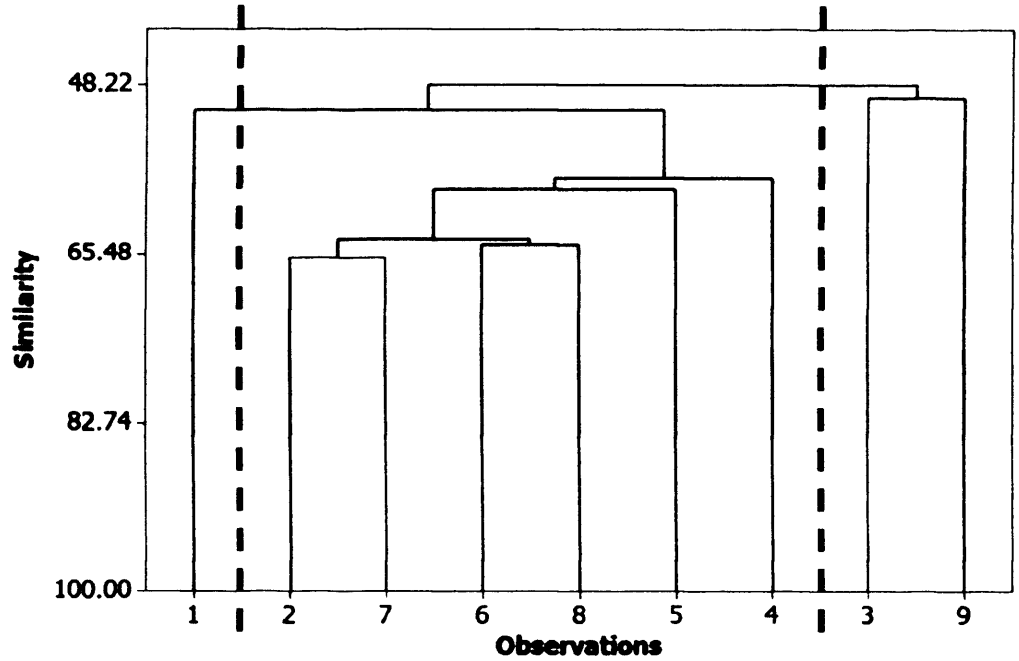


Figure 15. Similarity between research cruise CPUE during 1980s research cruises; 1 = October 1984, 2 = March 1985, 3 = May 1985, 4 = November 1985, 5 = January 1986, 6 = May 1986, 7 = May 1987, 8 = May 1988 and 9 = May 1989

Principle component analysis showed that PC1 and PC2 explained 66% of the dataset variance, therefore the result of the score and loading plots are valid. The score plot (Figure 16) showed that cruises October 1984, May 1985 and May 1989 were distributed away from that main group. The loading plot (Figure 17) showed that *C. limbatus* and *G. cuvier* CPUE were responsible for the isolation of October 1984, *N. brevirostris* and *S. tiburo* CPUE to be responsible for the isolation of May 1985, and *C. acronotus* and *C. limbatus* CPUE to be responsible for the isolation of May 1989.

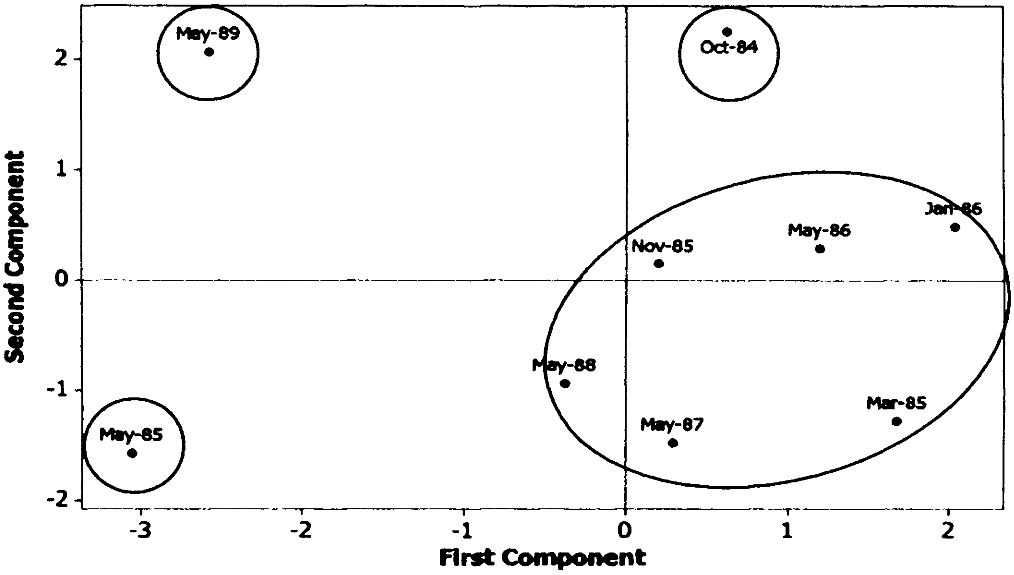


Figure 16. Score plot of all species' cruise CPUE, group encircled to show distribution

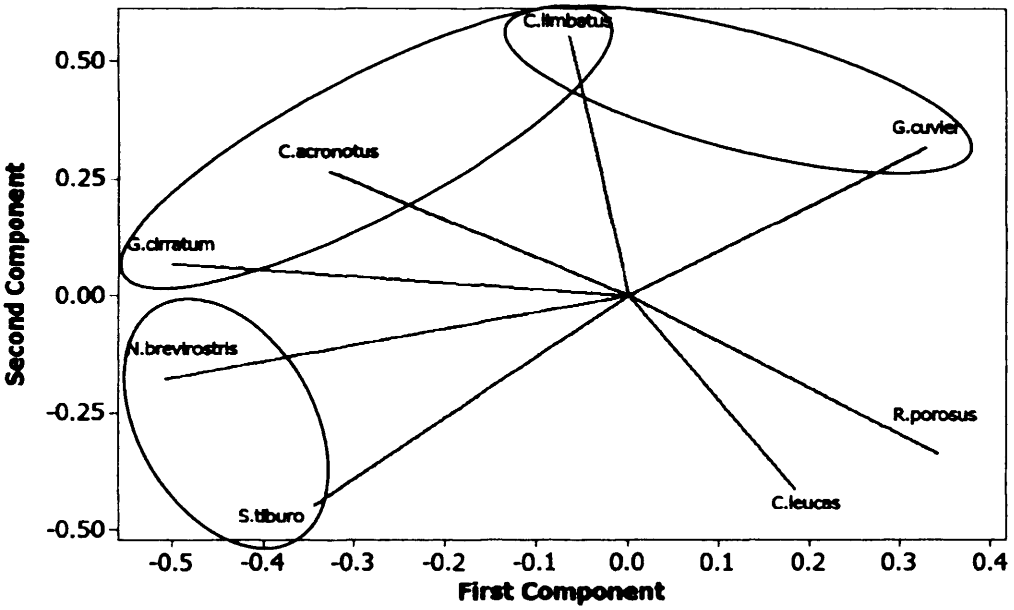


Figure 17. Loading plot of all species' cruise CPUE

2.3.3.4. Capture related mortality

No *N. brevirostris* capture related mortalities were recorded in the first four 1980s research cruises (Figure 18). Subsequent rates ranged from 9% on cruise May 1988 to 50% on cruises November 1985 and January 1986 (mean = 25.8 ± 4.0% s.e.).

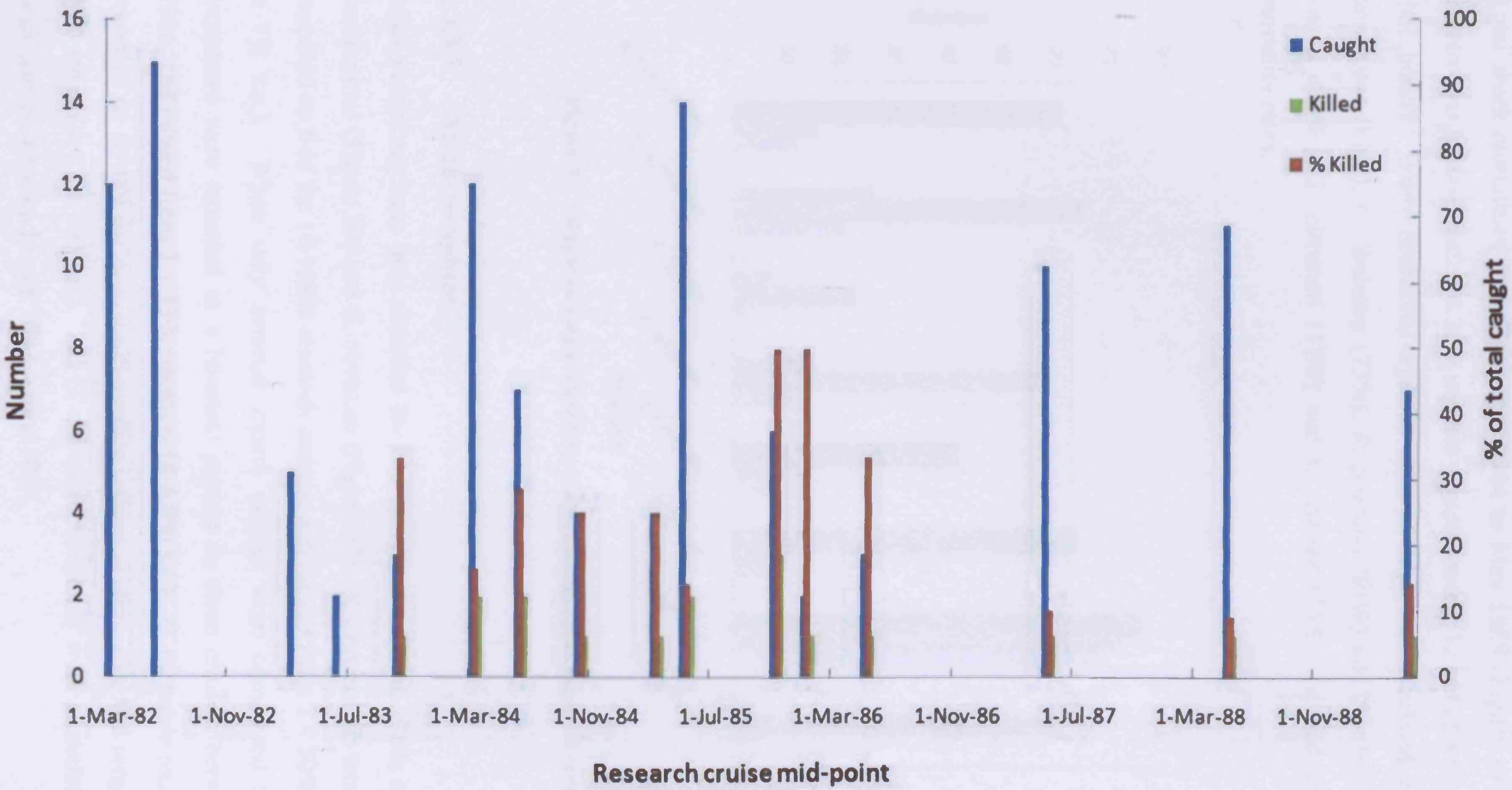


Figure 18. .Total *N. brevirostris* caught, killed and proportion killed during 1980s research cruises

Total shark mortalities from December 1984 to May 1989 (Figure 19), showed *N. brevirostris* to have suffered 20% mortality, representing 12 out of a total 61, during that period. Four additional species showed high catch related mortality; *C. acronotus* (81%), *C. limbatus* (73%), *R. porosus* (91%) and *S. tiburo* (75%). *C. leucas* (29%), *G. cirratum* (17%) and *G. cuvier* (13%), all had relatively low mortality rates.

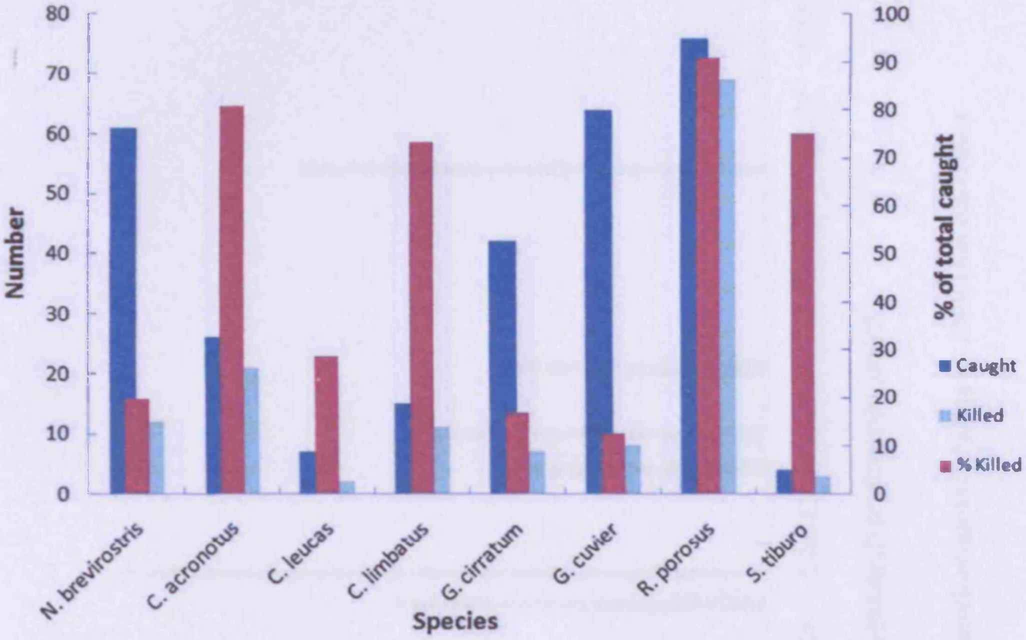


Figure 19. All species catch related mortality during 1980s research cruises

2.3.3.5. Mark-recapture

Mark-recaptures were only recorded for two species during the 1980s campaign, *N. brevirostris* (Figure 20) and *G. cirratum* (Figure 22). *N. brevirostris* recaptures were recorded on 6 of the 16 1980s research cruises, and ranged from 7 – 50% (mean = 31 ± 7% s.e.). When only summer month cruises were considered (Figure 21), recaptures were recorded as a biannual pattern on three cruises, between 1982 – 1986, and ranged from 7 – 33% (mean = 18 ± 8% s.e.). *G. cirratum* recaptures were recorded on five of the nine multi-species cruises (Figure 22), and ranged from 8 – 50% (mean = 27 ± 7% s.e.). All *G. cirratum* recaptures were recorded on back to back cruises between March 1983 – June 1984.

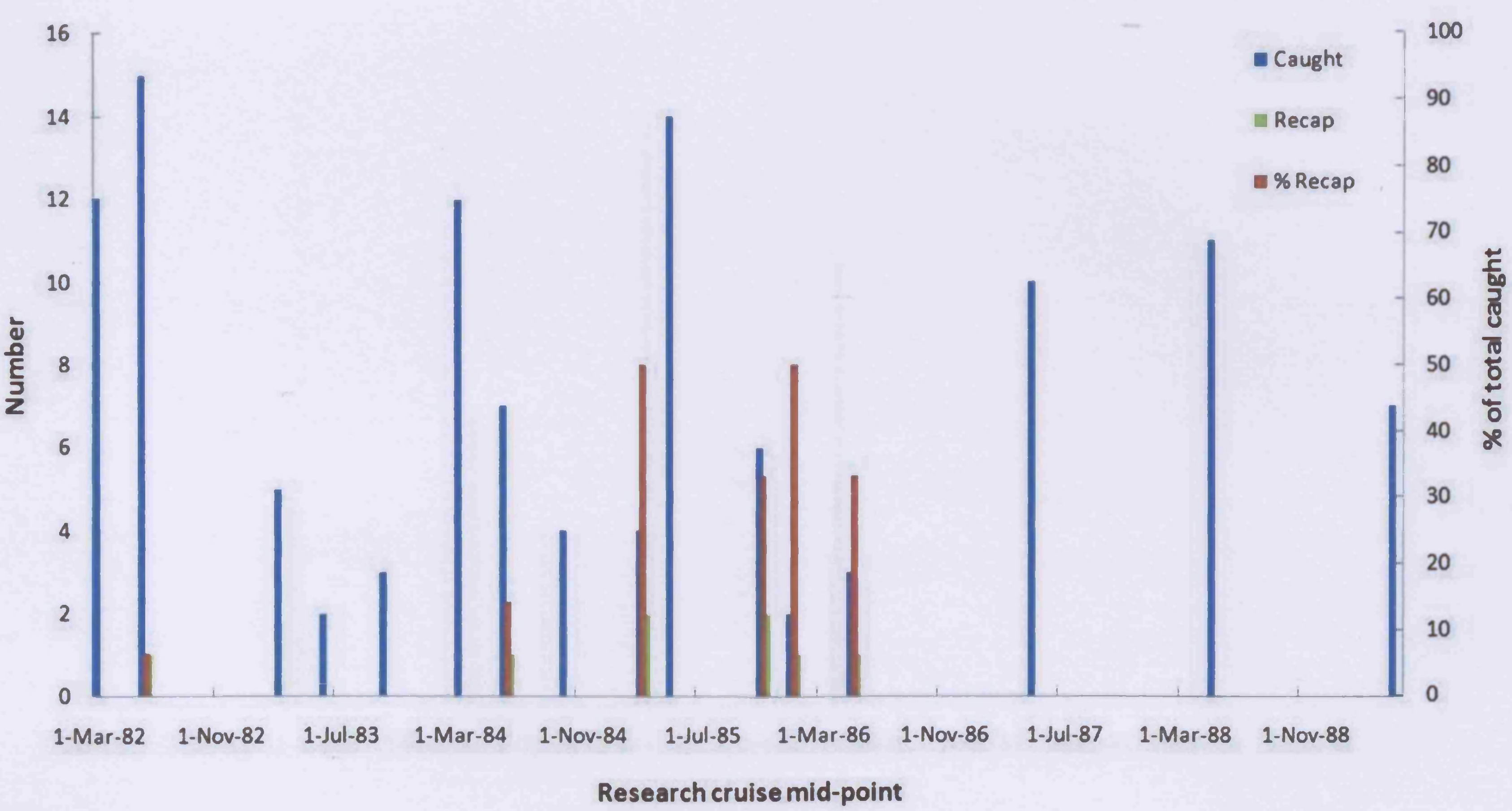


Figure 20. *N. brevirostris* **mark-recaptures during all 1980s research cruises**

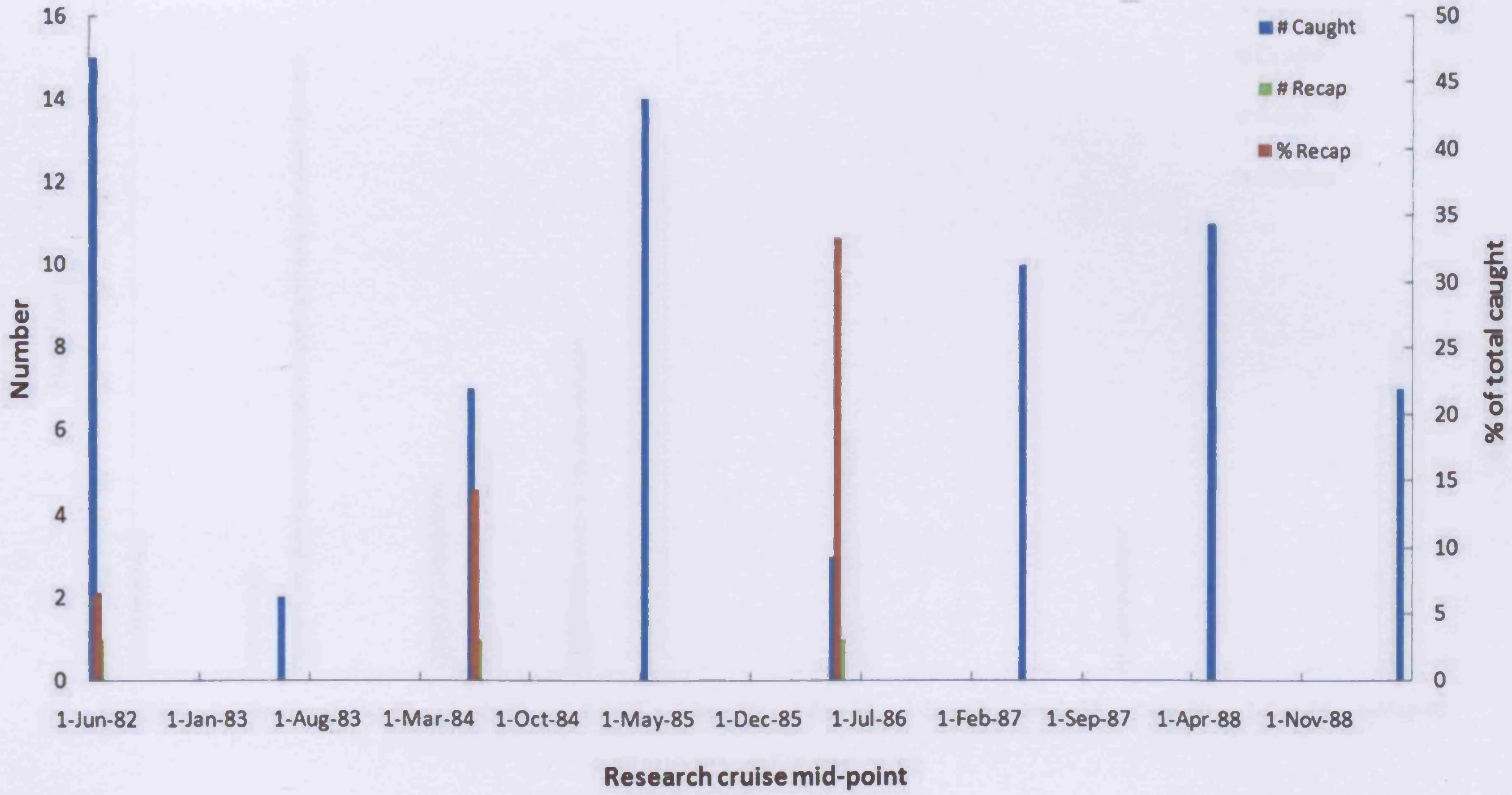


Figure 21. *N. brevirostris* mark-recaptures during summer month 1980s research cruises only

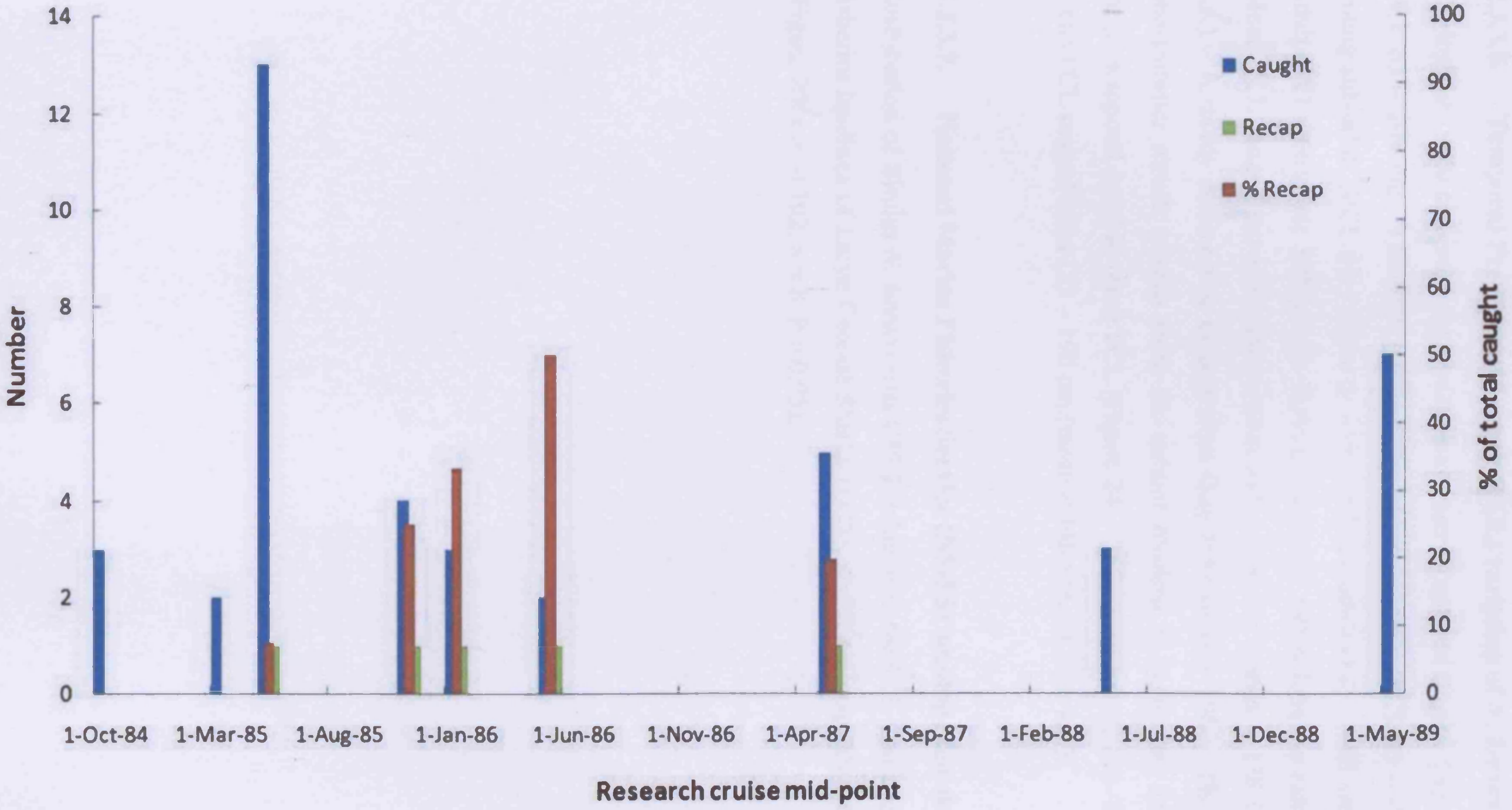


Figure 22. *G. cirratum* **mark-recaptures during 1980s research cruises**

2.3.3.6. Temporal Pre-Caudal Length (PCL) variation of *N. brevirostris*

During the 1980s campaign sizes of *N. brevirostris* captured (Figure 23) ranged from PCL 63 – 209 cm. Therefore all four life stages: juvenile (PCL 45 – 80 cm; 6%), young sub-adult (PCL 81 – 124 cm; 43%), old sub-adult (125 – 165 cm; 21%) and adult (PCL 166+ cm; 30%), were represented in the 1980s longline catch database. Mean PCL ranged between cruises from 103 – 190 cm (mean = 138.13 ± 6.5 cm s.e.). A steady decline was evident from May 1986 to May 1989. The removal of non-summer month records from the dataset resulted in a steadier and generally larger temporal trend in mean PCL (Figure 24). PCL ranged from 63 – 209 cm, and mean PCL ranged from 123 – 190 cm (mean = 148.91± 10.5 cm s.e.).

2.3.3.7. National Marine Fisheries Service (NMFS) landing records

Distribution of Bimini *N. brevirostris* CPUE relative to the U.S. east coast and Gulf fisheries landings of Large Coastal Sharks (LCS), showed no significant correlation (Figure 25; $r = -0.102$, $n = 8$, $P > 0.05$).

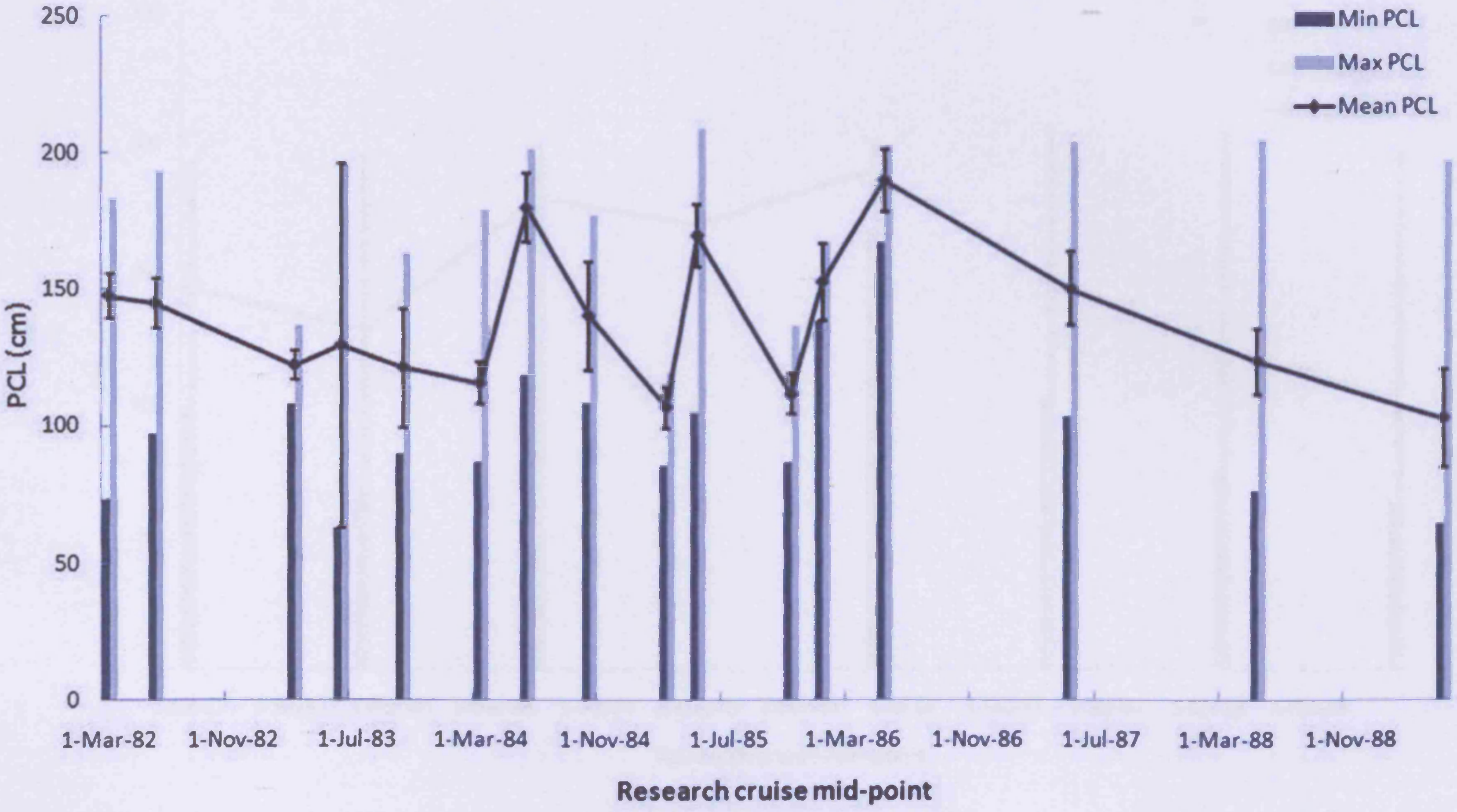


Figure 23. *N. brevirostris* **mean PCL variation over 1980s research cruises**

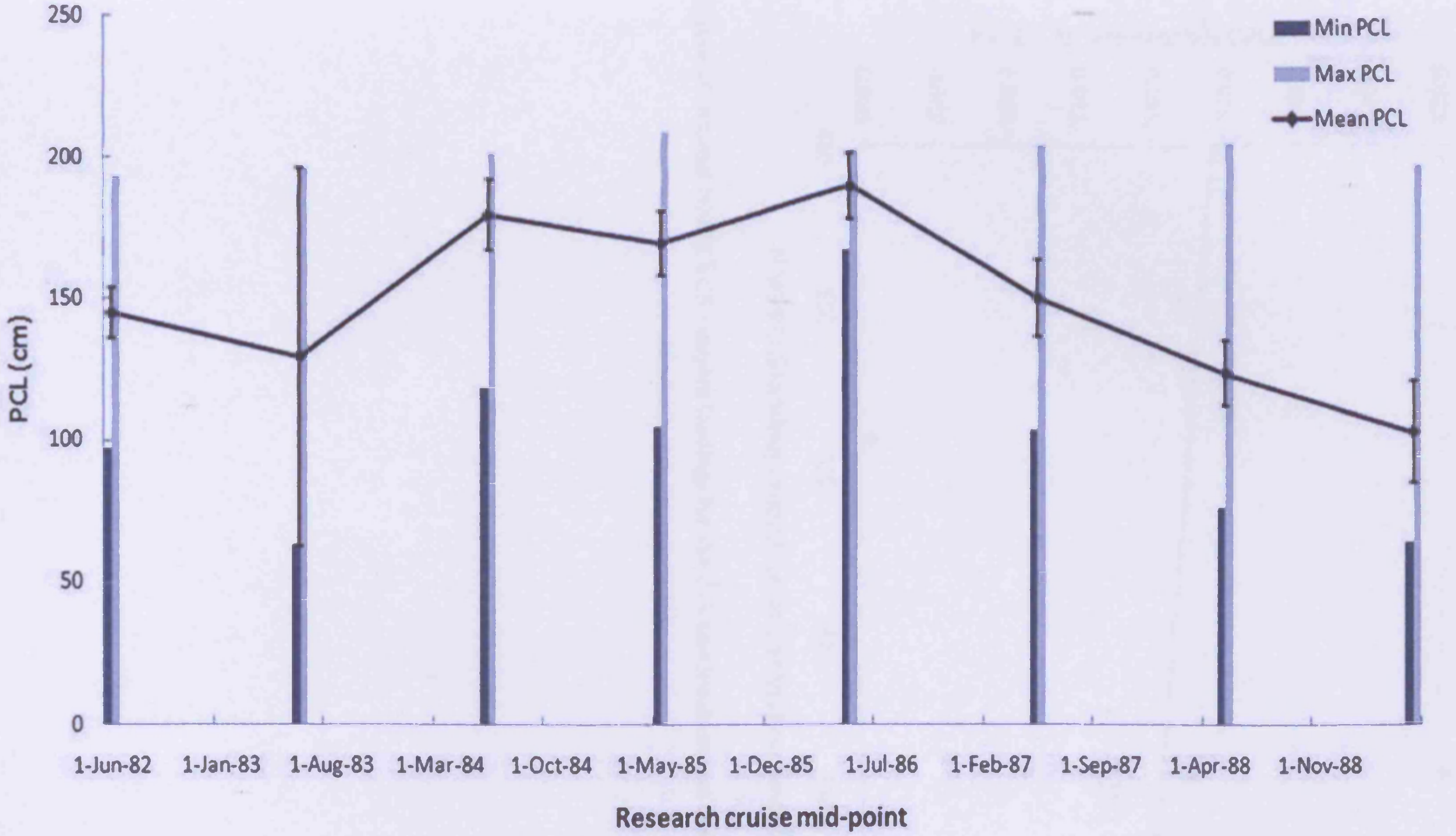


Figure 24. ***N. brevirostris*** **mean PCL variation over 1980s summer month research cruises**

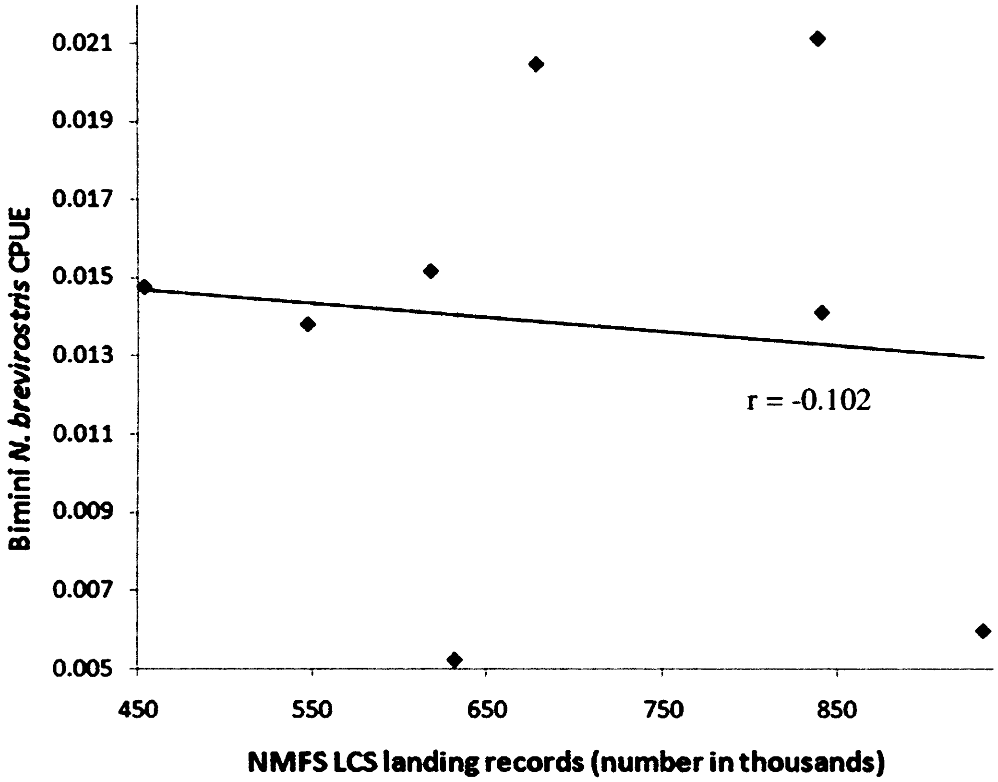


Figure 25. Annual NMFS LCS complex landings for the U.S. east landings and Gulf fisheries vs Bimini *N. brevirostris* CPUE

2.3.4. Discussion

2.3.4.1. Unit Effort (UE)

The large variation in UE between research cruises (Figure 6) inevitably provided a disproportionate representation of total catches for each research cruise (Table 2). This was the result of a lack of structure in research design, as the longlining activities were, during this research period, employed simply to obtain specimens and not to assess the population dynamics. Subsequent analysis was conducted by CPUE to account for the large UE variation between cruises. However, despite the conversion of catch records into CPUE, the disproportionate structure, and variation in amount, of UE still likely influenced the results and may well have contributed towards the scattered distribution of *N. brevirostris* CPUE (Figure 9) throughout the period.

2.3.4.2. Catch proportions

The lowest *N. brevirostris* catch proportion (6%; Figure 7) occurred when UE was focused in late January 1986 during the fishing of cruise January 1986. The low proportion therefore can be attributed to generally low winter catches (see section 3.3.4) in addition to unusually low catches for all fishing efforts in the year 1986. Conversely, the highest catch proportion (36%) occurred when the UE was focused in May 1985. The high proportion can be attributed to high seasonal *N. brevirostris* catches in summer months (see section 3.3.4), particularly at the beginning of the summer when the mature females travel to the island to give birth (Feldheim et al., 2002a). The inconsistent *N. brevirostris* catch proportions and absence of a pattern throughout the 1980s campaign suggests a lack of stability in community structure across that period. This inconsistency can also be in part attributed to seasonal variation (see section 3.3.4), although when only summer month UE was considered there is still a range of 16% (mean = 23.8 ± 2.7% s.e.), again suggesting instability in community structure.

Of the three additional species to *N. brevirostris* that were in high abundance throughout the 1980s campaign (Figure 8), *G. cuvier* had the highest potential for direct influence on the *N. brevirostris* population. The influence would have been in the form of direct predation and therefore a potential reduction in numbers of *N. brevirostris* (Lowe et al., 1996). *R. porosus* are too small to pose a direct threat of predation even on new born *N. brevirostris* (Compagno, 1988), but could possibly have influenced the juvenile population by competition for prey resources. It is possible that a large *G. cirratum* could predate a smaller *N. brevirostris*. *G. cuvier* could additionally have influenced the *N. brevirostris* population through competition for prey resources as they do share a number of the same prey items (Newman, 2003, Lowe et al., 1996, Wetherbee et al., 1990, Cortes and Gruber, 1990).

The most notable inconsistencies are apparent in both of the 1986 research cruises, January 1986 and May 1986, with *N. brevirostris* displaying relatively low proportions and *G. cuvier* disproportionately high compared to other cruises. This resulted from, particularly in January 1986, an increased *G. cuvier* CPUE relative to a reduced *N. brevirostris* CPUE. There was a possible relationship between these two inconsistencies as, of all the species represented, *G. cuvier* presented the most direct threat of predation upon the *N. brevirostris* population (Lowe et al., 1996), consequently an increased number of *G. cuvier* could have resulted in increased predation and therefore lower incidences of *N. brevirostris* (Frisk et al., 2001, Hassell, 1976). However, an increase in the occurrence of *G. cuvier* in the geographic target area could result in avoidance of habitat utilisation in that target area by *N. brevirostris* due to increase predation risk (Hassell, 1976, Simpfendorfer et al., 2005). Accordingly the encounter rates of *N. brevirostris* with the longline gear would be reduced, resulting in a reduction in catchability for that period and therefore only an apparent, not a true, decline in the *N. brevirostris* abundance.

2.3.4.3. Catch Per Unit Effort (CPUE)

N. brevirostris CPUE (Figure 9) showed no definitive temporal pattern between 1982 - 1989. Assuming standard fishing efficiency throughout, this indicated a disrupted and unstable *N. brevirostris* population. The instability was likely caused, at least in part, by catch related mortalities throughout the research period (see section 2.3.3.4). Seasonal variation in UE would also likely have caused dissimilarity between *N.*

brevirostris CPUE between research cruises as the result of seasonal variation in *N. brevirostris* abundance (see section 2.3.3.1).

Total (all shark species) CPUE from December 1984 to May 1989 was, similar to *N. brevirostris* CPUE, randomly distributed with no apparent pattern (Figure 9), both for all cruises and with only summer UE records considered. *N. brevirostris* catches represented 21% and 24% respectively, of total catch, suggesting unstable shark abundance around the Bimini Islands during that research period. With seasonal influence removed, most sharks showed no significant pattern. *C. limbatus* ($r = 0.675$, $n = 5$, $P < 0.05$) and *C. acronotus* ($r = 0.855$, $n = 5$, $P < 0.05$) however, both showed a significant increase in seasonal CPUE. Both *C. limbatus* and *C. acronotus* have very defined breeding cycles (Capape et al., 2004, Sulikowski et al., 2007, Heupel, 2007) explaining a large seasonal influence over their CPUE. Both species were, however, represented in relatively low proportions, 4% and 8% of total catch respectively. *C. limbatus* and *C. acronotus* are both small in anatomical size relative to *N. brevirostris* posing little to no predation risk (Compagno, 1988), therefore it is unlikely that this temporal increase would have had a direct effect on defining the abundance of *N. brevirostris*.

The lack of variation between the full and the seasonally sensitive results suggests no seasonal influence over correlation. The significant correlation between *N. brevirostris* and *G. cirratum* ($r = 0.774$, $n = 9$, $P < 0.05$; Figure 11) may be the result of any or all of the following factors. Positively, there is little evidence of predation risk between the two species (Castro, 2000, Cortes and Gruber, 1990, Newman, 2003, Wetherbee et al., 1990), allowing them to inhabit the same areas at the same time; therefore either species' presence in the target area would not pose a negative influence on the other species presence. A possible negative relationship between the two species would be in relation to competition of prey resources (Cortes and Gruber, 1990, Motta et al., 2008, Hassell, 1976, Stoner, 2004); therefore it would appear that prey availability in the region was not limited. As a result, if prey targeted by both species is plentiful in a given area, such as numerous longline baits in the target area, this could draw both species equally. The two species may also cue off each other's movements and activity to seek out prey, thus if one was drawn to, or feeding from, the longlines, it could bring in the other in increasing their relative CPUE (Stoner, 2004).

The cluster analysis for species based CPUE (Figure 12) showed that *N. brevirostris, G. cirratum, C. acronotus, C. limbatus, C. leucas* and *S. tiburo* all share a high degree of similarity, hereafter referred to as 'Group 1'. The close relationship between *N. brevirostris* and *G. cirratum* further supports the results of the correlation and strengthens the theory of a positive relationship between the two species. The relatively close similarity between these two and the other four species, suggests neither a positive or negative relationship between species within this group. It is possible that if significant size differences between *N. brevirostris* and the other species occurred, then some level of predation risk from either side may occur. However, based on size (see section 2.3.3.6), the only great predation threat for the majority of the *N. brevirostris* sampled would have come from *C. leucas* (Habegger et al., 2009). Only seven *C. leucas* were sampled throughout the entire campaign, therefore *C. leucas* abundance was not high enough to cause a significant negative relationship.

Group 2, containing *G. cuvier* and *R. porosus*, was largely separated in similarity from Group 1. The most logical justification of the negative relationship between *N. brevirostris* and *G. cuvier* was the direct predation risk posed by *G. cuvier* on *N. brevirostris*. As outlined above, this can either be a true impact in that *G. cuvier* are predating *N. brevirostris*, or an apparent impact in that the presence or *G. cuvier* in the target area posed predation risk on *N. brevirostris*. This would cause avoidance of this area by *N. brevirostris*, reducing their true catchability, and reflecting apparent reduction in population size through the CPUE, if interpreted with each species having a constant catchability between research cruises. The most likely cause for this overall group separation was also predation risk, in that *G. cuvier* would pose an overall threat of predation for many size classes of species in Group 1, and in turn these other species would pose a predation threat over *R .porosus*. *G. cuvier* would also pose a big threat of predation on *R. porosus*, (Cortes, 1995, Lowe et al., 1996) which would suggest that a negative relationship between the two species would be more logical. However, of all the eight species, *G. cuvier* is documented to most commonly predate on other elasmobranchs (Meyer et al., 2009, Lowe et al., 1996), therefore it is possible that they would actively follow high abundances of *R. porosus*, the smallest of the eight species, into the target area, resulting in a positive association (Stoner, 2004).

The isolation of *N. brevirostris* and *G. cirratum* can be explained by cruises May 1985, November 1985 and May 1989. CPUE for these cruises showed similar values for both species. CPUE was identical for *N. brevirostris* and *G. cirratum* during the cruise May 1989, which as a summer month cruise *N. brevirostris* CPUE was expected to be higher due to the birthing season (Feldheim et al., 2002a). *G. cirratum* CPUE could have been elevated relative to the other species due to the identified positive relationship between *N. brevirostris* and *G. cirratum.* Both species were shown to produce higher CPUE in summer months (see section 3.3.4). CPUE was low for all species in cruise November 1985, and therefore similar for *N. brevirostris* and *G. cirratum.* This was most likely due to low water temperatures in the winter months leading to slow metabolisms, and resulting in a reduced desire to feed (Bernal et al., 2003, Dowd et al., 2006a). Data also showed that *G. cuvier* and *R. porosus* were grouped and isolated from the other species as the result of the rest of the cruises; October 1984, March 1985, January 1986, May 1986, May 1987 and May 1988. This can be attributed to high CPUE for both species, relative to CPUE for the other species, during these cruises. This supports the theory of a positive relationship between the two species that invariably had a negative influence, most likely due to the predation risk associated with the presence of *G. cuvier* upon the other species. This negative relationship has also been identified, in different geographic locations, for *G. cuvier* with other marine species; not just elasmobranchs (Heithaus et al., 2009, Wirsing et al., 2007).

The cluster analysis (Figure 15) revealed three outlying cruises, October 1984, May 1985 and May 1989; this is further investigated by the score and loading plots. The score and loading plots (Figure 16 and Figure 17) showed that cruises October 1984, May 1985 and May 1989 were distributed away from that main group and isolated from each other. The isolation of October 1984 was the result of high catches for both *C. limbatus* and *G. cuvier.* It is likely that the unusually high catch activity of the smaller *C. limbatus* would have drawn into the study area, more of the larger *G. cuvier* (Lowe et al., 1996), into the study area. The isolation of May 1985 is the result of the highest *N. brevirostris* and *S. tiburo* CPUEs for all cruises in the research period. As the highest *S. tiburo* catch represents only two sharks (No. = 2), it is the unusually high *N. brevirostris* CPUE that is the main cause for the difference. This was a summer month cruise and the combination of a high site-attached sub-adult catch and a high mature breeding population catch for this cruise resulted in the overall high CPUE for this species. The isolation of May 1989 was the result of high *C. acronotus*, *C. limbatus* and *G. cirratum* CPUE, relative to the other species. CPUE for *C. limbatus* and *C. acronotus* are unusually high for the month of May (see section 3.3.4), when this UE was focused. This appears to have been combined with a seasonally early high (see section 3.3.4) in *G. cirratum* CPUE relative to the other species, to cause the isolation of May 1989 from the main group.

2.3.4.4. Capture related mortality

The absence of *N. brevirostris* catch related mortalities during the first four cruises (Figure 18) is unusual, as in elasmobranch studies based on longline surveys mortality rates are normally highest in the early stages of fieldwork (Abel et al., 2007). This usually results from the time taken to reach the balance between the disruptive nature of checking the gear for captures and the survival window for specimens captured on the gear. Later mortalities were largely attributed to the research experiments requiring *N. brevirostris* sacrifices. These were both for anatomical, and age and growth studies (e.g. Brown and Gruber, 1988). For the age and growth study, specimens were injected with tetracycline over a period of repeated recaptures. The intention was to see how frequently, relative to the time of dose, the tetracycline was laid down in the rings of each shark's vertebrae. Therefore, in order to yield the results of the study, it was necessary to sacrifice the specimen and remove the vertebrae (Brown and Gruber, 1988, Gruber et al., 1985).

Tetracycline experiments accounted for much of the catch related mortality from cruise October 1983 onwards, as by that time some sharks caught on previous cruises would have received a satisfactory number of doses to justify their harvest (Brown and Gruber, 1988). Most other sharks that were not sacrificed were dosed and released for future harvest, hence the continued mortality rates for the rest of the period. Despite this, the maximum number of *N. brevirostris* killed in a single cruise as a direct result of the longline fishing, was three. With such a low number it is unlikely that this would impose a significant impact on *N. brevirostris* population levels. It does not appear for *N. brevirostris*, that increased catch rates in the summer months (see section 3.3.4) resulted in an increase in catch related mortality.

Total shark mortalities form December 1984 to May 1989 (Figure 19) showed *N. brevirostris* to have suffered 20% mortality. Although 20% is relatively high, there was no significant relationship of Mortality Per Unit Effort (MPUE) on subsequent years CPUE. High mortalities for *C. acronotus*, *C. limbatus* and *R. porosus* were to be expected, as all are ram ventilators with high metabolic requirements, small mouths and low stress tolerances (Morgan and Burgess, 2007), thus the capture induced stress, which combined with the restriction of movement caused by attachment to the mainline could quickly result in their fatality. Fortunately, all four species have relatively short life histories, with low ages of maturity (Compagno, 1988), meaning that of all species sampled these are the most able to recover from fisheries related population decline. *C. acronotus* and *C. limbatus* mortality is of little concern as these are high proportions of relatively low numbers, 26 and 15 respectively, and neither species' numbers are likely to have a strong influence over the *N. brevirostris* population. *R. porosus* and its close relative *R. terraenovae* are the most abundant of all small coastal shark (SCS) species recorded in the U.S. east coast fisheries (Morgan et al., 2009). Of all four species it has the shortest life-history and lowest age at maturity, thus it is the most able to recover from population decline. High mortalities for this species resulted mainly from a very short period for successful release after capture, often missed by the intermittent checks. *S. tiburo* mortality rates are high due to the previously described common factors influencing these four species; however 75% of only four individuals is unlikely to have any long-term effect upon the species' local abundance.

Though *C. leucas* mortality rates were reasonably high, they represented only 2 of 7 specimens. *G. cirratum* mortality was almost equal to *N. brevirostris* (3% separation), therefore whether there was a positive, negative or the absence of relationship between the two species, the longline fishing did not result in a change in intra-species influences. Total catches of *N. brevirostris* and *G. cuvier* for the period were similar, 61 and 64 respectively, yet *N. brevirostris* mortalities were 7% higher. Since the most significant direct negative influence upon the *N. brevirostris* population has been identified as being imposed by the *G. cuvier* population, it is possible that the higher mortality rate for *N. brevirostris* would have, through the increase in abundance ratio, been magnified by the 1980s research campaign.

2.3.4.5. Mark-recapture

Mark-recaptures were only recorded for two species during the 1980s campaign: *N. brevirostris* (Figure 20) and *G. cirratum* (Figure 22). This would suggest that these two species are more site-attached, while the other species are more nomadic in their movements. In addition, in Bimini, *N. brevirostris* show a strong site attachment to the nursery grounds at the juvenile life stage (Franks and Gruber, 2007, Morrissey and Gruber, 1993b), a high level of site attachment to the island's surrounding water at the sub-adult life-stage (Chapman et al., 2009, Sundström et al., 2001, Gruber et al., 1988) and philopatry at the adult life-stage (Feldheim et al., 2004). *G. cirratum* have also been shown at all life stages to have strong site-attachment (Pratt and Carrier, 2007, Castro, 2000).

Incidences of tagging and the number of catches were two low for *C. leucas* and *S. tiburo* to make any assessment of site attachment. Mortality rates were too high; therefore, successful releases of tagged individuals were too low to make any assessment for *C. acronotus*, *C. limbatus* and *R. porosus*. Successful releases of tagged *G. cuvier* were plentiful, yet not a single mark-recapture was recorded. Thus it can be concluded that *G. cuvier* present in the target area for this period were predominantly nomadic animals passing through, or extremely large home ranges for this species as documented in Hawaii (Holland et al., 1999). This is supported by the many documented large scale movements by this species (Kohler et al., 1998).

For both species, *N. brevirostris* and *G. cirratum*, no mark-recaptures were recorded in the first year of fishing, which would be an unlikely event and require an individual to be captured twice in a given fishing period. *N. brevirostris* mark-recapture rates increased toward the middle of the campaign. The increase was logical as progressively more tagged individuals would be released into the population as the result of the previous cruises longline efforts. The increase was inconsistent, most likely the result of continued sacrifices of recaptured individuals for the age and growth experiments, therefore reducing the potential for multiple recaptures of the same individual over the years. This may also explain complete absence of mark-recaptures for the final three cruises, as animals dosed with tetracycline towards the beginning of the campaign would have been reaching their most suitable time for harvest during the three prior cruises (Brown and Gruber, 1988). When non-summer month records were removed (Figure 21), *N. brevirostris* showed a more temporally incremental increase in recapture rates, prior to their absence in the last three cruises. This suggests a more seasonal pattern of recapture susceptibility for this species. Also, the biannual pattern between June 1982 and May 1986 could thus be explained by the biannual breeding philopatry of the mature females (Feldheim et al., 2002a, Feldheim et al., 2004) in the summer months. *G. cirratum*, due to the lack of consistent mark-recapture harvesting experienced by the *N. brevirostris*, showed a more expected incremental increase in mark-recapture rates. This incremental increase started, and was likely boosted by, the large number tagged, during cruise May 1985. The absence of any recaptures for the final two cruises however, is a mystery.

2.3.4.6. Temporal Pre-Caudal Length (PCL) variation of *N. brevirostris*

Temporally, within the mean PCL range, there was little consistency between cruises (Figure 23), thus reflecting the wide range of size classes present in the target area. There was an apparent steady decline across the last four cruises, each of which was a year apart. This may have been a reflection of the previous and continued harvest of larger recaptured individuals for the age and growth experiment. The removal of these larger specimens resulted in steady decline in the mean PCL of the Bimini *N. brevirostris* population, a documented indicator of fishing pressure (de Lestang et al., 2003, Webster, 2004). During the 1980s the lagoon *N. brevirostris* population was dominated by young sub-adults (43%); juveniles comprised 6%, older sub-adults 21% and adults 30%. This suggests a strong recruitment of young sub-adults from the nursery areas, and a number of the older sub-adults to have matured into the adult population. These size class levels have formed the bases for temporal comparison over the next two campaigns, to analyse for a shift in size class proportions.

The removal of non-summer month records from the dataset resulted in a steadier and generally larger temporal pattern in mean PCL (Figure 24). It has removed the pattern of high/low variation between summer and non-summer month catches. This is explained by the increased presence of the mature philopatric females in the summer months and their almost complete absence outside of the birthing season (Feldheim et al., 2002a). As all four final cruises took place during summer months, the temporal decline at the end of the campaign is still represented and appears even more apparent with the steadier pattern that precedes it.

2.3.4.7. National Marine Fisheries Service (NMFS) landing records

When NMFS landing records for the U.S. east coast and Gulf fisheries LCS complex (NOAA/NMFS, 2006) were correlated to Bimini temporal *N. brevirostris* CPUE records from the same period (Figure 25), no significant relationship was found. The lack of a significant correlation was most likely the result of erratic CPUE distribution throughout the 1980s research campaign (Figure 9). The erratic CPUE distribution was largely caused by sacrificial research techniques, which may well have clouded any external influences from the U.S. east coast and Gulf fisheries landings of Large Coastal Sharks (LCS).

2.4. 1992 – 2003 research campaign

2.4.1. Background

Following the 1980s research campaign the 1992 – 2003 longline efforts targeted an *N. brevirostris* population that could no longer be considered as 'relatively unaffected' by anthropogenic influences. The main influence was a direct result of previous research itself, predominantly from the sacrificial techniques used in the 1980s campaign, with sacrifices of *N. brevirostris* specimens numerous to contribute to the various life-history based studies, most notably the age and growth study.

Throughout the 1980s and subsequent 1992 – 2003 campaign, artisanal and recreational fishing activities remained relatively constant and minimal and therefore were not considered as an external factor contributing to changes in *N. brevirostris* population dynamics. However, in 1997 Bimini Bay Development work started. This involved large-scale alterations to the Bimini marine ecosystem both sub-tidally, in the form of heavy dredging (initiated in 1999), and in the littoral zone *N. brevirostris* nursery grounds, with the removal of large areas of the fringing mangroves (Jennings et al., 2007, Gruber, 2002). In terms of significant events in the development, the most intense dredging activities were conducted in March 2001 (Feldheim and Edren, 2002, Jennings et al., 2007).

The opening of the Bimini Biological Field Station (BBFS) in 1990 was followed by a two year period without any longline survey work as the station was still being established and developed. Following the 1980s cruises, research foci were still grouped under the overall aim of "the elucidation of the role of the lemon shark (*Negaprion brevirostris*) as a top predator in the tropical marine environment" (BBFS, 2008). They did however move completely away from sacrificial research techniques. This would have instantly reduced the direct research-related impacts upon the resident *N. brevirostris* population. A number of studies were conducted over that decade and the following three years of the station's research activities including: diet studies, ecosystem dynamics, telemetry and homing studies. These research projects focused predominantly on the juvenile life stage and, to a much lesser extent, the sub-adults (BBFS, 2008). This meant that there were minimal direct impacts from the research activities to the longline target populations.

During this research period longline activities were conducted to providing specimens for university based elasmobranch field biology courses and film crews making nature documentaries. Field biology courses were conducted at the BBFS intermittently throughout the course of each year. In addition, through the 1990s, media interest in elasmobranchs proliferated and the BBFS received a large amount of media interest (BBFS, 2009a). Both the university courses and the film crews required larger shark specimens than the usual research techniques produced, therefore the larger specimens were obtained through the employment of the same shallow water longlines utilised during the 1980s research campaign. Around three university courses were conducted each year and up to 10 film crews, which resulted in relatively frequent longline efforts throughout the duration of each research year. As in the previous campaign the purpose of the longline effort was not to conduct a population study, however, the frequent efforts and standardised approach has allowed for the data to be analysed for population patterns over the period.

2.4.2. Methodologies

2.4.2.1. Longlines

The same longline gear was used as in the 1980s campaign. As in the 1980s individual elements were replaced as needed. For example, hooks were replaced if cut and the stainless steel cable element of the gangions were often replaced if damaged by the shark capture or processing. The most significant gear change was the switch from 9/0 J hooks to 16/0 circle hooks (Plate 1) in 1996. *Scomber scombrus* was no longer utilised as bait as it was hard to obtain from the island base. *Sphyraena barracuda* was still predominately utilised in combination with various jack species (*Carangoides sp.* and *Seriola sp.*). Check incidences were increased from twice daily to once every four hours, which, following some trial and error was found to be the best balance between minimum disturbance and maximum survival of captured specimens. Fishing locations were similar to those of the 1980s (Figure 4), although sets were conducted with the use of visual references so minor discontinuity in exact location occurred.

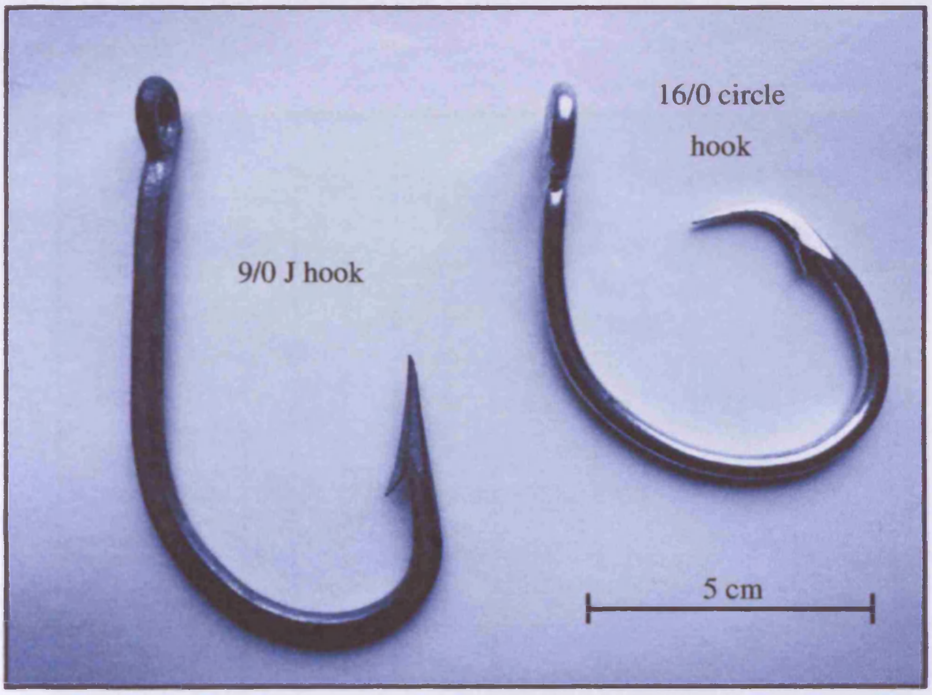


Plate 1. 9/0 J hook (left) and 16/0 circle hook (right)

2.4.2.2. Shark processing

The processing of captured sharks remained almost identical to that employed in the 1980s (section 2.3.2.3), bar a few minor exceptions. For *N. brevirostris* new Passive Integrated Transponder (PIT) tags were utilised. The decision to switch from external NMFS M-type dart tags to the new PIT tags was made due to their size (Plate 2). This made it possible to issue all *N. brevirostris* from neonate to fully mature with the same tag (Feldheim et al., 2002b). Therefore, between 1992 – 2002, external dart tags were only issued to fully mature *N. brevirostris*. Later in 2003 the benefits of double tagging all suitable *N. brevirostris* was realised due to the potential longevity of the external tags from sub-adult to maturity when they were more likely to undertake large scale movements/migrations (Kohler and Turner, 2001). The minimum TL for M-type dart tag application was decided to be 140 cm as by this size, for most species, enough muscle had been developed to safely lodge the dart (personal communications Gruber 2008). Therefore from 2003 onwards all *N. brevirostris* of TL > 140 cm were issued with both a PIT and M-type dart tag. Finally in 1995 the Bimini genetics bank was initiated, therefore a genetic sample in the form of a small fin clip (~0.5 cm^2) was taken from all captured *N. brevirostris* regardless of size.

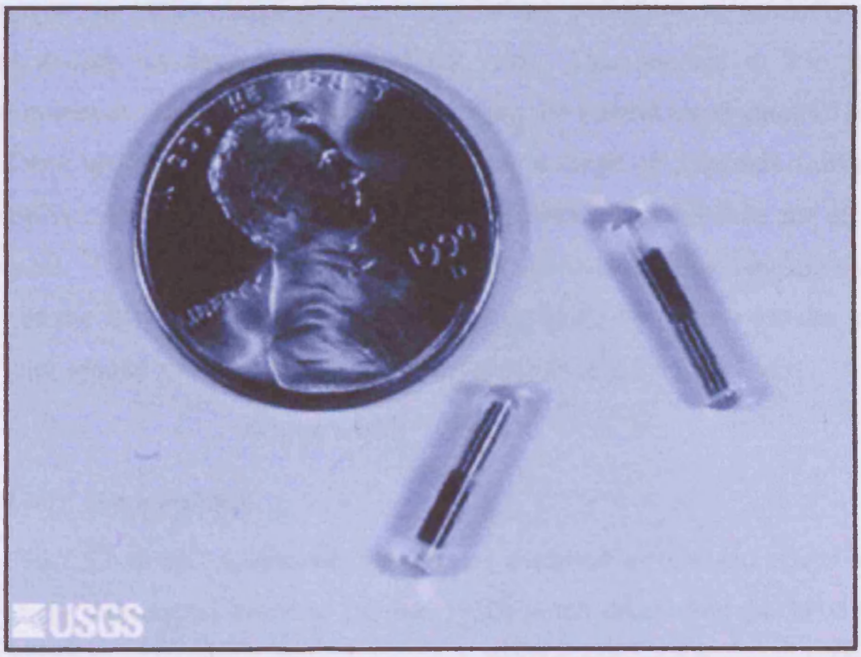


Plate 2. Passive Integrated Transponder (PIT) tag

2.4.2.3. Dataset

Similar to the 1980s the 1992 – 2003 workable dataset was assembled and truthed from a number of sources. Unlike the 1980s, the database was already transcribed onto an excel spreadsheet. Following a given fishing period the data were transcribed directly onto the database by the research team, maintained by the Principal Investigators. The first step was to take the existing database, comprising all BBFS sampled sharks, and remove all records that represented a gear or capture type other than longlining. This was a relatively simple process as almost all records had an entry in the 'gear' field. Questionable records were cross-referenced with hard copy catch records and hook books as well as the methods for other captures on that date. Once all non-longline records were removed, the dataset was cross-referenced against the backlog of data books from the period. The final dataset represented a total of 202 *N. brevirostris* and an additional 367 sharks of other species.

2.4.2.4. Analytical methodologies

2.4.2.4.1. Deduction of Unit Effort (UE)

Compared to the 1980s campaign, individual fishing periods were generally shorter, but more evenly distributed throughout the year. This resulted in less potential seasonal influence over CPUE levels and a more even annual representation between years. Once again UE had to be deduced from a range of available information. This comprised the cross-referencing and truthing between data books and electronic spreadsheets. Deduced efforts were finally checked with the past resident staff and scientist of the BBFS, who were running the longlining operations for the research period, with special attention to areas of uncertainty within the data books.

2.4.2.4.2. Assumptions

Section 2.3.2.5.2 details a number of variables assumed to have no effect over the results of the subsequent sections for the 1980s catch data. For the 1992 – 2003 catch data many of these assumptions over variables remained the same. However, increased field recording of some of these variables allowed investigation into their influence. These variables are re-listed below, with explanations only provided when they differ for those of the 1980s dataset:

A. **Movements and migrations**;
B. **Fishing location**;
C. **Fishing-master experience** – though many of the research cruise crew members had moved on by this point and new personnel were staffing the BBFS, the overall experience of the science director, Dr. S. Gruber, would have been ever increasing, potentially producing temporal increases in fishing efficiency;
D. **Operation time** – operation times were generally shorter with less back to back fishing efforts, reducing the potential of influence;
E. **Bait loss**;
F. **Gear saturation**;
G. **Detection of gear** – it is possible that, for the more site-attached *N. brevirostris* and *G. cirratum*, repeated exposure may have increased the possibility of gear detection;
H. **Hunger**;
I. **Competition among gears**;
J. **Bait type** – following the establishment of the BBFS, mackerel was no longer used as bait. Barracuda was still used in combination with various jack species (*Carangoides sp.* and *Seriola sp.*);
K. **Bite-off**;
L. **Activity**;
M. **Environmental factors**;
N. **Diel**;
O. **Lunar** - The effects of lunar phase on catch rates are investigated in section 2.4.3.2;
P. **Hook type** - The effects of hook type on catch rates are investigated in section 2.4.3.3;

It is assumed for the subsequent results and analysis that variables A to N had no effect upon the catch records included in the dataset, with the effects of O and P investigated prior to any further population analysis. In a given, section should a variable be accounted for, or additional variable assumed to have no further effect, this will be stated at the beginning of the analytical methodology.

2.4.2.4.3. Lunar effect

The effects of lunar phase on the behaviour and activities, including feeding, are well documented for many fish species (Dewar et al., 2008, Graham et al., 2006, Hernandez-Leon, 2008, Kraus and Rooker, 2007, Kuparinen et al., 2009, Nanami and Yamada, 2009, Oliveira et al., 2009, Whitty et al., 2009). For the 1980s data set results and analysis, no influence of lunar phase was assumed, yet it is entirely possible that this variable may have affected the results. Partial lunar phase data was recorded during the 1992 – 2003 research campaign. This prompted the completion of lunar phase for catch records by reference to the NASA historical lunar records (NASA, 2008). For a given catch record, the number of days within the current lunar cycle were recorded, then the number of days relative to the date of the catch record from new to full moon were recorded. The number of days from new to full moon was then converted into a percent of full moon for that particular date by the following:-

$$\sum = \frac{No.\,days\ new\ to\ full}{No.\,days\ in\ lunar\ cycle} \times 100$$

These results were then grouped into 10% bins for total catches of all shark species. Since fishing efforts were not designed around lunar phases, fishing efforts for each lunar percentile group were not equally distributed. It was therefore necessary to normalise these results by the number of days fished within each percentile group to give a CPUE per bin. This was achieved for each 10-percentile bin by applying the following:-

$$\sum = \frac{No.\,sharks\ caught\ in\ bin}{No.\,days\ fished\ in\ bin}$$

Variations relative to the wax and wane state of the lunar phase were investigated. Records with waning percentiles were converted to negative values. The records were then regrouped into their new bins and the normalisation process was repeated. Finally *N. brevirostris* records were isolated and the entire process was repeated.

2.4.2.4.4. Hook type

Hook type is well documented to have effect over catchability (Bolten et al., 2002, Cooke et al., 2003a, Cooke and Suski, 2004, Cooke et al., 2003b, Falterman and Graves, 2002, Galeana-Villasenor et al., 2008, Hand, 2001, Huse and Ferno, 1990, Malchoff et al., 2002, McEachron et al., 1985, Prince et al., 2002, Skomal et al., 2002). In 1996 the BBFS switched from 9/0 J hooks to 16/0 circle hooks. This was in response to reduced mortality, coupled with similar catch rates on experimental circle hook longlines, conducted by the Virginia Institute of Marine Science (VIMS; personal communications Grubbs 2003). Elsewhere circle hooks have been documented to alter catch and mortality rates for elasmobranchs by 14.4% (Yokota et al., 2006) and 15.4% (Kerstetter and Graves, 2006) respectively. It was therefore necessary to explore the effects of the change in hook type. The data was then tested for normality and a t-test test was conducted for CPUE data pre and post hook change.

2.4.2.4.5. Catch proportions

The same methodology described in section 2.3.2.5.4 was used, with data grouped by year, rather than cruise, given the more consistent distribution of annual effort. Proportions were then displayed by species relative to the proportions from the previous campaign, and analyses for temporal change.

2.4.2.4.6. Catch Per Unit Effort (CPUE)

The same methodology described in section 2.3.2.5.5 was used. *N. brevirostris* temporal CPUE variation was plotted only as a scatter graph. This showed a distinct trend was immediately apparent. A linear trend-line was fitted to the plot but was replaced by a polynominal trend-line, fitted using Excel 2007® software. This decision was as a result of the scatter distribution and the distinct possibility that carrying capacity for the ecosystem had been reached; therefore a linear trend-line would be an inappropriate fit for a population that has no further possibility of substantial increase.

2.4.2.4.7. Capture related mortalities

The same methodology, as described in section 2.3.2.5.6 was used, with data was grouped by year rather than cruise given the more consistent distribution of annual effort. With the absence of scientific sacrifices, all mortalities were the direct result of capture on the longlines.

2.4.2.4.8. Mark-recapture

In addition to all previously stated variables A – M, zero tag loss was assumed, relative to a proven retention for PIT tags of 88% (Feldheim et al., 2002b). The same methodology, described in section 2.3.2.5.7 was used, except for the following alteration. *N. brevirostris* recaptures were truthed using the PIT tag records, not the M-type dart tags, accept for occurrence of recaptures between research periods.

2.4.2.4.9. Temporal Pre-Caudal Length (PCL) variation of N. brevirostris

The same methodology described in section 2.3.2.5.8 was used, with data grouped by year, rather than cruise, given the more consistent distribution of annual effort.

2.4.2.4.10. National Marine Fisheries Service (NMFS) landing records

The same methodology described in section 2.3.2.5.9 was used, with data grouped by year, rather than cruise, given the more consistent distribution of annual effort.

2.4.3. Results

2.4.3.1. Deduction of Unit Effort (UE)

UE varied greatly between 1992 and 2003 (Figure 26), being low for the first two years 1992 – 1993 (135 and 120 respectively) and unusually high during 1996 (2160) and 1997 (2760). Following this inconsistent period UE remained fairly constant between 1998 - 2003. The disproportionate effort logically resulted in disproportionate catches between years (Table 3).

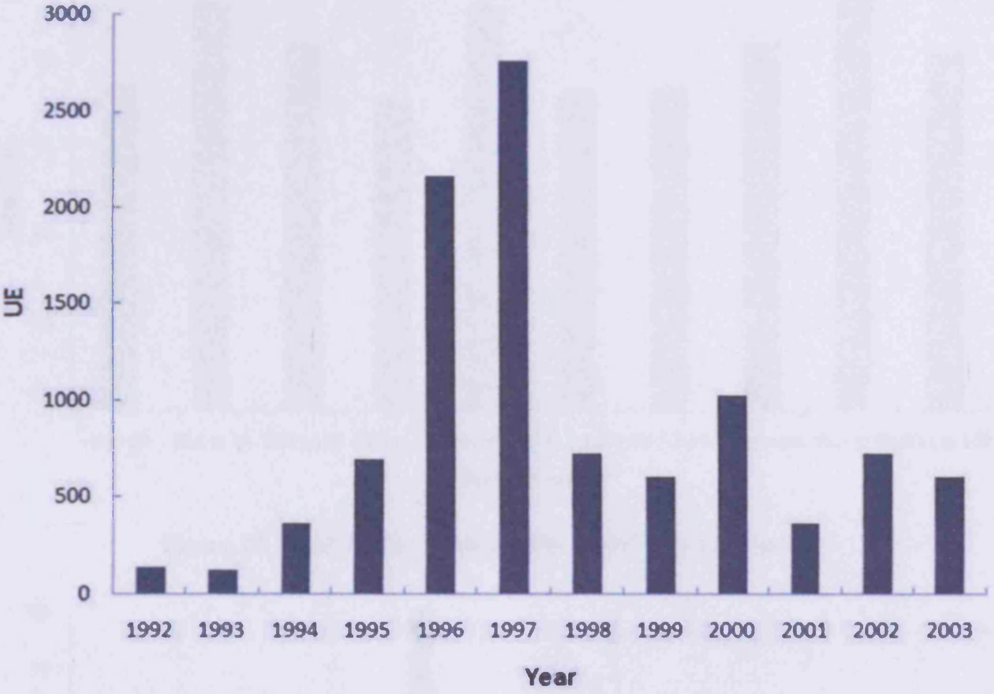


Figure 26. UE by year as a product of number of hooks multiplied by number of days fishing

Table 3. Number of sharks caught by species and total from 1992 – 2003

Species	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	Total
N.brevirostris	1	0	5	8	53	45	13	15	27	9	14	12	202
C.leucas	1	0	0	0	2	2	1	0	0	0	1	0	7
C.limbatus	0	0	4	4	13	6	2	6	11	2	19	5	72
G.cirratum	1	2	3	5	10	17	7	3	8	4	25	22	107
G.cuvier	1	4	2	8	40	29	5	28	28	3	19	6	173
R.porosus	0	0	0	0	1	2	0	1	0	2	0	2	8

2.4.3.2. Lunar effects

Total CPUE relative to the binned lunar phases (Figure 27), showed no distinct pattern. Total CPUE relative to binned normalised lunar phases, with waxing and waning state considered (Figure 28), also showed no distinct pattern. Results for *N. brevirostris* CPUE, both of total lunar phase (Figure 29), and with waxing and waning state considered (Figure 30), also revealed no distinct influence of lunar variations over this species' catch rates.

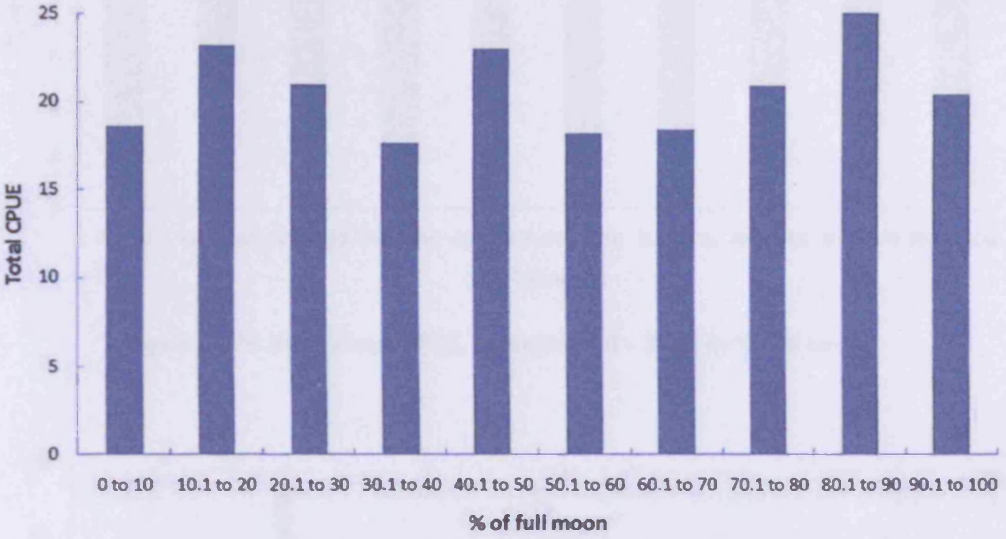


Figure 27. Total CPUE, between 1992 – 2003, by % full moon

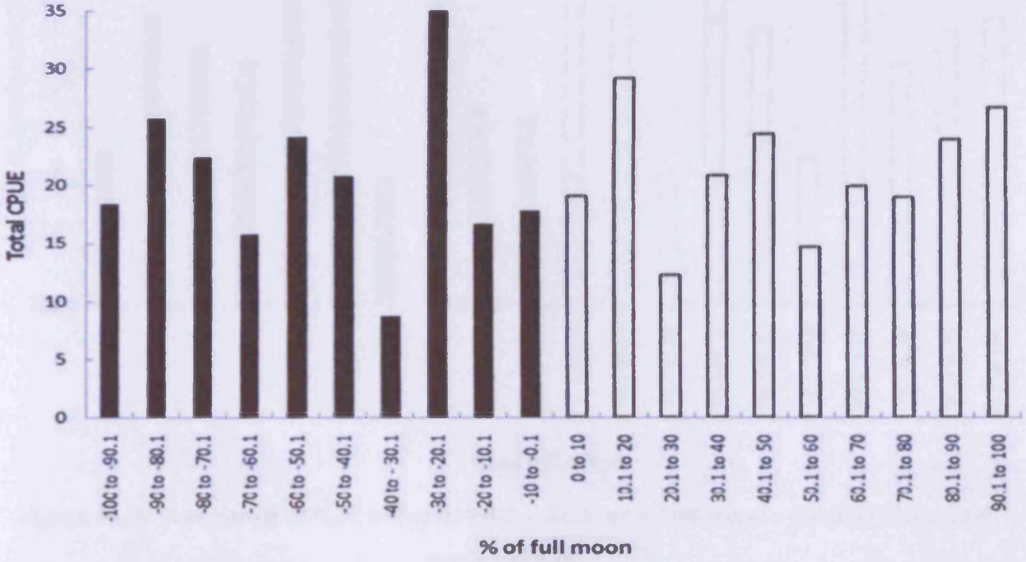


Figure 28. Total CPUE, between 1992 – 2003, by % full moon - waxing (white) and waning (black)

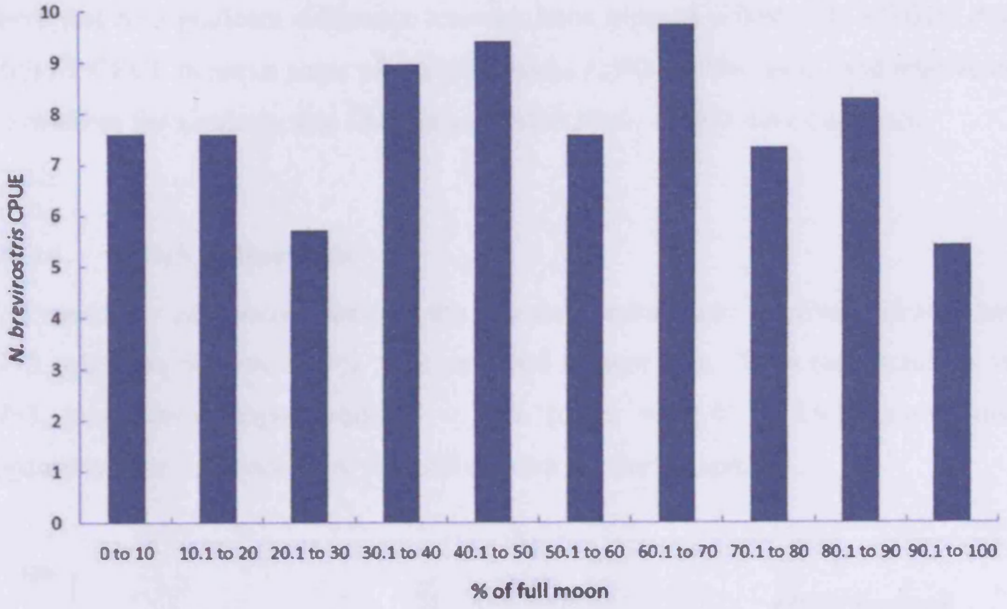


Figure 29. ***N. brevirostris*** **CPUE, between 1992 – 2003, by% full moon**

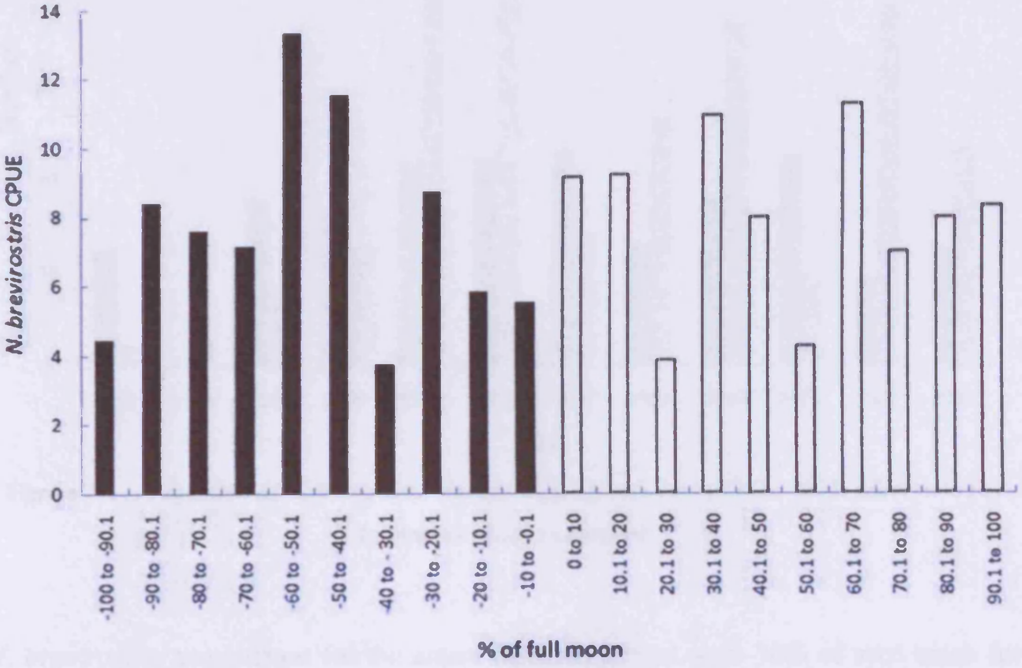


Figure 30. ***N. brevirostris*** **CPUE, between 1992 – 2003, by% full moon - waxing (white) and waning (black)**

2.4.3.3. Hook type

There was no significant difference between hook types (t = 0.84, dif. = 0.015, $P > 0.05$) for CPUE between years where 9/0 J hooks (1992 – 1996) were used relative to years where the similarly size 16/0 circle hooks (1996 – 2003) were employed.

2.4.3.4. Catch proportions

N. brevirostris proportions through the research period were relatively steady, bar 1993, when no *N. brevirostris* were captured (Figure 31). With the exclusion of 1993, proportions ranged from 18 – 46% (mean = 31.41 ± 3.92% s.e.), with apparently little influence from the total number of sharks captured.

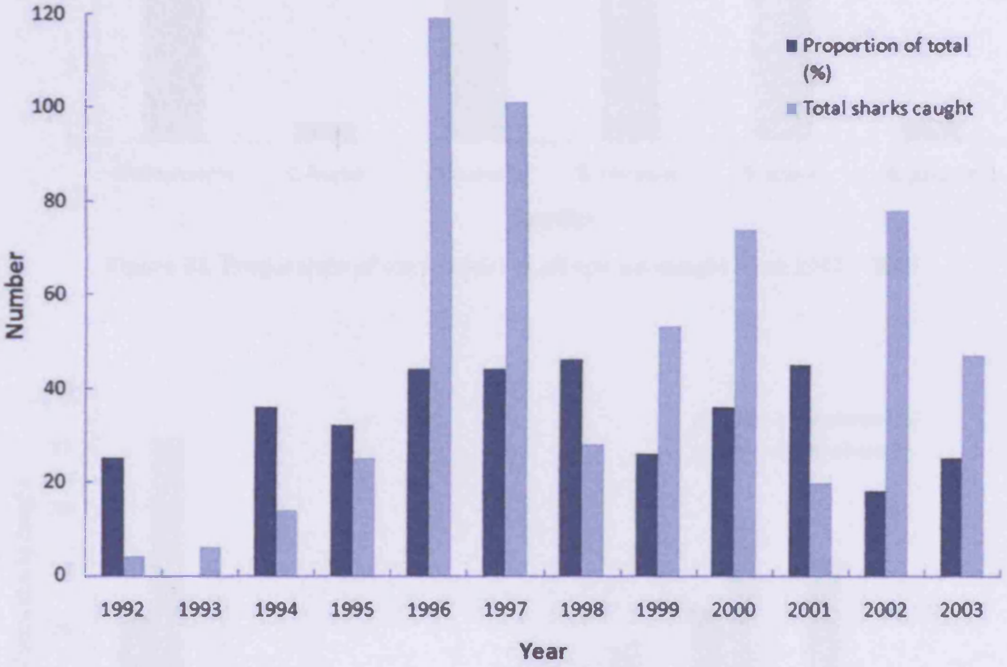


Figure 31. . Proportion of *N. brevirostris* caught on longlines, from 1992 - 2003, relative to the total of all sharks captured

N. brevirostris proportions for the entire research period were 36% of total catch for all species (Figure 32). Overall, the four species with the highest catch proportions were: *N. brevirostris* (36%), *G. cuvier* (30%), *G. cirratum* (19%) and *C. limbatus* (13%). Changes in catch proportions between the 1982 – 1989 and the 1992 – 2003 research periods (Figure 33) showed an increase in abundance for: *N. brevirostris*

(15%), *C. limbatus* (8%), *G. cirratum* (5%) and *G. cuvier* (8%), and a decrease in abundance for: *C. acronotus* (9%), *C. leucas* (1%), *R. porosus* (25%), and *S. tiburo* (1%).

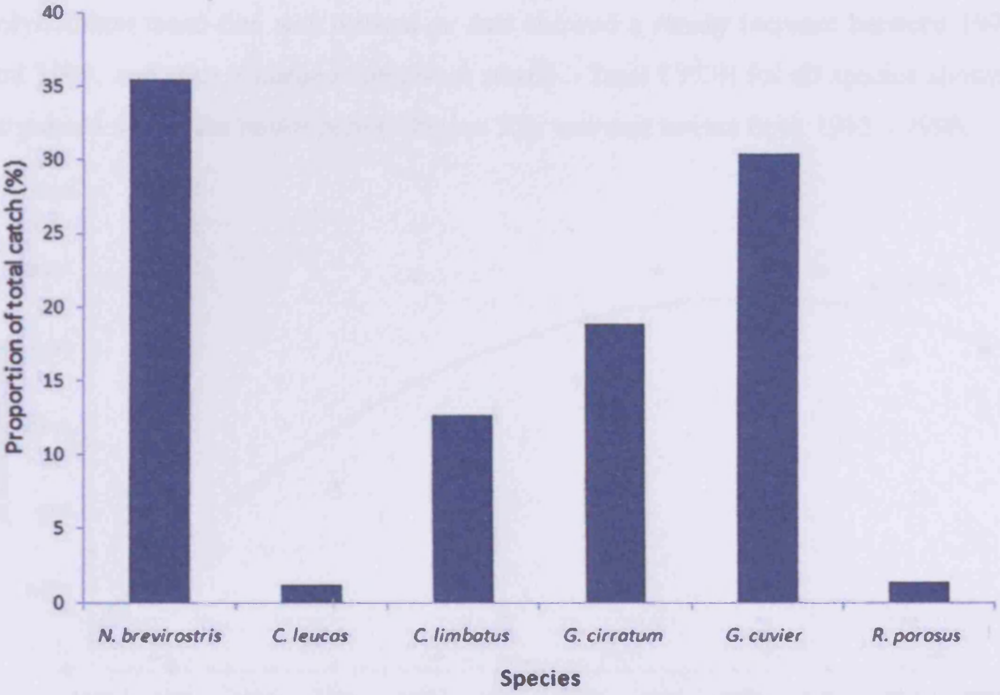


Figure 32. Proportions of total catch for all species caught from 1992 – 2003

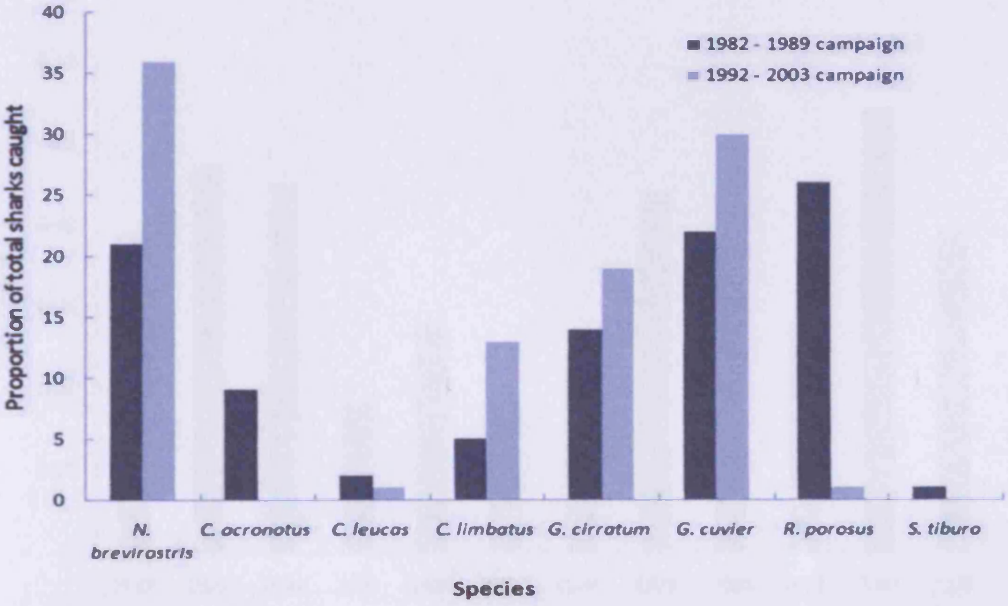


Figure 33. Species change in proportion of catch between the 1982 - 1989 and 1992 - 2003 campaigns

2.4.3.5. Catch Per Unit Effort (CPUE)

N. brevirostris CPUE values between 1992 and 2003 showed a distinct and significant ($r^2 = 0.726$, $n = 12$, $P < 0.01$) temporal increase (Figure 34). The polynominal trend-line was utilised as data showed a steady increase between 1992 and 1999, and then remained somewhat steady. Total CPUE for all species showed no pattern across the entire period (Figure 35), and was lowest from 1995 – 1998.

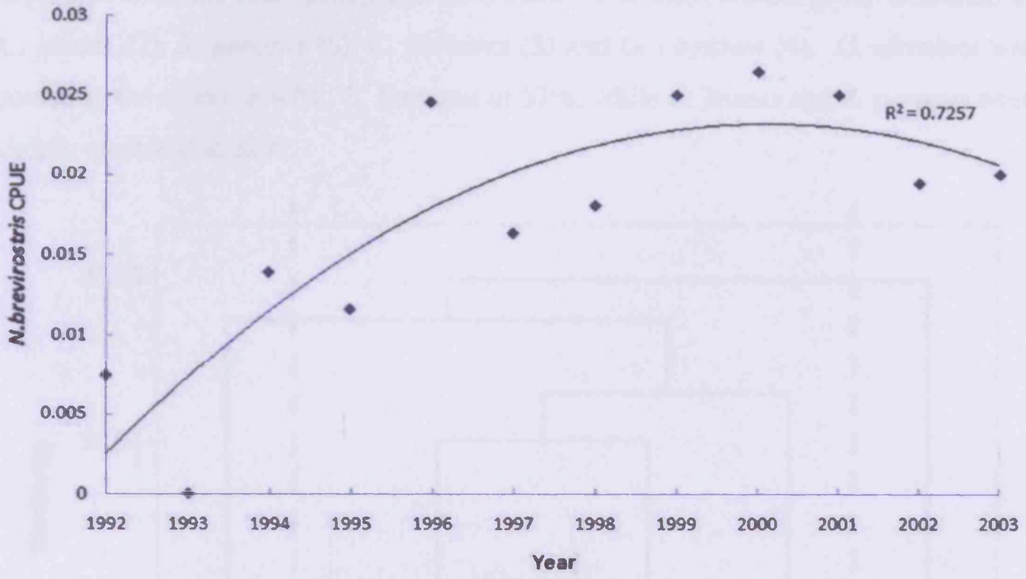


Figure 34. ***N. brevirostris*** **CPUE on longlines conducted from 1992 – 2003**

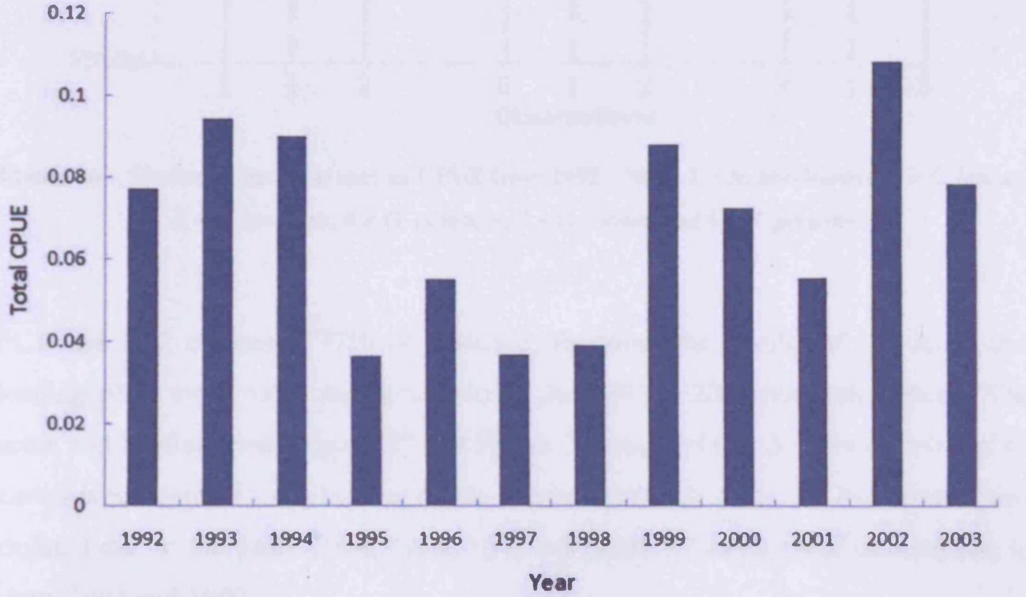


Figure 35. Total CPUE for all species on longlines conducted from 1992 - 2003

The results of the CPUE correlation analysis showed no relationships, positive or negative, for any of the species for this research period. The results for correlation between years showed most years to be significantly correlated to the years before and after, except for 1992, 1993, 1998 and 2001. The cluster analysis for species based CPUE (Figure 36) showed *N. brevirostris* (1) and *G. cuvier* (5) to be clearly separated from the main group and each other. The main central group consisted of *C. leucas* (2), *R. porosus* (6), *C. limbatus* (3) and *G. cirratum* (4). *G. cirratum* was joined to the others at 47%, *C. limbatus* at 57%, while *C. leucas* and *R. porosus* were tightly clustered at 82%.

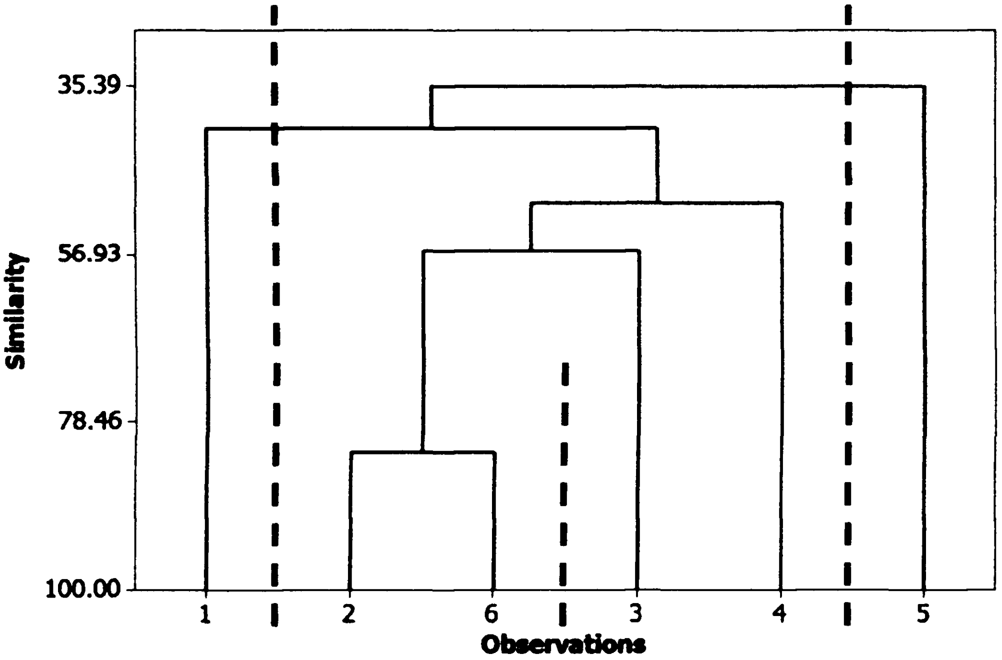


Figure 36.. Similarity between species CPUE from 1992 - 2003; 1 = *N. brevirostris*, 2 = *C. leucas*, 3 = *C. limbatus*, 4 = *G. cirratum*, 5 = *G. cuvier* and 6 = *R. porosus*

PC1 and PC2 explained 77% of variance, therefore the results of the score and loading plots are a valid representation of the 1992 – 2003 research period. The score and loading plots (Figure 37 and Figure 38) showed that *N. brevirostris* and *G. cuvier* were isolated from the rest of the species and each other. *N. brevirostris* was isolated due to the years 1994, 1998, 2001 and 2003. *G. cuvier* was isolated due to years 1993 and 1999.

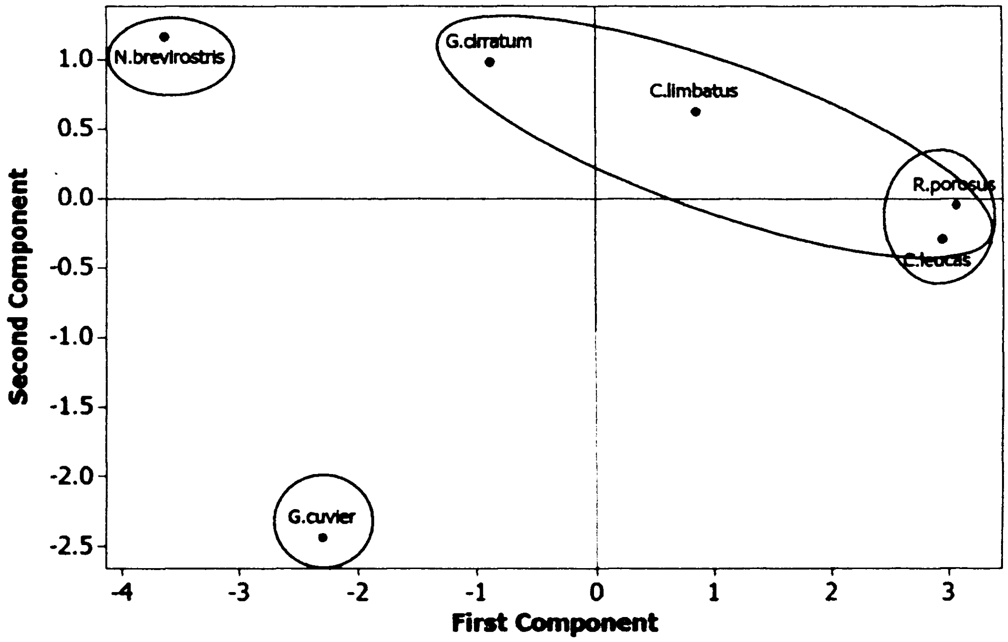


Figure 37. Score plot of research years' 1992 - 2003 species CPUE, groups encircled to show distribution

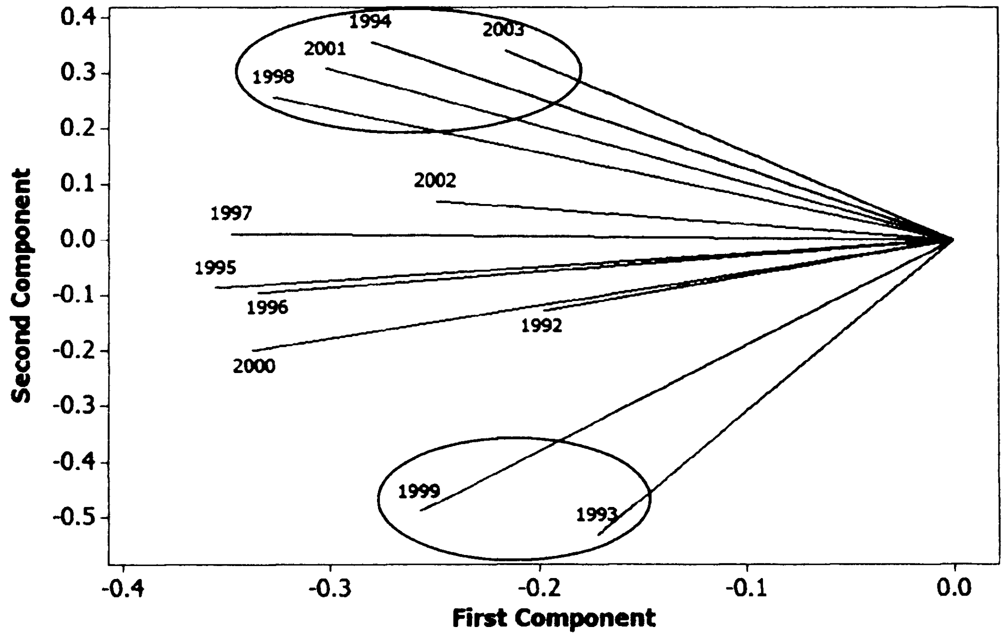


Figure 38. Loading plot of research years' 1992 - 2003 species CPUE, groups encircled to show distribution

The cluster analysis for year based CPUE (Figure 39) revealed a distinctly similar group comprising in order, the years: 1992, 1994, 1995, 1997, 1998, 2001, 1996 and 2000. This was separated from the rest of the cruises: 1999, 2002, 2003 and 1993, which showed strong dissimilarity to the grouped years, as well as between themselves. Of the grouped years, 1997 and 1998 showed the greatest similarity at 88%.

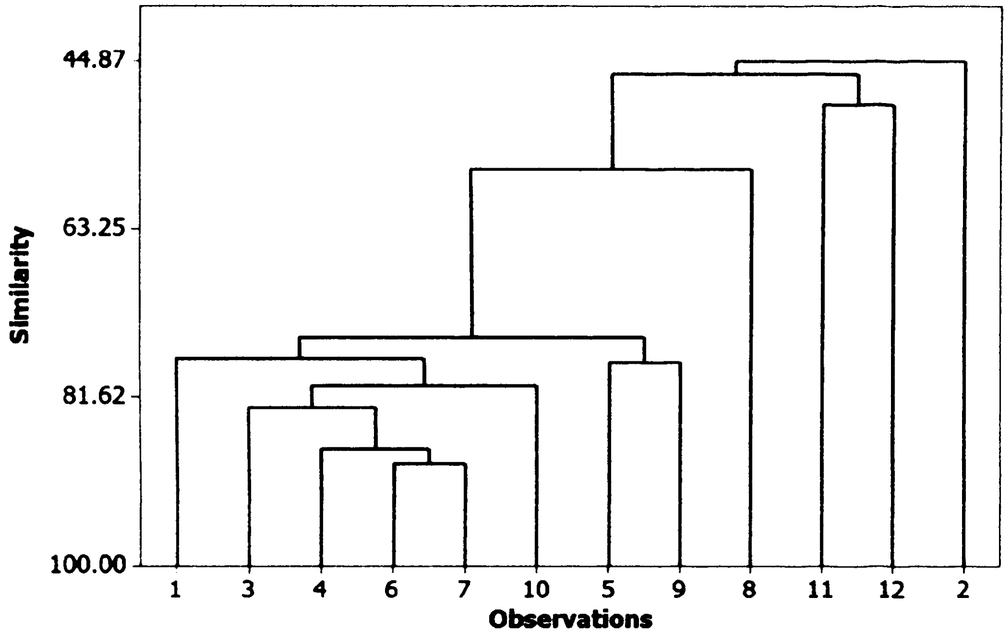


Figure 39. Similarity between research year CPUE from 1992 - 2003; 1 – 12 = 1992 - 2003

PC1 and PC2 explained 60% of variance; therefore the results of the score and loading plots are a valid representation of the 1992 – 2003 research period. The score plot (Figure 40) showed all years to be centrally grouped, except 1992, 1999, 2002 and 2003. The loading plot (Figure 41) shows the isolation of 1992 was the result of *C. leucas* CPUE in this year. The isolation of 1999 was the result of *N. brevirostris*, *G. cuvier* and *R. porosus* CPUE in this year. The isolation of 2002 and 2003 was the result of *C. limbatus* and *G. cirratum* CPUE in these years.

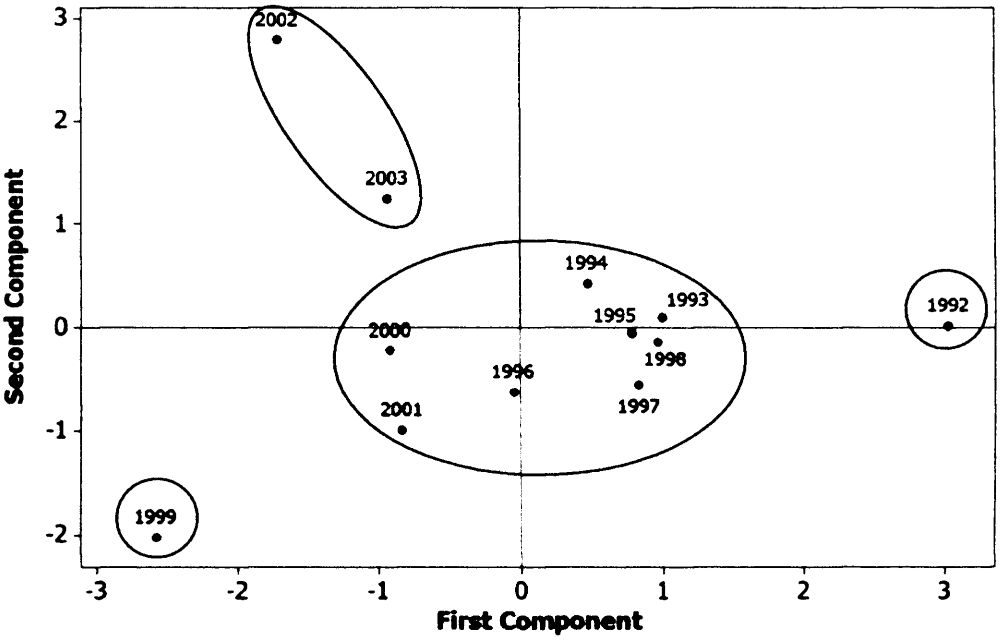


Figure 40. Score plot of all species' year CPUE, groups encircled to show distribution

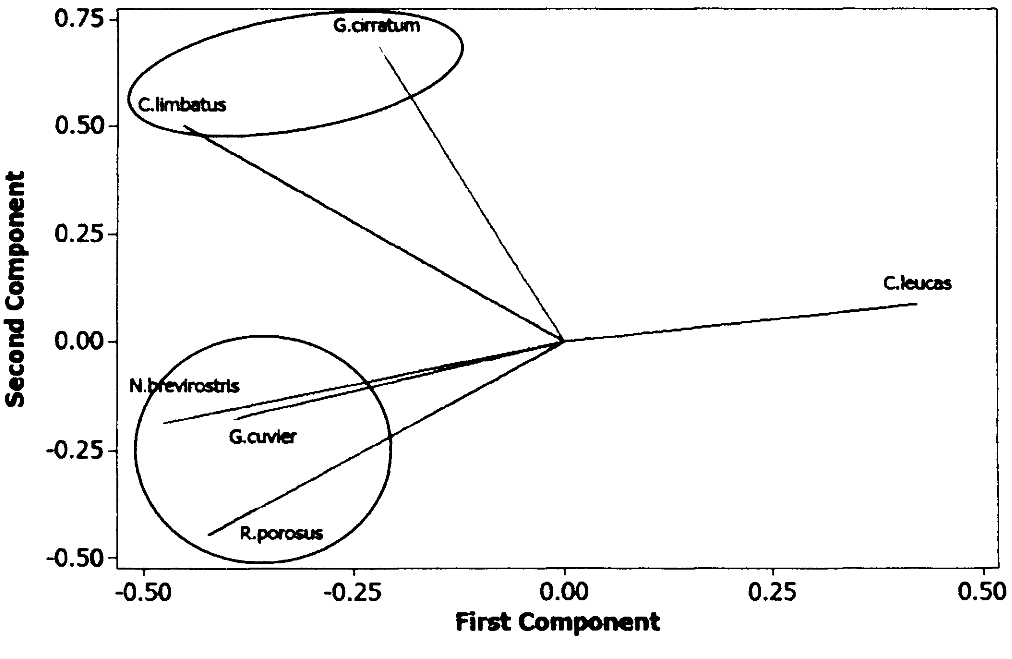


Figure 41. Loading plot of all species' year CPUE, groups encircled to show distribution

2.4.3.6. Capture related mortality

N. brevirostris catch related mortalities were very low during the 1992 – 2003 research campaign. Capture related mortalities for *N. brevirostris* were only present during four years: 1996 (18%), 1997 (6.5%), 2001 (11%) and 2003 (8%). The correlation between catch related *N. brevirostris* mortality and CPUE the following year showed no significant effect on population levels (r = -0.046, n = 4, P > 0.05). Total mortalities for all species during the 1992 – 2003 research campaign (Figure 42) were considerably lower than in the 1980s (Figure 19) for all recoded species. Most notably *R. porosus* mortalities were 12.5% compared to 91%, and *C. limbatus* mortalities were 16.5% compared to 73%, in the 1980s campaign. Mortalities were present for all species except for *G. cuvier*.

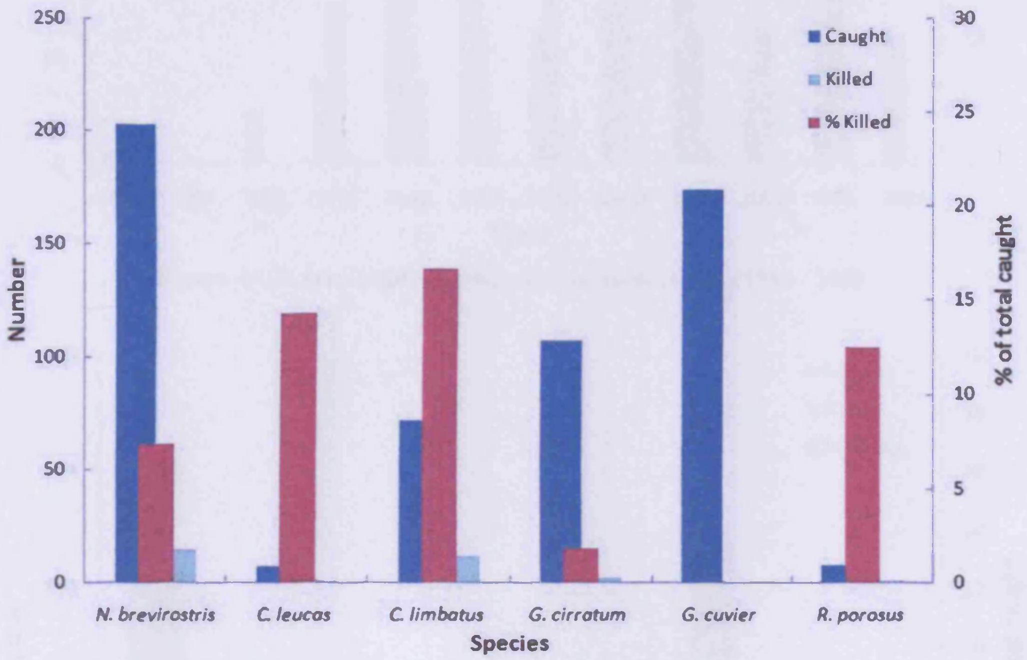


Figure 42. All species longline catch related mortality from 1992 - 2003

2.4.3.7. Mark-recapture

As in the 1980s, no *N. brevirostris* mark-recaptures were recorded at the beginning of the research campaign, with the first occurring in 1995 (Figure 43). Following this, recaptures were recorded in: 1995 (12.5%), 1996 (15%), 1997 (11%), 1998 (31%), 1999 (13%), 2000 (11%) 2001 (11%) and 2002 (14%). No *N. brevirostris* recaptures were recorded in 2003. During the entire 1992 – 2003 research period, four species: *N. brevirostris* (12%), *C. limbatus* (1%), *G. cirratum* (3%) and *G. cuvier* (3%) all provided mark-recaptures (Figure 44).

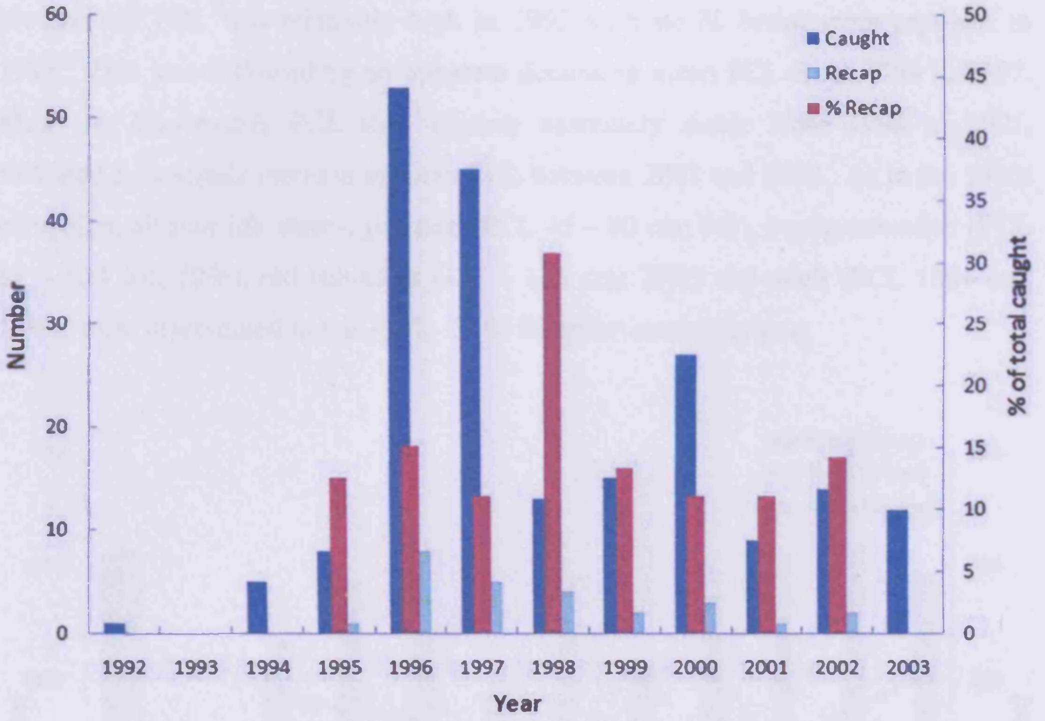


Figure 43. *N. brevirostris* longline mark-captures from 1992 - 2003

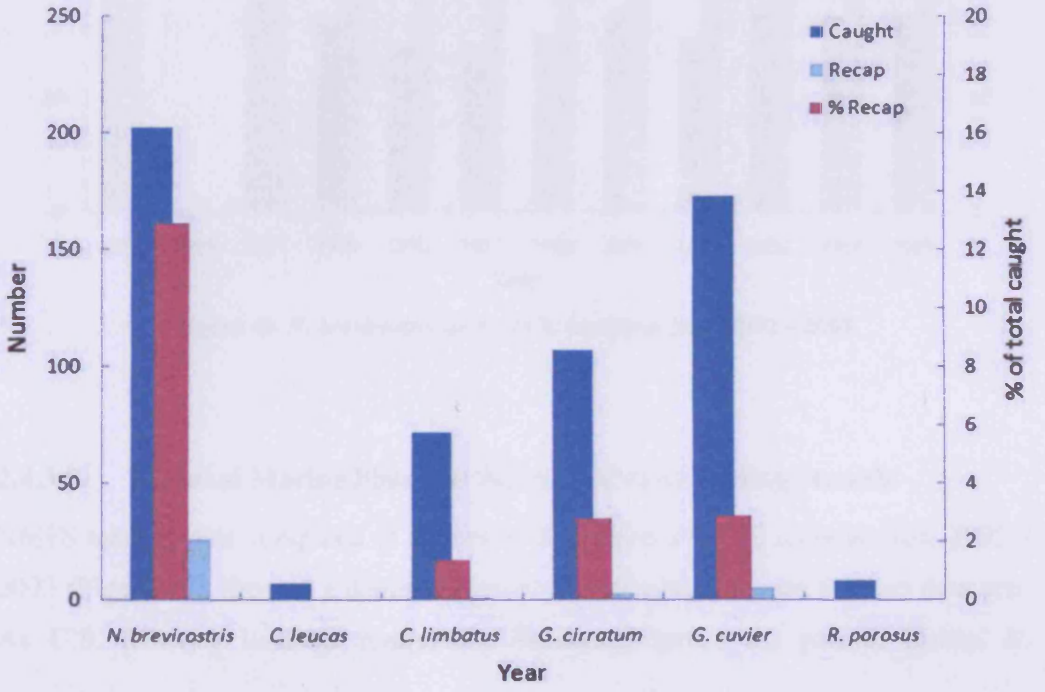


Figure 44. All species longline mark-captures from 1992 - 2003

2.4.3.8. Temporal Pre Caudal Length (PCL) variation of *N. brevirostris*

Mean *N. brevirostris* PCL was relatively stable throughout the 1992 – 2003 research campaign (Figure 45), with standard error generally low throughout. Mean *N. brevirostris* PCL was relatively high in 1992 with no *N. brevirostris* captured in 1993. This was followed by an apparent decline in mean PCL from 1994 to 1997. Mean *N. brevirostris* PCL then became extremely stable from 1998 to 2001, followed by a steady increase in mean PCL between 2001 and 2003. As in the 1980s campaign, all four life stages: juvenile (PCL 45 – 80 cm; 5%), young sub-adult (PCL 81 – 124 cm; 52%), old sub-adult (125 – 165 cm; 29%) and adult (PCL 166+ cm; 13%), were represented in the 1992 - 2003 longline catch database.

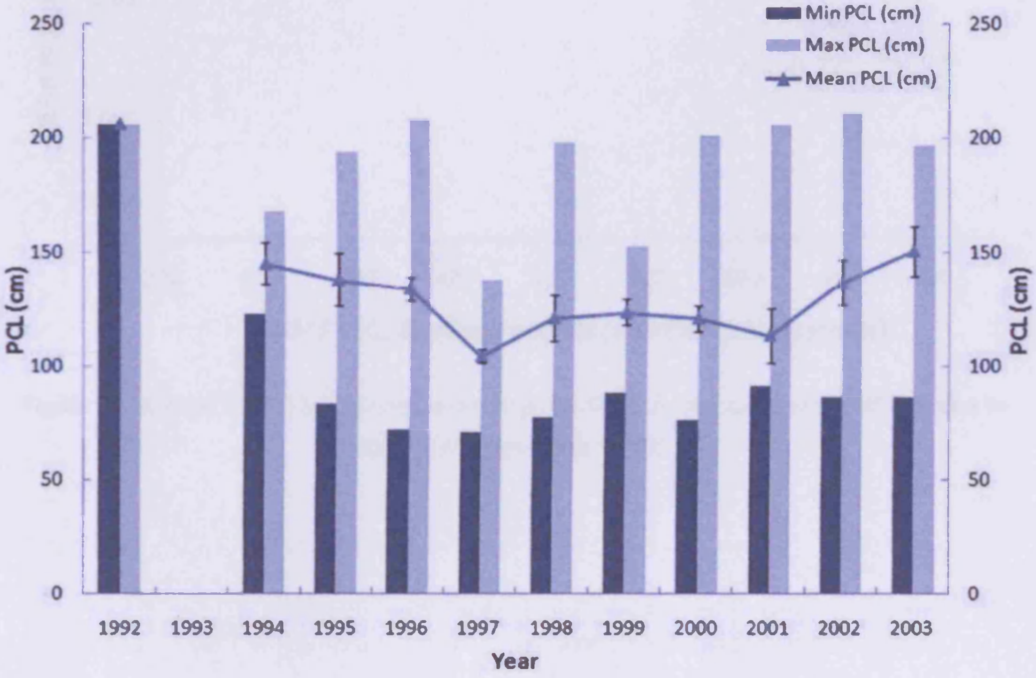


Figure 45. *N. brevirostris* mean PCL variation from 1992 – 2003

2.4.3.9. National Marine Fisheries Service (NMFS) landing records

NMFS landing data compared to Bimini *N. brevirostris* CPUE records, from 1992 – 2003 (Figure 46), showed a distinct negative relationship between the two data sets. As U.S. fisheries landings temporally decreased across the period, Bimini *N.*

brevirostris CPUE significantly increased ($r = -0.77$, $n = 12$, $P < 0.05$) over the same temporal period.

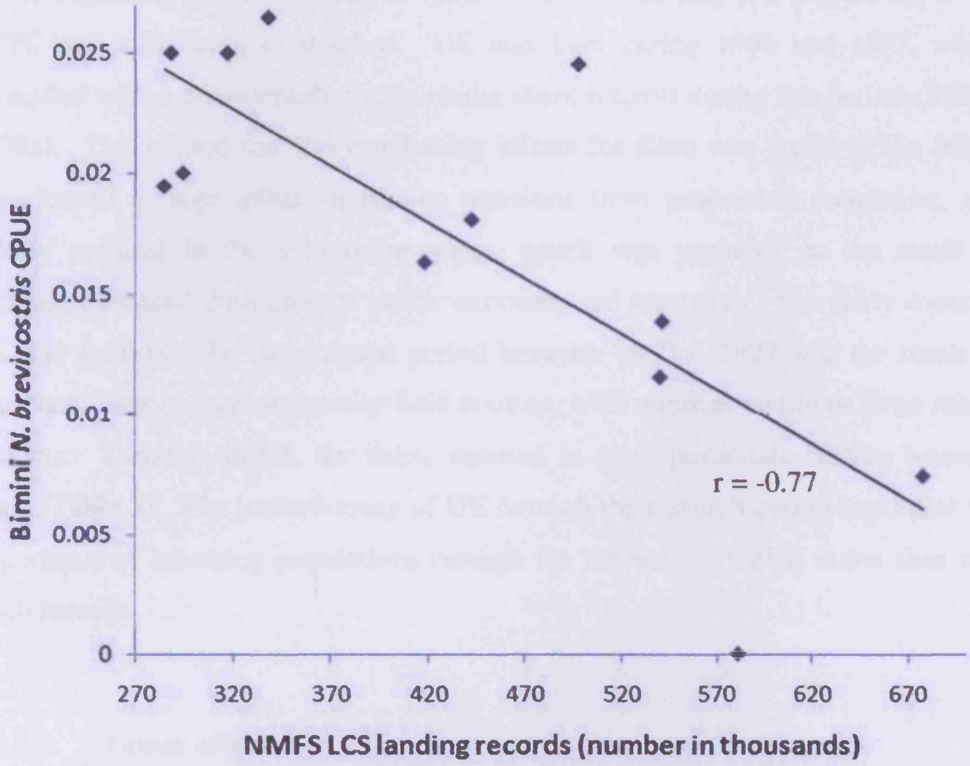


Figure 46. Annual NMFS LCS complex landings for the U.S. east coast and Gulf fisheries vs Bimini *N. brevirostris* CPUE

2.4.4. Discussion

2.4.4.1. Deduction of Unit Effort (UE)

At the beginning of the campaign in 1992 -1993 UE was very low (Figure 26) as the BBFS was still being established. UE was high during 1996 and 1997, which coincided with a considerable rise in media shark interest during this period (BBFS, 2009a). This caused the elevated fishing efforts for these two years, as the BBFS experienced a large influx in filming activities from production companies, and greatly reduced in the subsequent years, which was probably as the result of decreased demand through over public exposure and saturation. The fairly constant UE that followed the inconsistent period between 1992 – 1997 was the result of consistent year-on-year university field courses, with minimal additions from media projects. Variation in UE inevitably resulted in disproportionate catches between years (Table 3). The inconsistency of UE through the research period highlights the importance of assessing populations through the medium of CPUE rather than raw catch records.

2.4.4.2. Lunar effects

The absence of any distinct patterns (Figure 27 – 30) suggests the lunar phase relative to proportion of full moon had no influence over shark catch rates around the Bimini Islands. It would be an expected outcome for lunar phase to affect CPUE as it has commonly been shown to affect marine species behaviour (Bigelow et al., 1999, Dewar et al., 2008, Hammond and Welsh, 2009, Hernandez-Leon, 2008, Kraus and Rooker, 2007). However, lunar driven behaviours tend to be displayed at the mature life-stage, often as a function of reproduction (Graham et al., 2006, Ikegami et al., 2009, Kuparinen et al., 2009, Lowry et al., 2007, Nanami and Yamada, 2009, Oliveira et al., 2009), with the majority of the Bimini lagoon N. brevirostris population comprised of immature individuals. Thus the fact that lunar phase was not considered in the planning on longline sets throughout the entire research period 1982 – 2008 should not have lead to any false patterns or cause an inability to detect true patterns in population statistics.

2.4.4.3. Hook type

The absence of a significant difference in CPUE between 9/0 J hook (1992 - 1996) and 16/0 circle hooks (1996 - 2003) utilisation resulted in separate hook types concluded as a single continuous dataset. In many other studies, hook type has been found to effect catch and survival rates (Cooke et al., 2003a, Cooke and Suski, 2004, Cooke et al., 2003b, Falterman and Graves, 2002, Galeana-Villasenor et al., 2008, Hand, 2001, Kerstetter and Graves, 2006, Malchoff et al., 2002, McEachron et al., 1985, Prince et al., 2002, Rice, 2006, Yokota et al., 2006). The absence of a significant effect in this study is likely due to the relatively low catch rates throughout the research period, compared to longline based hook assessments with relatively high catch rates (Bigelow et al., 1999, Falterman and Graves, 2002, Kerstetter and Graves, 2006, Yokota et al., 2006). Thus catch rates of the Bimini longline efforts were likely too low to be subject to any significant effects of the change in hook type in 1996.

2.4.4.4. Catch proportions

A relative consistent proportion of *N. brevirostris* (Figure 31), despite an inconsistent in UE (Figure 26), and resultant total catch suggests a general stability of the *N. brevirostris* throughout the 1992 - 2003 research campaign. The complete absence of *N. brevirostris* in 1993 was the result of a relatively very low UE in that year. A total of only two days fishing was conducted, one of which was in February when the water temperatures were low and season low catches of *N. brevirostris* were usually recorded (see section 3.3.4). The other UE was in May when catches were normally higher. Of the three species, *G. cuvier*, *G. cirratum* and *C. limbatus*, that together with *N. brevirostris* represent the most abundant shark species around the Bimini Islands for this research period, the large abundance of *G. cuvier* and the resultant predation risk this species poses were, similarly to the 1982 - 1989 research period, most likely to effect the dynamics of the *N. brevirostris* population (Chase et al., 2002).

Proportions of *N. brevirostris* increased by a disproportionately large amount, relative to the other species (Figure 33), suggesting an increase in the size of the *N.*

brevirostris population relative to those of the other species. This indicates that the scientific sacrifices were restricting *N. brevirostris* *r*-intrinsic (the maximum potential of a population to expand) rates (Gedamke et al., 2007). The complete disappearance of *C. acronotus* was of concern as they previously represented a relatively large proportion of the total catch. The huge reduction in *R. porosus* was also of concern. Both of these reduced species, *C. acronotus* and *R. porosus*, suffered high catch related mortalities in the 1980s campaign and may not have fully recovered during the following research period. Also, increases in *N. brevirostris* and *G. cuvier* could also have lead to increases in predation pressures. Through these increases and decreases the relative shark abundances have altered between the two research periods, and now showed a more *N. brevirostris* dominated shark community structure.

2.4.4.5. Catch Per Unit Effort (CPUE)

The temporal pattern of CPUE between 1992 – 2003 (Figure 34) indicates a steady population increase until the carrying capacity of the ecosystem was reached. It is likely that although apparently steady throughout the 1980s campaign, population levels were below what is considered equilibrium within the ecosystem. It is completely possible that the nature of the sacrificial research being conducted on *N. brevirostris* throughout, although not causing a significant decline in the population, did not allow the population to reach its maximum sustainable capacity (Gedamke et al., 2007). Following the sacrificial based research of the 1980s cruises, all research conducted by the BBFS was based on non-sacrificial techniques, with every effort to keep the test specimens alive during and after capture. It appears that this allowed the population to reach its full potential for the Bimini Islands. It is possible that the decline of *N. brevirostris* CPUE from 2000 to 2001 can be attributed to the intensive dredging conducted by the Bimini Bay Development in the *N. brevirostris* nursery (Feldheim and Edren, 2002, Jennings et al., 2007). This resulted in increased mortality in the juvenile population (Jennings et al., 2007) that could have lead to direct reductions in CPUE through decreased recruitment from the nursery areas. Also, the disturbance to the nursery area during the breeding months could have disturbed the activities of the mature breeding female population (Feldheim et al., 2002a) that often comprise a number of the longline catches during this period.

Relatively low total CPUE between 1995 – 1998 (Figure 35) has no apparent cause for the years 1995 and 1998. However, for 1996 and 1997 it is possible that the high level of UE neared sample saturation of the shark population, thus reducing catch rates relative to UE (Ward et al., 2004).

The absence of correlation for the years 1992, 1993, 1998 and 2001 was justified in part by UE. Reference to the CPUE results (Figure 35) showed that 1992 and 1993 had generally low CPUE for most species, as very low UE focused only in a few months, in both these years (Figure 26). Therefore seasonal variations in CPUE (see section 3.3.4) lead to less accurate annual representation causing dissimilarity relative to other years. Also 1993 also saw the unusual occurrence of zero *N. brevirostris* CPUE making it instantly dissimilar to all other years. An increase in total CPUE from 1998 to 1999 caused dissimilarity between the two years. Dredging related to the Bimini Bay Development started in 1999 on the west side of the lagoon (Jennings et al., 2007, Feldheim and Edren, 2002). It is possible that this disturbance to the marine environment in the west of the lagoon could have caused a displacement, the result of avoidance, of sharks in the west of the lagoon to the east, where they would have received increased encounter rates with the longline (see section 4.4.2). This could therefore have increased the relative CPUE the increased encounterability (Ward, 2008, Stoner, 2004), compared to the previous year, when the west lagoon was left untouched. The discontinuity between 2001 and 2002 can be attributed to the period of most intensive dredging, relating to the Bimini Bay Development, in the west of the lagoon (Jennings et al., 2007, Gruber, 2002, Feldheim and Edren, 2002). Again, this could have displaced many sharks from the west to the east of the lagoon where the longlines are set.

This separation of *N. brevirostris* in the cluster analysis (Figure 36) reflected the disproportionately high increase in *N. brevirostris* CPUE relative to the other species. This allowed *N. brevirostris* to become the most abundant shark species in the catch records for the 1992 – 2003 research campaign. The closely clustered species of *C. leucas* and *R. porosus*, both represent relatively and similarly small catches, seven and eight individuals respectively, which provided cause for the similarity. There was also the potential that *R. porosus* presence on the longlines could have drawn *C. leucas* to the area resulting in simultaneous captures (Stoner, 2004).

N. brevirostris CPUE was isolated from the other species due to the years 1994, 1998, and 2001 (Figures 37 and 38). These are all years that *N. brevirostris* CPUE was considerably higher and often double that of the other species; therefore it is predominantly the catches in these years that resulted in the *N. brevirostris* representing the highest proportion of catches for this research period. *G. cuvier* was isolated due to the years 1993 and 1999, in which its CPUE was also considerably higher and double that of any other species. The *G. cuvier* proportion increase relative to the 1980s campaign can therefore be predominantly attributed to these two years. This increase would most likely have influenced the reduction in the numbers of smaller shark species (Lowe et al., 1996, Chase et al., 2002).

The years 1997 and 1998 were most strongly grouped by the cluster analysis (Figure 39). *N. brevirostris* CPUE appeared to be approaching carrying capacity for the ecosystem (Figure 34), indicating a relative stability at this time of the campaign. This stability was then disrupted by the beginning of the Bimini Bay Development dredging activities in 1999 (Jennings et al., 2007, Gruber, 2002, Feldheim and Edren, 2002), a year that was shown to have a high degree of dissimilarity to the grouped years. Again this has suggested that the Bimini Bay Development caused disruption to the Bimini shark population dynamics. 1993 showed the highest degree of dissimilarity to the grouped years, which is logical as only two species, *G. cirratum* and *G. cuvier*, were recorded at all. This could have been the result of unusual catches over the relatively low UE for that year. The dissimilarity of the 2002 and 2003 catches from the group, may have been due to effects of the intense dredging that took place in 2001 and the continuing detrimental nursery habitat alterations associated with the overall development (Gruber, 2002, Jennings et al., 2007). These would represent the time-lagged results that would be expected from a bottom up population decline starting in the nursery areas.

The isolation of year 1992 (Figure 39) is the result of *C. leucas* CPUE (Figure 40 and 41); this however represents a single *C. leucas* catch that made up 25% of the four sharks caught in a year of very low overall UE. Therefore, the influence of *C. leucas* over the local shark population has been over-represented by the unusually low total CPUE for that year. From the loading plot it becomes apparent that the isolation of 1999 is the result of unusual combined high CPUE of *N. brevirostris* and *G. cuvier*, with the addition of a relatively high *R. porosus* CPUE. However, *R. porosus* CPUE was still very low in relation to most other species, and therefore poses little influence. *N. brevirostris* and *G. cuvier* CPUE have been shown to ordinarily pose a negative relationship upon each other through the predation risk that *G. cuvier* poses over *N. brevirostris*. A likely avoidance mechanism would be for the *N. brevirostris* to move to the west of the lagoon, over the very shallow waters of the central lagoon, where it would be much more difficult for the generally larger *G. cuvier* to access.

As a result, the west of the lagoon is an area where very few, if any, *G. cuvier* sightings, or capture from other fishing methods in the area, have been made (personal observations 2002 - 2008). However, the initiation of the Bimini Bay Development dredging in 1999 would have caused instant disturbance and increased turbidity in the west of the lagoon (Gruber, 2002). This would have rendered the area much less suitable or desirable as a refuge, possibly forcing the *N. brevirostris* to remain in the east of the lagoon where the water depths are suitable even at low tide. Thus, in contrast to other years, both species would have been abundant in the target area during the same fishing periods, allowing multiple simultaneous captures to occur. The loading plot showed high catches of *G. cirratum* and *C. limbatus* to be the cause for the isolation of 2002 and 2003. Many of the fishing efforts in 2002 and 2003 occurred during summer months when *C. limbatus* and *G. cirratum* are usually in high numbers (see section 3.3.4), resulting in disproportionately high catches for these species.

2.4.4.6. Capture related mortality

The reduction in catch related mortalities between the 1982 – 1989 and the 1992 – 2003 research campaigns was the direct result of the move away from sacrificial based research techniques and alterations to the checking regime. From 1992 onwards every effort was made to keep the study sharks alive during all conducted research. Checking periods were altered from twice a day to every four hours, greatly reducing the average time that each shark remained on the line and therefore increasing survival rates (Ward et al., 2004). Also the permanent research base in the form of the BBFS meant that, unlike the research cruises, set periods could be more carefully chosen to avoid serious weather effects that may prevent the checking of the lines for long periods. The mortalities that occurred between 1992 – 2003 curiously came after the switch from J to circle hooks, which elsewhere have been proven to reduce shark mortality (Falterman and Graves, 2002). The highest rate in 1996 can be attributed to the very large *N. brevirostris* catch (No. = 53) that year. Therefore, as there is an inherent risk of mortality with any shark capture; the more *N. brevirostris* caught, the greater the chance a portion will die.

Many of these mortalities came when multiple sharks were caught on the same checks. The processing time, in addition to the 4 h period between, meant that some of the sharks remained on the lines for extended periods resulting in mortality. The 1997 mortalities, though less in number, can be attributed to the same cause. The high mortality rate in 2001 could be the result of the intense dredging occurring in the west of the lagoon that year. The dredging activity in the west resulted in high catch rates in the east, while turbid waters resulting from the dredging compromised environmental conditions. Turbidity commonly lowers oxygen levels available in the water column (Zale and Merrifield, 1989), which increases the possibility of suffocation caused by restricted movements on the lines. The 8% mortality rate in 2003 relates to a single shark that was released alive, but then found dead the next day, and identified by the external tag. This mortality remains somewhat of a mystery as the shark was released in good condition and the mortality cannot be attributed to anything recorded in the comments during processing.

Total mortalities for all species during the 1992 - 2003 research campaign (Figure 42) were considerably lower than in the 1980s (Figure 19). Dramatic reductions in *R. porosus* and *C. limbatus* mortality was most likely the direct result of increased check occurrences to once every four hours during the 24 h fishing period (Ward et al., 2004). *N. brevirostris* mortalities were also greatly reduced from 20% in the 1980s to 7%. This was the result of a combination of the move to no sacrificial study approaches and the increased check ratios. No correlation between catch related mortality and subsequent CPUE, indicates that low catch related mortality had no significant effect over the *N. brevirostris* population dynamics. This in turn contributed to the increase in population level to near ecosystem capacity through the period. Therefore, it appears that during the 1980s, study related mortalities posed the greatest influence over *N. brevirostris* population levels at the Bimini islands. In contrast to the 1982 – 1989 research campaign when a number of species were subject to high levels of catch related mortality (Figure 42), with now minimal effects to other elasmobranch species *N. brevirostris* still emerged as the most abundant shark species present in the waters (Figure 32). The absence of any *G. cuvier* mortalities is logical, as this species is one of the more robust species in relation to prolonged periods on the longlines (Cortes et al., 2008, Holland et al., 1999).

2.4.4.7. Mark-recapture

In the case of the 1980s campaign, the low *N. brevirostris* mark-recapture rate during the first three years (Figure 43) was logical, as prior to this there were no *N. brevirostris* tagged in the area. However, in the 1992 – 2003 campaign it would be expected that individuals tagged in the 1980s campaign would still be instantly available for recapture at the start of longlining in 1992 (Chapman et al., 2009). This can be explained as there was a sustained level of catch related mortality right up until the end of the 1980s campaign, thus less *N. brevirostris* were tagged and released. There was also the period between 1990 and 1992 where no sharks at all were caught and tagged under the longline activities. Numbers of captured *N. brevirostris* were also low at the beginning of the 1990s longlining efforts, thus few tagged sharks were available for capture in the area. It is also possible that many of the larger sharks would have reached maturity and left the target area (Feldheim et al., 2002a, Sundström et al., 2001) between the time of last recapture in the 1980s and 1995. This would have further reduced the number of tagged sharks present in the target area.

Once the levels of tagged sharks within the population increased, and recaptures began to be recorded in 1995, levels remained relatively stable until 2003 when no mark-recaptures were recorded. This suggest that for this period, the *N. brevirostris* population was consistently stable, with new sharks repeatedly being added to the population and other tagged sharks dying, or leaving the area. Since mark-recapture proportions were remaining stable relative to the temporal changes in CPUE, this supports the theory that the population steadily increased and then levelled out as it reached the carrying capacity of the ecosystem. The highest recapture proportion was recorded in 1998, which is logical as it followed two years of intense fishing efforts and thus *N. brevirostris* catches (Figure 43), which resulted in more tagged individuals available for recapture that year. The absence of any mark-recapture in 2003 can be partially attributed to the fact that these catches only represent efforts between January and July. It could also be attributed to the chance that the *N. brevirostris* sampled represented a disproportionately untagged number within the site-attached population (Chapman et al., 2009).

Of the four species that provided mark-recaptures in the 1992 – 2003 campaign, *N. brevirostris* showed considerably the highest rate at 12%, supporting the evidence provided by Chapman et al. (2009) that they displayed a high level of site-attachment to the waters of the Bimini Islands. This is also similar to the 10% proportion recorded in the 1980s. Levels would be expected to be higher due to the absence of scientific sacrifices. However it was generally larger individuals that were sacrificed in the 1980s and these mortalities may be accompanied by natural mortalities and the departure of maturing individuals over the longer time period (Sundström et al., 2001). Curiously, *G. cirratum* mark-recapture declined from 12% between 1982 – 1989, to just 2% between 1992 - 2003. This could be partly due to the nature of the *G. cirratum* feeding behaviour that lead to considerable external tag losses (Motta et al., 2002). The low incidences of *C. limbatus* and *G. cuvier* recapture strengthens the theory that these comprise the more nomadic species that make up significant proportions of the community structure (Figure 44).

2.4.4.8. Temporal Pre-Caudal Length (PCL) variation of *N. brevirostris*

The relatively stable, compared to the 1980s campaign, mean *N. brevirostris* PCL throughout the 1992 – 2003 research campaign (Figure 45) reflects the proportionally large catch rates (Figure 34). The relatively high *N. brevirostris* PCL in 1992 was only representative of one relatively large shark (No. = 1). No *N. brevirostris* were captured on the longlines in 1993; therefore, there were no records for this year. The apparent decline in mean PCL, from 1994 to 1997 suggests an influx of smaller sub-adults, maturing from the various nursery areas, into the lagoon population. The steady increase in mean PCL between 2001 and 2003 can be attributed to the dredging activity that took place between 1999 and 2001. The dredging resulted in a documented decline in juvenile survival rates for the period (Jennings et al., 2007), which would have reduced the amount of juveniles maturing into the lagoon population. At the same time the group, whose influx caused the decline between 1994 and 1995, would have been closely approaching maturity, resulting in increased predation risk to individuals at the smaller end of the population size distribution (Webster, 2004). Increased predation risk, in addition to reduced juvenile survival rates, caused by the development activity, would have magnified the increase in mean PLC. This reversal at both ends of the size classes would have caused the increase in mean PCL.

Relative to the data from the 1980s campaign (Figure 23) mean PCL was most similar to the more stable seasonal catches. This is logical as the non-summer catches in the 1980s data caused the variations; and the 1992 – 2003 efforts were more evenly distributed over each year, resulting in little to no seasonal influence over catches. During the 1992 – 2003 research campaign the lagoon *N. brevirostris* population was dominated by young sub-adults (52%), while juveniles comprised 5%, old sub-adults 29% and adults 13%. The proportional increase of both size classes of sub-adults, relative to the proportions in the 1980s (see section 3.3.9), reflects the increase in *N. brevirostris* CPUE throughout the research period. Size class figures also support the theory that the ecosystem had approached carrying capacity, as both sizes classes of sub-adult display higher site-attachment than the adults (Sundström et al., 2001, Gruber et al., 1988, Chapman et al., 2009), which have proportionally decreased relative to the sub-adults.

2.4.4.9. National Marine Fisheries Service (NMFS) landing records

The significant negative correlation between NMFS landing records and Bimini *N. brevirostris* CPUE records (Figure 46) provides strong evidence for a single north-western Atlantic *N. brevirostris* stock, as suggested from the results of the past genetics studies conducted by Feldheim et al. (Feldheim et al., 2001a). Thus U.S. east coast and Gulf landings of Large Coastal Sharks (LCS) can directly affect the later life-stages of *N. brevirostris* that are directly linked to the Bimini population. The impact from the U.S. east coast and Gulf landings would have the most direct influence on the adults, and to a lesser extent, a proportion of the larger sub-adults. Indirectly, the effect would have come from a reduction in the mature breeding population that provided the population with juvenile *N. brevirostris* at the base level, resultantly supplying the lagoon population by recruitment. This also suggests that it was not only catch related mortality that restricted *N. brevirostris* population growth during the 1980s, but more likely a combination of catch related mortality and the U.S. east coast and Gulf fisheries. The decrease in U.S. fisheries landings could have also combined with increased juvenile mortality (Jennings et al., 2007), to result in the increase in mean PCL towards the end of the research period.

2.4.5. Conclusions

The apparent lack of stability of *N. brevirostris* CPUE through the 1980s research campaign can be most strongly attributed to the sacrificial nature of many of the research projects. Despite the identified effect upon the disruption of a temporal population pattern, it is unlikely that at the recorded levels *N. brevirostris* catch related mortalities would have had a substantial impact upon population abundance. Throughout the 1992 – 2003 research campaign, the absence of sacrificial research techniques, and the subsequent low *N. brevirostris* catch related mortality, allowed a stable pattern in CPUE to emerge. The 1992 – 2003 period saw a steady increase in *N. brevirostris* CPUE, which appeared to level off as the ecosystem reached carrying capacity at the top trophic level. This suggests that with the absence of direct anthropogenic influences *N. brevirostris* abundance will be stable at carrying capacity within the ecosystem. Disruption during the 1992 – 2003 period came directly from the Bimini Bay Development activities, with multiple negative impacts identified. Therefore it appears that the Bimini Bay Development has not only caused the identified reduction in primary nursery bound juvenile *N. brevirostris* survival rates, but also direct disruption to the secondary lagoon sub-adult and adult breeding *N. brevirostris* population dynamics.

Community structure between the 1980s and 1992 – 2003 also showed an increase in the relative abundance of *N. brevirostris* within the total multispecies shark population. All four dominant species within the community structure, *N. brevirostris*, *C. limbatus*, *G. cirratum* and *G. cuvier*, catch proportions' increased from the 1982 – 1989 to the 1992 – 2003 research periods. Therefore the interspecies relationships identified, positive between *N. brevirostris* and *G. cirratum* and negative between *N. brevirostris* and *G. cuvier*, should not have disproportionately influenced the increase of *N. brevirostris* proportion within the community structure. The high proportion of *N. brevirostris* within the community structure of the 1980s highlights its importance as a top predator in the Bimini marine ecosystem. Importance was reinforced when the *N. brevirostris* were uninfluenced by catch related mortality, in the 1992 – 2003 period, their abundance increased relative to the other species.

Temporal changes in mean PCL in the 1980s showed an alarming decrease toward the end of the period, most logically the result of scientific sacrifices of larger individuals. The mean PCL decrease also suggested a high level of recruitment from the juvenile population at the time, from the then undisturbed nursery areas. The strong recruitment continued through the beginning of the 1992 – 2003 research period, until it became disrupted by the Bimini Bay Development activities in the late 1990s. Increasing mean PCL would result in increasing predation risk for individuals at the lower end of the population size classes, in addition to decreased recruitment potential from the reduction in survival rates at the juvenile life-stage. Therefore, at the end of the 1992 – 2003 period the *N. brevirostris* lagoon population, as the result of decreased recruitment potential and increased predation risk, would have been positioned to most likely suffer a population decline over the coming years. Thus the documented negative impacts of the Bimini Bay Development, at the juvenile level, will over time, further negatively impact the entire local *N. brevirostris* population dynamics.

With the absence of any major anthropogenic influences, both from scientific sacrifices and resort development through the majority of the 1992 – 2003 period, it was possible to identify a significant negative relationship between U.S. east coast and Gulf fisheries LCS landings and Bimini longline *N. brevirostris* CPUE. This identified negative relationship, was in support of previously published genetic evidence suggesting a single unit stock for the north-western Atlantic *N. brevirostris* distribution (Feldheim et al., 2001a). Therefore, it is possible that the *N. brevirostris* population of Bimini, or *N. brevirostris* populations of similarly remote locations, could serve as an indicator of the broader distributed U.S. east coast *N. brevirostris* population status.

3. Recent longline catches

(2003 – 2008)

3.1. Chapter Introduction

In the early 2000s at the start of the research campaign, *N. brevirostris* Catch Per Unit Effort (CPUE) was at the highest recorded levels since research began in 1982. *N. brevirostris* CPUE reached its highest annual level in 2000, suggesting that the *N. brevirostris* population had reached carrying capacity for the ecosystem. This appeared to be partly in response to no direct anthropogenic influences throughout the majority of the 1992 - 2003 campaign. Research related sacrifices of *N. brevirostris*, from 1992 – 2003, were no longer in effect and in addition to increased longline check regularity, catch related mortalities were very low. Scientific approaches that required no *N. brevirostris* sacrifices were again adopted through the new 2003 – 2008 research campaign, resulting in minimal research impacts on local *N. brevirostris* abundance. As was the case throughout the 1980s and subsequent 1992 – 2003 campaign (Lutz et al., 2002), artisanal and recreational fishing activities remained relatively constant and minimal throughout the 2003 – 2008 research campaign (personal observations 2002 - 2008). Therefore local fisheries impacts were not considered as an external factor influencing the *N. brevirostris* population dynamics.

The Bimini Bay Development activities remained in operation throughout the 2003 – 2008 research campaign, with effects already documented following the initiation of the development in 1997 (Gruber, 2002) in the results of the 1992 – 2003 research campaign. The Bimini Bay Development activities remained as the most considerable local anthropogenic influence that may have affected the *N. brevirostris* population throughout the 2003 – 2008 research campaign. Most notable activities were substantial dredging of the eastern lagoon sub-tidal areas and the continued removal of the North Sound *N. brevirostris* nursery's fringing mangrove populations (Jennings et al., 2007). The Bimini Bay Development activities were found to have resulted in a reduction of nursery bound *N. brevirostris* survival rates, in addition to a reduction in the extent of seagrass beds, in a study where field research was concluded in 2005 (Jennings et al., 2007). It is most likely that continuing development activities resulted in a continued repression of juvenile *N. brevirostris* survival rates throughout the 2003 – 2008 research campaign.

It is the ontogenetic shift of *N. brevirostris* individuals from the island nursery areas that provided recruitment at the base level of the lagoon Bimini *N. brevirostris* population (Sundström et al., 2001, Feldheim et al., 2002a, Chapman et al., 2009). Therefore the identified reductions in survival rates at juvenile level would have resulted in a reduction in the recruitment potential for the lagoon Bimini *N. brevirostris* population. Of greatest concern was the scale of the development plans for the Bimini Bay Resort (Appendix 2; Puentes, 2004). These included full development of the terrestrial and near-shore sub-tidal areas surrounding the North Sound *N. brevirostris* nursery. Planned development includes land use such as a casino, condos and most worryingly a nine-hole golf course (Gruber, 2002). The development plans would involve the complete removal of all nursery fringing mangroves, land reclamation and continued dredging in both the *N. brevirostris* nurseries and east lagoon. The scale of the plans facilitated continued development, both terrestrial and sub-tidal throughout the 2003 – 2008 research campaign (personal observations 2003 – 2008).

From a research perspective, the 2003 – 2008 campaign overlapped annually with the 1992 – 2003 campaign. Following discussions with Dr. Gruber, the director of the Bimini Biological Field Station (BBFS), during the annual juvenile *N. brevirostris* population census in June 2003, a new longlining regime was agreed. For the first time in Bimini, as the result of the initiation of this study, the longlining activities would serve not as a tool for obtaining specimens for other studies/activities (e.g. Brown and Gruber, 1988, Sundstrom and Gruber, 2002, Sundstrom and Gruber, 1998, Chapman et al., 2009, Gruber et al., 1988, Nixon and Gruber, 1988, Wetherbee et al., 1990), but a focused research campaign. It was thus possible to design a structured effort schedule that would not only allow for general annual population analysis, but in addition more seasonal variations to be revealed. Research focused directly on the longlining activity also resulted in greater financial investment and thus the employment of additional scientific equipment to investigate more of the previously assumed variables. Also for the first time, the database would be managed carefully from start to finish, resulting in the greatest level of data confidence for all three of the research periods.

With the addition of the final research period, 2003 – 2008, it was then possible to address each research period individually, but also consider and analyse the entire 26 year long research period from 1982 – 2008 as a single temporal unit. The specific aims of the chapter were to a) assess the shark population dynamics, for both this period and the entire 26 year research campaign from 1982 - 2008, with specific focus upon *Negaprion brevirostris*, for temporal patterns in CPUE, catch proportions, catch related mortality, mark-recapture, mean Pre-Caudal Length (PCL) and size class proportions; and b) to assess the effects of external driving variables, including temperature, inter/intra-species relationships, and anthropogenic influences, with specific focus on the Bimini Bay Development, that dictated the local shark population dynamics. The aims were achieved by statistical analysis of both the 2003 – 2008 data set and the combined 1982 - 2008 Bimini longline database; the explanation of identified patterns and relationships using existing species life-history information; the incorporation of influencing historical information, both anthropogenic and environmental, including the peer reviewed literature on the environmental impact of the Bimini Bay Development.

3.2. Methodologies

3.2.1. Longline regime design

In order to achieve a seasonally representative dataset it was decided that two 24 hour longline sets would be conducted each month. Sets were conducted on the 7th and 22nd of each month, or as close to those dates as conditions permitted. In keeping with the previous research campaign, lines were set in the afternoon then hauled the following afternoon, 24 hours after the set, and checks were conducted every four hours. Twice monthly sets were executed from July 2003 – September 2008, weather conditions permitting. As the result of prolonged periods of bad weather and hurricane related field station evacuations, two sets each month were not always possible, therefore, and also to make this data set comparable to those from the previous research campaigns, it was again necessary to convert all catches into CPUE for analysis.

3.2.2. Alterations to longline sets

Longlines were set in accordance to the methodology described in sections 2.3.2.2 and 2.4.2.1 from July 2003 – September 2005. From September 2005 onwards, the following additions were made. Temperature profiling iButtons® were deployed on the first, last and centre floats of each line for the duration of the set, with water entry time recorded. Hook timers were added as a link between the main line and gangions. When a shark took the bait and pulled the gangion at in excess of 10 lbs of pressure, a magnetic switch would be released starting a digital counting unit that recorded time in hours and minutes, as employed by Rice et al. (2007). Longlines were set from GPS start and end points to standardise set locations between sets. Set times and GPS locations were taken for each gangion as it entered the water and the details of the bait type for each hook were also recorded. On hauling the longlines, for each gangion, time out of water, bait presence/absence and any comments relative to condition such as damage was recorded. Whether or not each hook timer was triggered, and if triggered the time displayed on the unit, was recorded. Time out of water for each iButton® was recorded.

3.2.3. Alterations to shark processing

Sharks were processed in accordance to the methodology described in section 2.3.2.3 and 2.4.2.2, with the following additions. On first encounter with the shark, the time displayed on the hook timer was recorded along with the current time. The line code and hook number that the shark was captured on was recorded. The hooking location, for example left or right corner of jaw or, in the event of a foul hooked shark the location of the foul hooking, and whether or not the shark was bleeding from the hook wound were recorded. Finally, for males, the in-seam and out-seam of the right clasper were measured, and the calcification status of the clasper was recorded as an indicator of maturity.

3.2.4. Analytical methodologies

3.2.4.1. Unit Effort (UE)

UE, and subsequent Catch Per Unit Effort (CPUE) were devised as described in section 2.3.2.5.1. Effort was grouped annually for temporal analysis by year and by month for seasonal analysis. For any incidences where analysis was conducted on the entire 26 year database a single temporal plot, UE and catch records were combined for 2003 to allow for a combined annual CPUE for that year.

3.2.4.2. Assumptions

Sections 2.3.2.5.2 and 2.4.2.4.2 detail a number of variables assumed not to influence the results of the 1980s and 1992 – 2003 catch data. For the 2003 - 2008 catch data, the majority of these assumptions over variables remained the same. However the initiation of a structured and focussed longline based study allowed for the influence of some further variables (Ward, 2008, Stoner, 2004) to be investigated. These variables are re-listed below, with explanations only provided where they differ from those of the previous datasets:

A. **Encounterability**;
B. **Fishing location**;
C. **Fishing-master experience**;

D. **Bait loss**;
E. **Gear saturation**;
F. **Detection of gear** – it is possible that, for the more resident *N. brevirostris* and *G. cirratum*, repeated exposure, and increased set regularity, may have further increased the possibility of gear detection through learned association (Guttridge et al., 2009b);
G. **Hunger**;
H. **Bite-off**;
I. **Activity**;
J. **Environmental factors**;
K. **Operation time** – operation time was standard throughout, at 24 hours per set with no back to back efforts, thus removing the potential for influence over catch rates;
L. **Competition among gears** – during the 2003 – 2008 campaign, all gear based research activities were halted during longline sets, thus removing the potential for influence over catch rates;
M. **Hook type** – hook type remained constant throughout the research period;
N. **Bait type** – the effects of bait type on catch rates are investigated in section 3.3.2;
O. **Diel** – the effects of time of day on catch rates are investigated in section 3.3.3;

It is assumed for the subsequent results and analysis that variables A to I had no effect upon the catch records included in the dataset. Variables J to M were accounted for in the experimental design of this research period and the effects of N and O were investigated prior to any further population analysis. In a given section should a variable be accounted for, or additional variables assumed to have no further effect, this will be stated at the beginning of the analytical methodology.

3.2.4.3. Bait variation

As within previous campaigns, it was not always possible to use the same bait type (teleosts species) or bait section (head, steak or tail). With the initiation of the new longline setting and shark processing, data was available for both number of each bait type/section used throughout, and the bait details that each shark were captured on. This was achieved by comparing the longline and hook number to the bait setting records. CPUE was calculated for each bait type and section. Chi^2 analysis was then conducted for each variable to assess whether or not bait type or section had any significant influence over CPUE, and therefore whether or not catches from different bait types/sections could be considered as a single dataset.

3.2.4.4. Capture and soak times

The addition of hook timers to the longline gear setup allowed for exact capture times to be calculated (Rice et al., 2007). When each shark was first encountered, the hook time was recorded along with the current time. By subtracting the hook time from the current time, the exact time the shark became captured was calculated. For capture times relative to hours of the day, shark catches were separated into six 4 h time periods. As effort was equal between time periods, it was not necessary to convert shark numbers into CPUE. The time periods were 16:31 – 20:30, 20:31 – 00:30, 00:31 – 04:30, 04:31 – 08:30, 08:31 – 12:30 and 12:31 – 16:30. Time period were arranged so that the first time period corresponded to the first period following the longline sets. 4 h periods were utilised so as to contain the entire annual time variation in crepuscular periods with dusk in 16:31 – 20:30 and dawn in 04:31 – 08:30. Soak times were calculated by subtracting the exact time the hook each shark was captured on entered the water from the devised exact shark capture times. Catches where then grouped into 2 h soak periods. Results for both capture and soak times were plotted and analysed for patterns.

3.2.4.5. Seasonal Catch Per Unit Effort (CPUE) variation

Catches and UE were grouped by month rather than year, and then CPUE was recalculated. Mean *N. brevirostris* Pre-Caudal Lengths (PCL) and size class proportions were calculated by month. Monthly mean water temperature was calculated by grouping the iButton temperature profiler results by month, which were then compared to CPUE. Spearman's rank correlation was used to test the relationship between total shark CPUE, and individually by species, with mean monthly temperature and then compared to CPUE.

3.2.4.6. Catch proportions

The same methodology described in section 2.3.2.5.4, was used. Proportions were then displayed by species relative to the proportions from the two previous campaigns, and analyses for temporal change. Results were descriptive and no statistical tests were conducted as the results between periods were based on a dissimilar amount and distribution of unit effort and therefore were not statistically comparable.

3.2.4.7. Catch Per Unit Effort (CPUE)

Datasets from all three research periods were combined into one continuous 27 year long dataset, spanning from 1982 – 2008. Results were then plotted and examined for temporal patterns. For *N. brevirostris,* three distinct temporal patterns were observed, the first from 1982 – 1989, the second from 1992 – 2000 and the third from 2000 – 2008. The combined results were then considered as three separate datasets, based on these temporal pattern separations, and Spearman rank correlations between CPUE and research year were conducted to test for significance across each. From 2005 – 2008, data for specific longline capture relative to latitude were available for each recorded shark. It was thus possible to separate catches by longline latitude and analyse for latitudinal influence over CPUE, with a Spearman's rank correlation test between latitude and CPUE.

3.2.4.8. Catch related mortality

The same methodology, as described in section 2.3.2.5.6, was used. With the absence of scientific sacrifices, all mortalities were the direct result of capture on the longlines.

3.2.4.9. Mark-recapture and *N. brevirostris* population estimates

For mark-recapture analysis, the same methodology, as described in section 2.3.2.5.7, was used. Due to the low number of year-on-year mark-recaptures, it was not possible to employ the standard Lincoln-Petersen method for annual *N. brevirostris* population estimates across the 1982 – 2008 research campaign. By considering larger temporal periods as single mark-recapture efforts, it was possible to obtain more realistic estimates using the Lincoln-Petersen method. However to account for the grouping of multiple efforts, it was necessary to alter the model relative to the temporal efforts. Thus the adapted Lincoln-Petersen model utilised was as follows:-

$$N = \left(\frac{MC}{R}\right) \div Y$$

Where N = estimate of mean population size for any given year within the research period, M = total number of *N. brevirostris* marked, C = total number of *N. brevirostris* captured, R = number of *N. brevirostris* recaptured, and Y = number of years longlining effort took place within the research period. Estimates were made for three progressively longer periods, 1982 – 1989, 1982 – 1999 and 1982 – 2008.

3.2.4.10. Temporal Pre-Caudal Length (PCL) and size class variation of *N. brevirostris*

For PCL analysis, the same methodology, as described in section 2.3.2.5.8, was used. In addition, datasets from all three research period were combined into one continuous 27 year long dataset, spanning from 1982 – 2008. Results were then plotted and examined for temporal patterns. Spearman's rank correlation was conducted between mean *N. brevirostris* PCL and year from 1994 – 2000, with the removal of the high recruitment year in 1997, to test for significance. Mean *N. brevirostris* PCL from 2000 – 2008 showed a distinct pattern of peaks and troughs, with trough values representing years of high recruitment. The trough values from 1997, 2001, 2004 and 2007 were isolated and a Spearman's rank correlation was conducted between mean *N. brevirostris* PCL and year to test for temporal significance. For *N. brevirostris* size class proportions, datasets from all three research periods were combined into one continuous 27 year long dataset, spanning from 1982 – 2008. Results were then plotted and examined for temporal patterns and connections to temporal variations in mean *N. brevirostris* PCL.

3.2.4.11. National Marine Fisheries Service (NMFS) landing records

Unfortunately no NMFS landing records were available for this period, so no comparison to the Bimini longline catch records could be made.

3.3. Results

3.3.1. Unit Effort (UE)

UE was relatively consistent throughout the 2003 – 2008 research campaign (Figure 47), with the exceptions of 2003 and 2008, which represented years where effort was not conducted in every month. UE ranged from 675 in 2003 to 1500 in 2007 (mean = 1250 ± 126.5 s.e.).

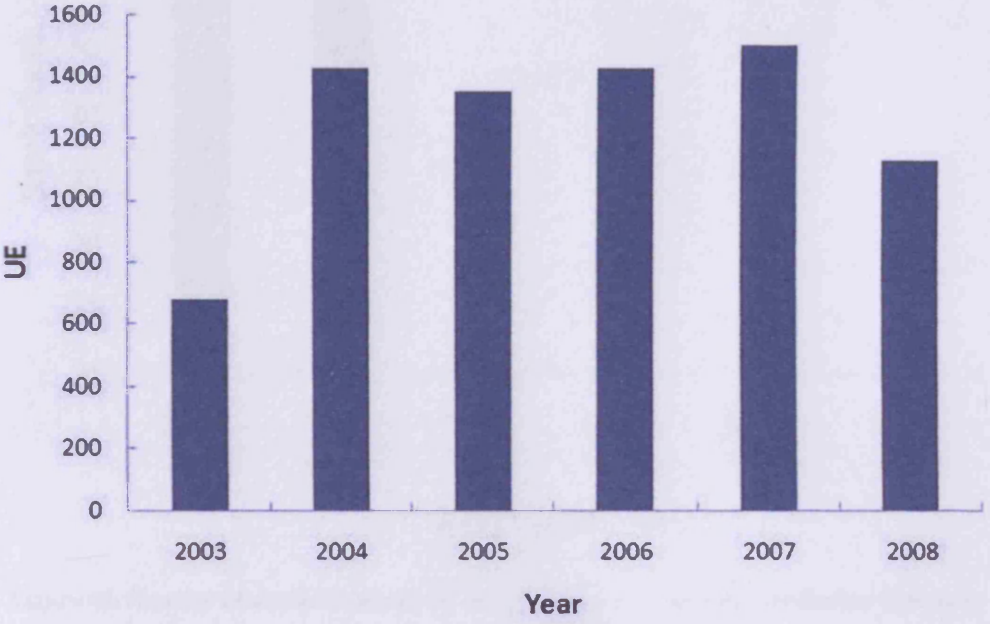


Figure 47. Unit Effort (UE) by year from July 2003 - September 2008

3.3.2. Bait variation

For total sharks caught no significant effect of bait type ($\chi^2 = 7.15$, d.f. = 8, $P > 0.05$) or bait section ($\chi^2 = 4.28$, d.f. = 4, $P > 0.05$) on CPUE was found. For *N. brevirostris* caught no significant effect of bait type ($\chi^2 = 6.63$, d.f. = 8, $P > 0.05$) or bait section ($\chi^2 = 0.211$, d.f. = 4, $P > 0.05$) on CPUE was found.

3.3.3. Capture and soak times

For Total sharks (i.e. all species captured), catches were highest for the first time period (74 sharks), including the dusk period, and second highest for the second time period (71 sharks) leading up to midnight (Figure 28). Catches were considerably lower, following the high rates in the first two time periods, decreasing across the subsequent three with a slight increase in the final time period. Catches ranged between periods from 12 – 74 sharks (mean = 38 ± 10.99 s.e.) per time period.

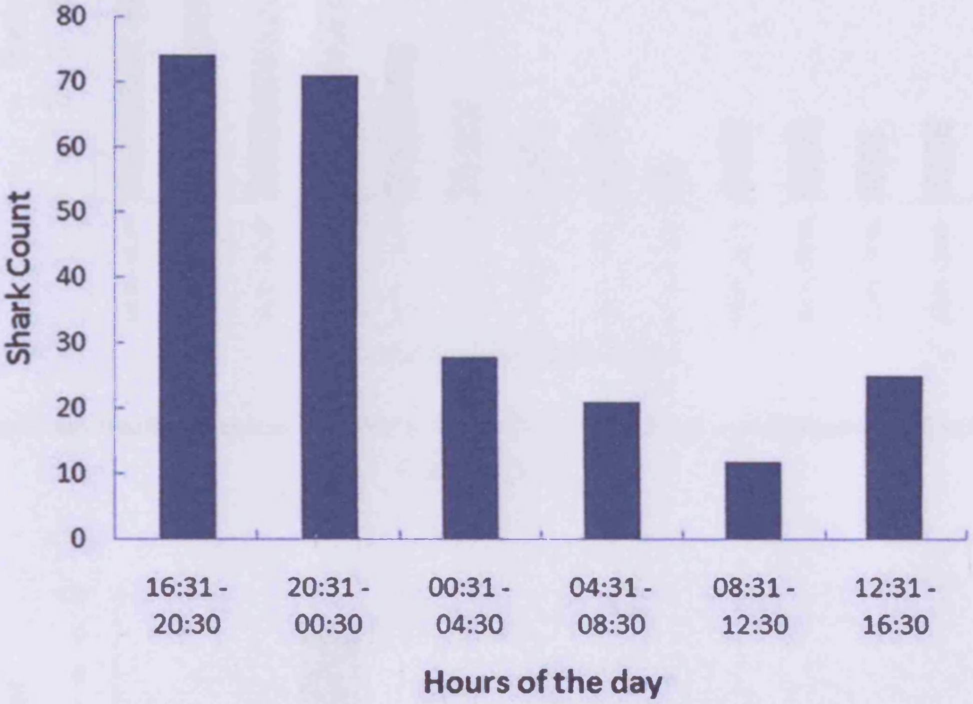


Figure 48. Number of sharks captured by time of day period between September 2005 and September 2008

Captures were greatest from 0 – 8 h soak time (Figure 49). Following the first eight hour period of high catches, catch rates decline between 8 - 14 h, then remained stable thereafter. Catch rates between soak time periods range from four to 36 sharks (mean = 15 ± 3.2 s.e.). *N. brevirostris* catches were highest for the second time period (9 individuals) leading up to midnight (Figure50). *N. brevirostris* catches were generally low for the other time periods with an absence of catches in the 08:31 – 12:30 time period. *N. brevirostris* catch rates were second highest in the final time period (5 individuals). *N. brevirostris* catches ranged between periods from 0 – 9 individuals (mean = 3 ± 1.4 s.e.).

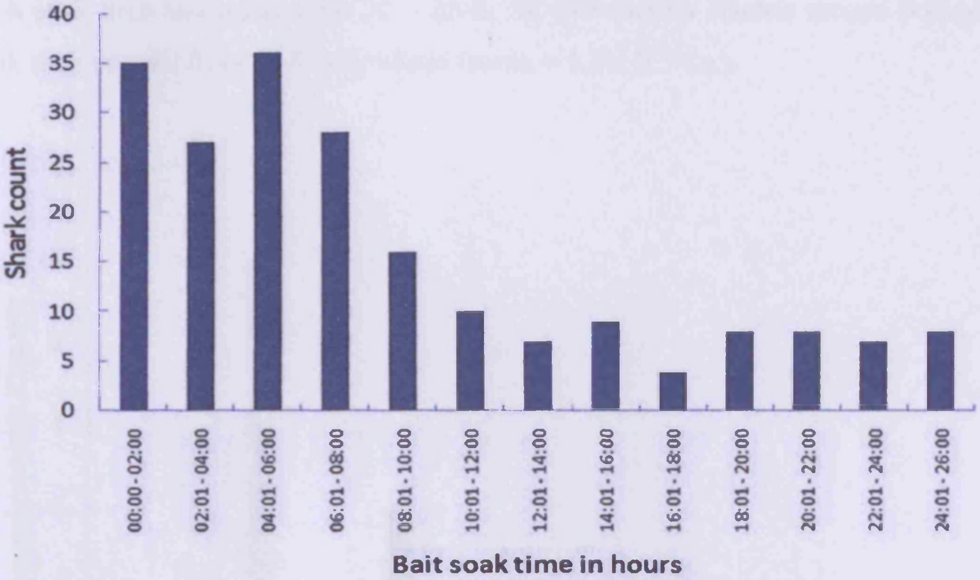


Figure 49. Number of sharks captured by bait soak time period between September 2005 and September 2008

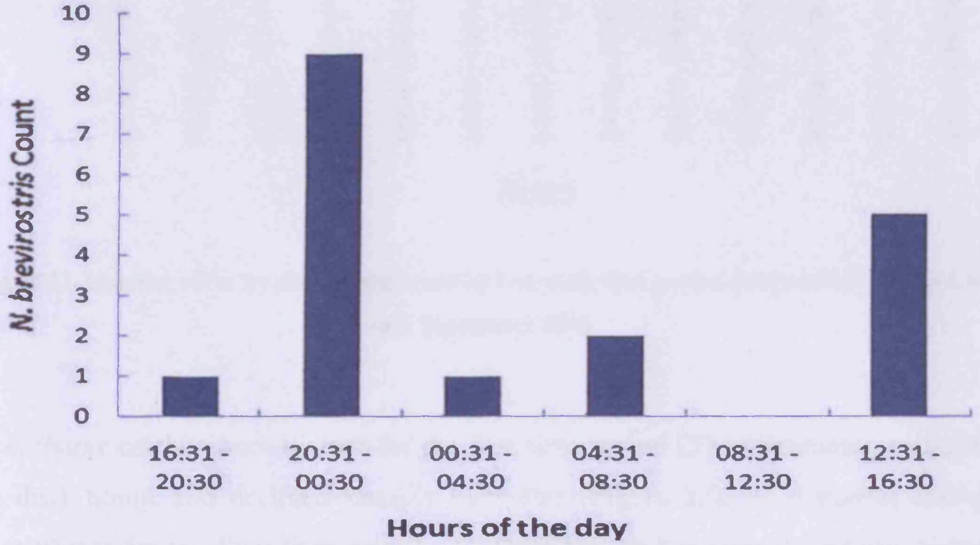


Figure 50. Number of *N. brevirostris* captured by time of day period between September 2005 and September 2008

N. brevirostris captures were recorded in only half of the bait soak time periods (Figure 51). *N. brevirostris* captures were absent for the first four hours, then highest from 4 – 6 h (6 individuals). *N. brevirostris* capture were also absent between 12 –

18 h soak time and again from 22 – 26 h. *N. brevirostris* catches ranged between soak time periods from 0 - 6 individuals (mean = 1.2 ± 0.5 s.e.).

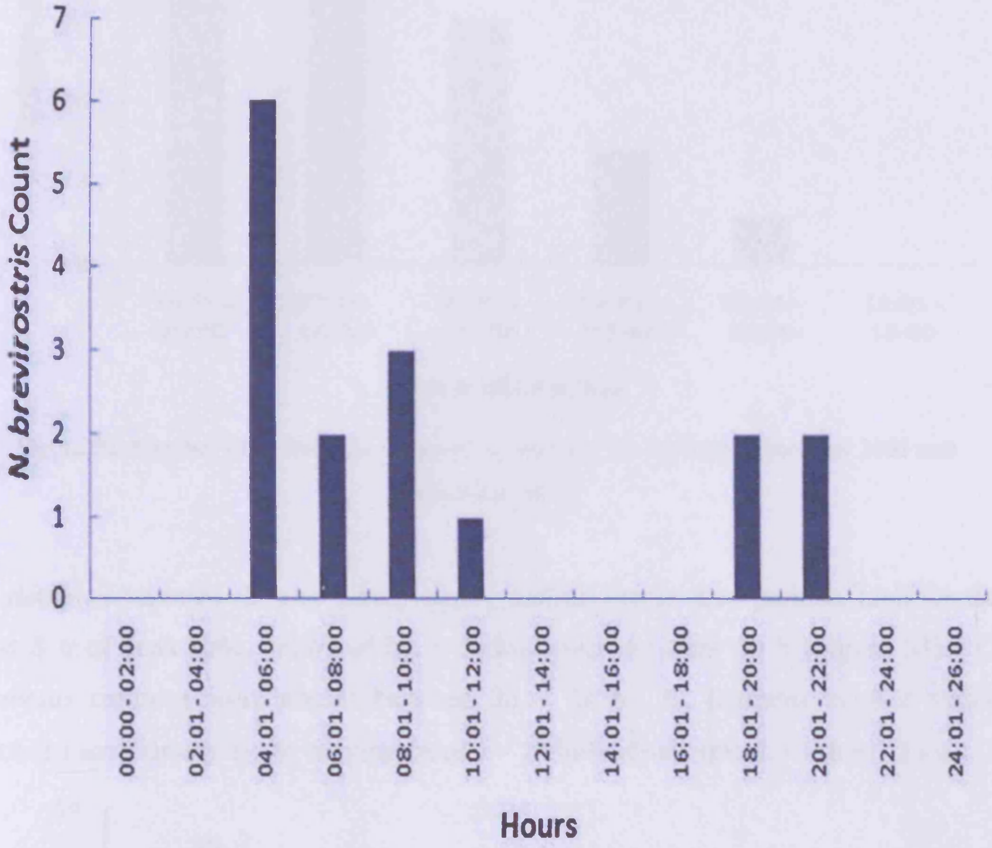


Figure 51. Number of *N. brevirostris* captured by bait soak time period between September 2005 and September 2008

C. limbatus catches were highest for the first time period (23 individuals), including the dusk hours, and declined steadily thereafter (Figure 52). *C. limbatus* catches were absent for the final time period. *C. limbatus* catches ranged between periods from 0 - 23 individuals (mean = 11 ± 3.8 s.e.).

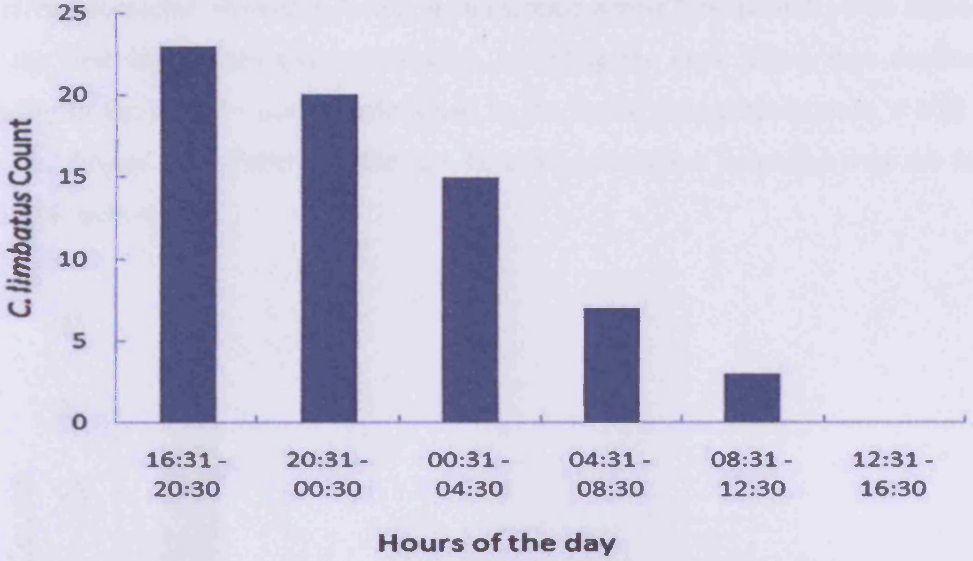


Figure 52. Number of *C. limbatus* captured by time period between September 2005 and September 2008

C. limbatus captures showed a very steady decline across time periods, high for the first 8 h of soak time, followed by a decline over the next 10 h (Figure 53). *C. limbatus* captures were absent between 20 – 24 h. *C. limbatus* catches varied between soak time periods, ranging from 0 – 13 individuals (mean = 4.8 ± 1.3 s.e.).

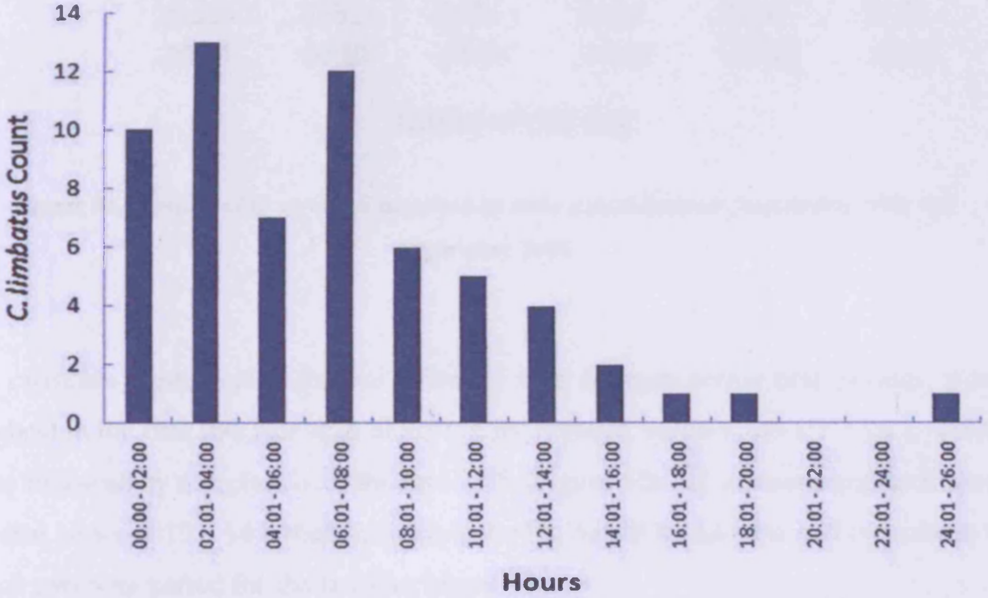


Figure 53. Number of *C. limbatus* captured by bait soak time period between September 2005 and September 2008

G. cirratum catches showed a decline then increase across time periods, were highest for the first time period (31 individuals), including the dusk hours, then declined steadily to the lowest value (1 individual) in the fourth time period (mean = 10.8 ± 4.6 s.e.; Figure 54). Following the low *G. cirratum* catches increased over the last two time periods.

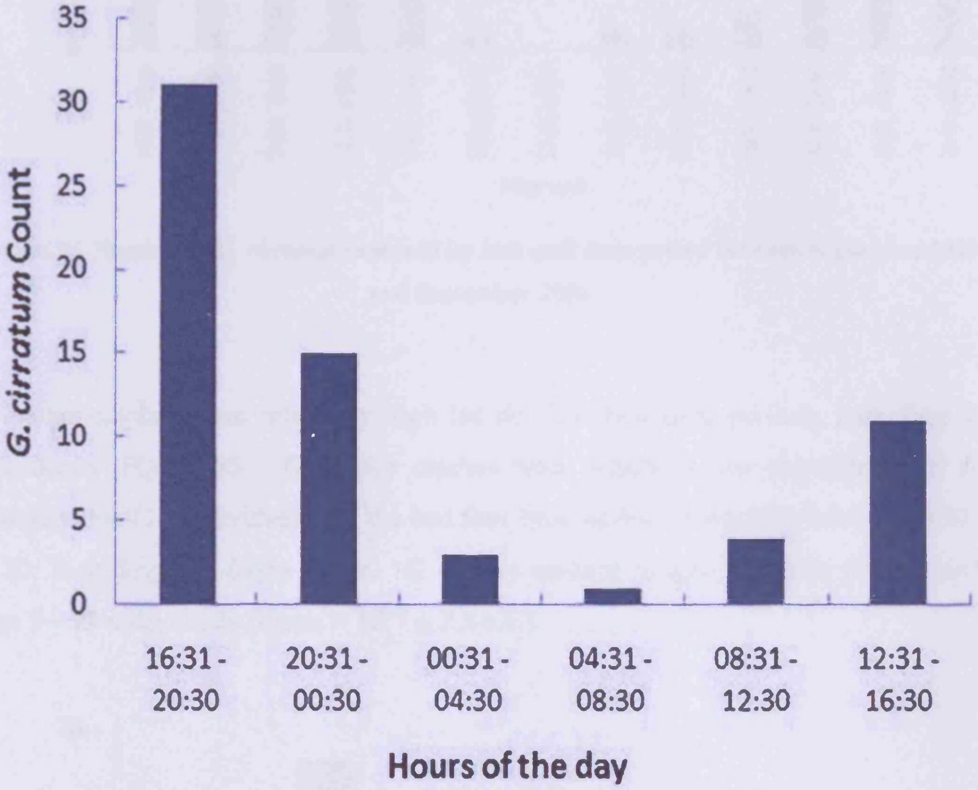


Figure 54. Number of *G. cirratum* captured by time period between September 2005 and September 2008

G. cirratum captures also showed a decline then increase across time periods, were highest in the first two bait soak hours (16 individuals; mean = 4.6 ± 1.2 s.e.), which was followed by a decline over the next 10 h (Figure 55). *G. cirratum* captures were absent between 12 – 14 h then increased over the next 8 h and remained constant at 4 each two hour period for the last four hours.

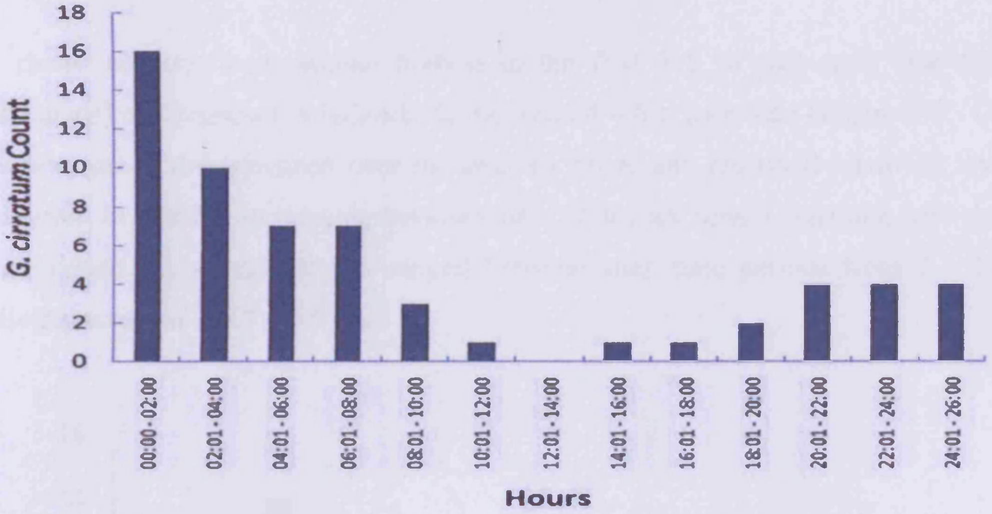


Figure 55. Number of *G. cirratum* captured by bait soak time period between September 2005 and September 2008

G. cuvier catches were relatively high for the first two time periods, including the dusk hours (Figure 56). *G. cuvier* catches were relatively low thereafter with the highest value (11 individuals) of the last four time periods recorded between 04:31 – 08:30, including the dawn hours. *G. cuvier* catches ranged between time periods from 5 - 23 individuals (mean = 12.7 ± 2.8 s.e.).

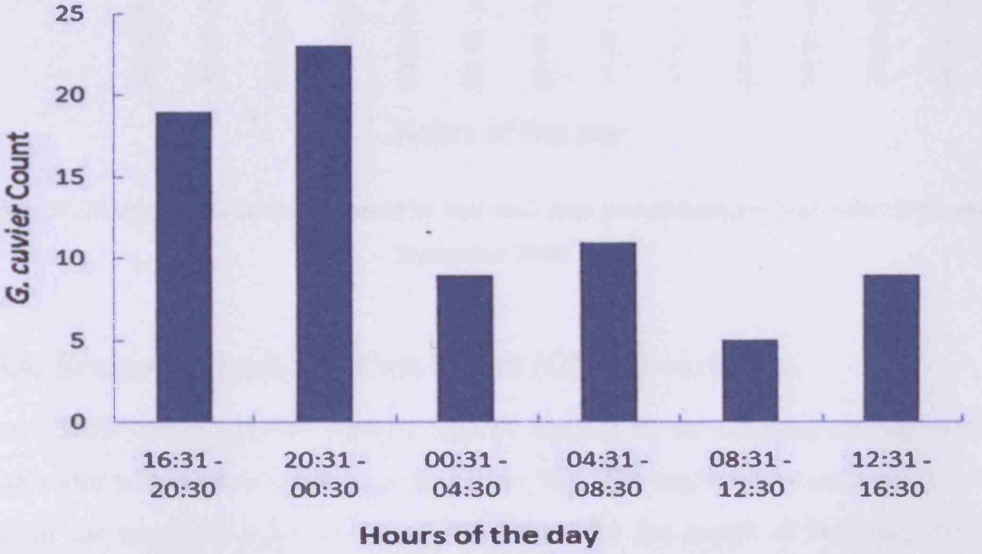


Figure 56. Number of *G. cuvier* captured by time period between September 2005 and September 2008

G. cuvier captures were second highest in the first 2 h of bait soak time (19 individuals) and highest (14 individuals) between 4 – 6 h soak time (Figure 57). *G. cuvier* captures then declined over the next six hours and remained relatively low thereafter, except for an increase between 14 – 16 h soak time, coinciding with the dawn period. *G. cuvier* catches ranged between soak time periods from 2 - 14 individuals (mean = 4.7 ± 0.9 s.e.).

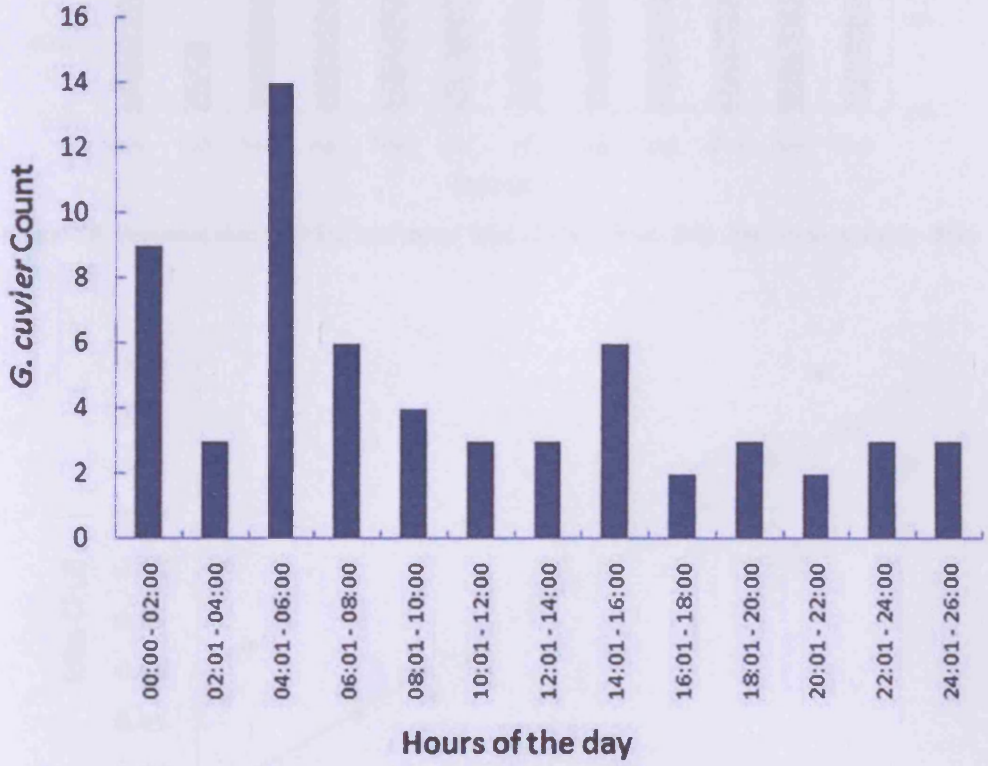


Figure 57. Number of *G. cuvier* captured by bait soak time period between September 2005 and September 2008

3.3.4. Seasonal Catch Per Unit Effort (CPUE) variation

Total CPUE for all species showed highest catches in the summer months when mean water temperatures were highest (Figure 58). The highest seasonal total CPUE was for the month of June (0.12) and the lowest for the month of February (0.02; mean = 0.07 ± 0.008 s.e.). Total CPUE showed a highly significant correlation with mean monthly water temperature (r = 0.875, n = 12, P < 0.01; Figure 59).

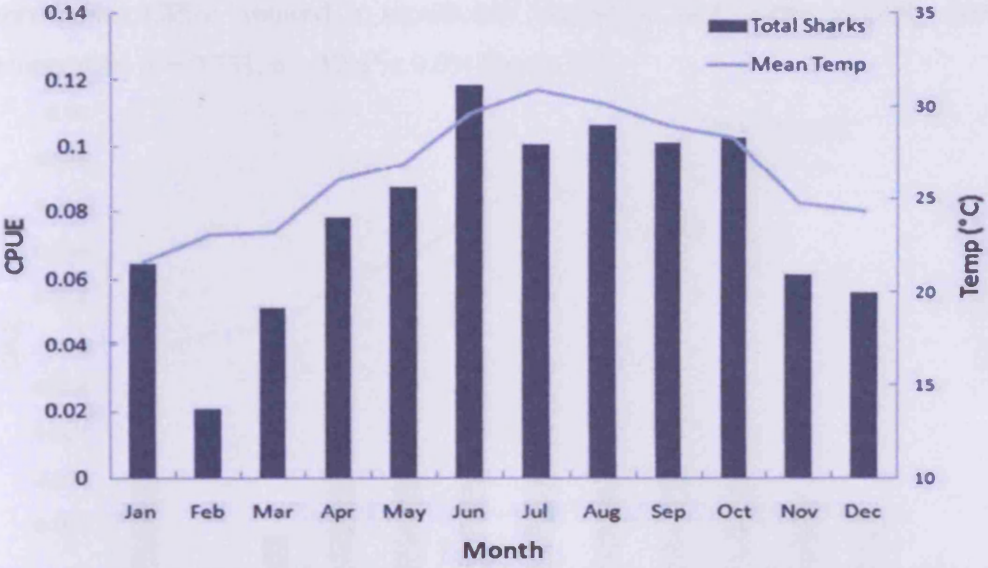


Figure 58. Seasonal shark CPUE and mean temperature from July 2003 to September 2006

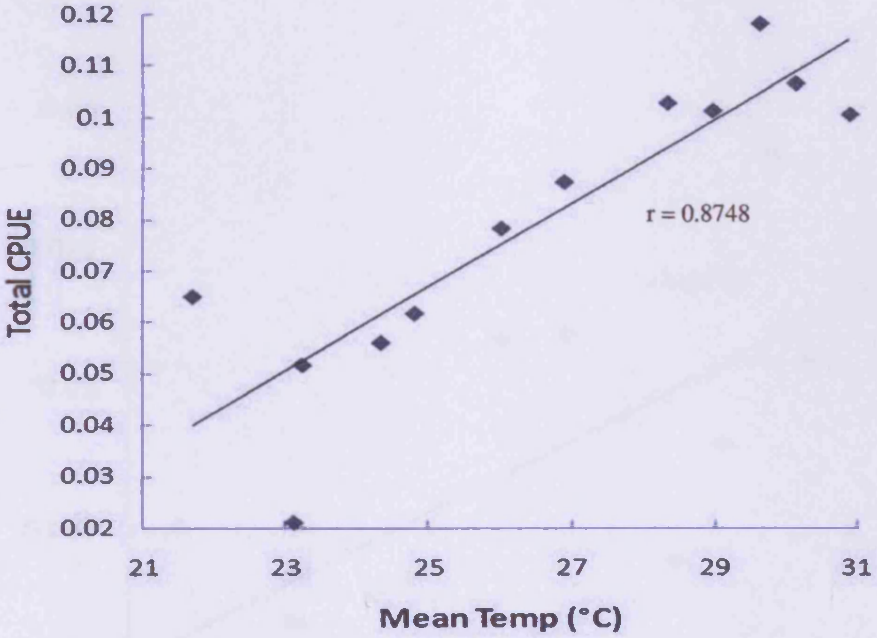


Figure 59. Total monthly CPUE vs mean temperature from July 2003 to September 2008

N. brevirostris CPUE showed a seasonal pattern, with the highest levels recorded in summer months (Figure 60). The highest seasonal *N. brevirostris* CPUE was, like total CPUE, for the month of June (0.018) and *N. brevirostris* were completely absent in the catch records for the month of February (mean = 0.008 ± 0.002 s.e.). *N. brevirostris* CPUE showed a significant correlation with mean monthly water temperature (r = 0.731, n = 12, $P < 0.05$; Figure 61).

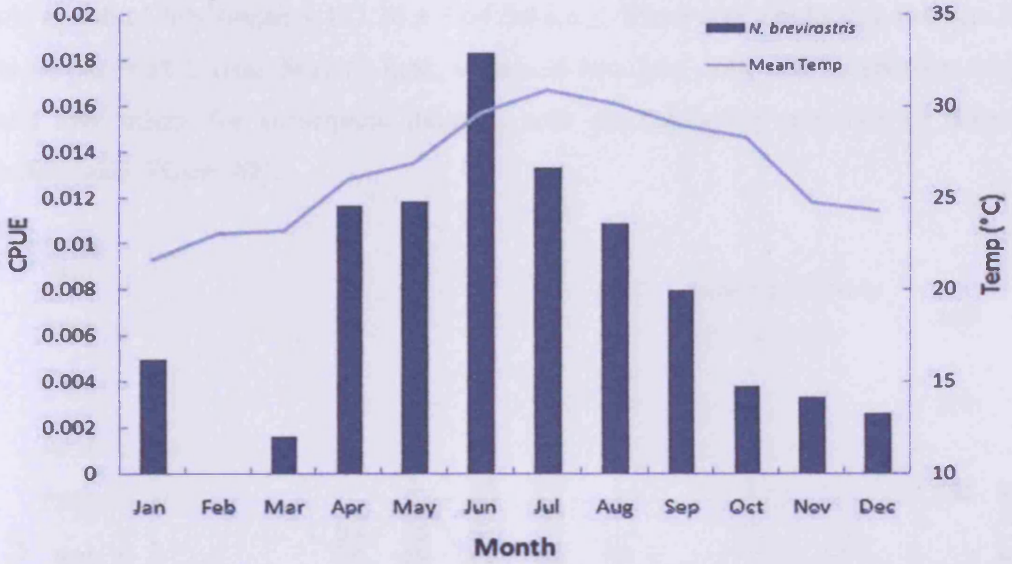


Figure 60. Seasonal *N. brevirostris* CPUE and mean temperature from July 2003 to September 2006

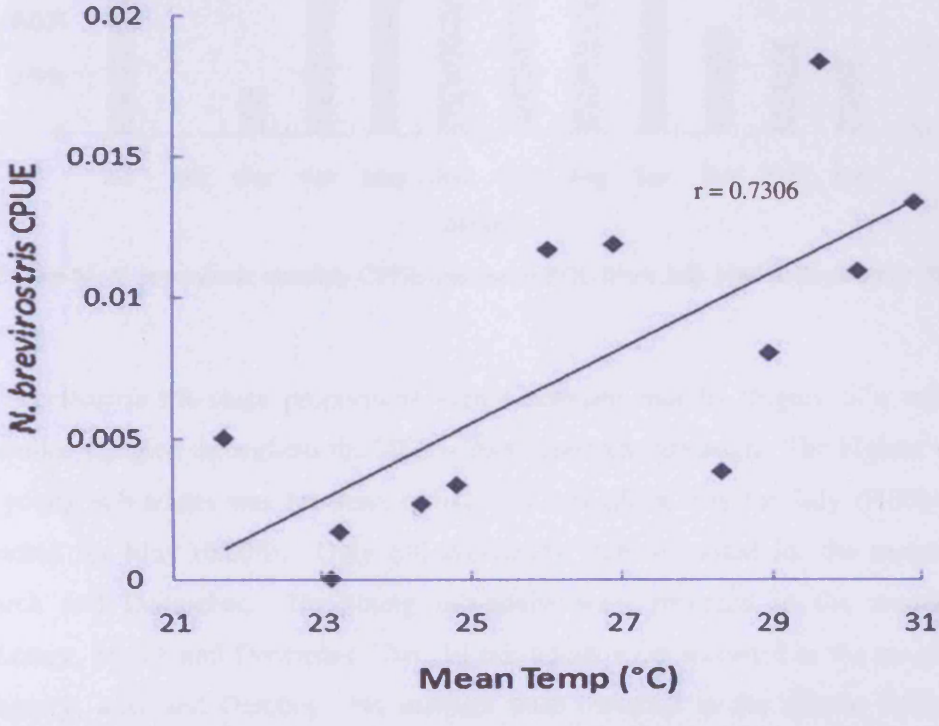


Figure 61. *N. brevirostris* monthly CPUE vs mean temperature from July 2003 to September 2008

N. brevirostris mean PCL varied between months (Figure 62). For months with multiple catches mean *N. brevirostris* PCL was highest for May (152.75 cm) with the presence of mature females for parturition (Figure 63), and lowest (122.45 cm) for the month of July (mean = 137.26 ± 3.64 cm s.e.). There was a reduction in mean *N. brevirostris* PCL from May to June, sustained into July, followed by alternate high and low values for subsequent months, with the bimonthly presence of mature individuals (Figure 62).

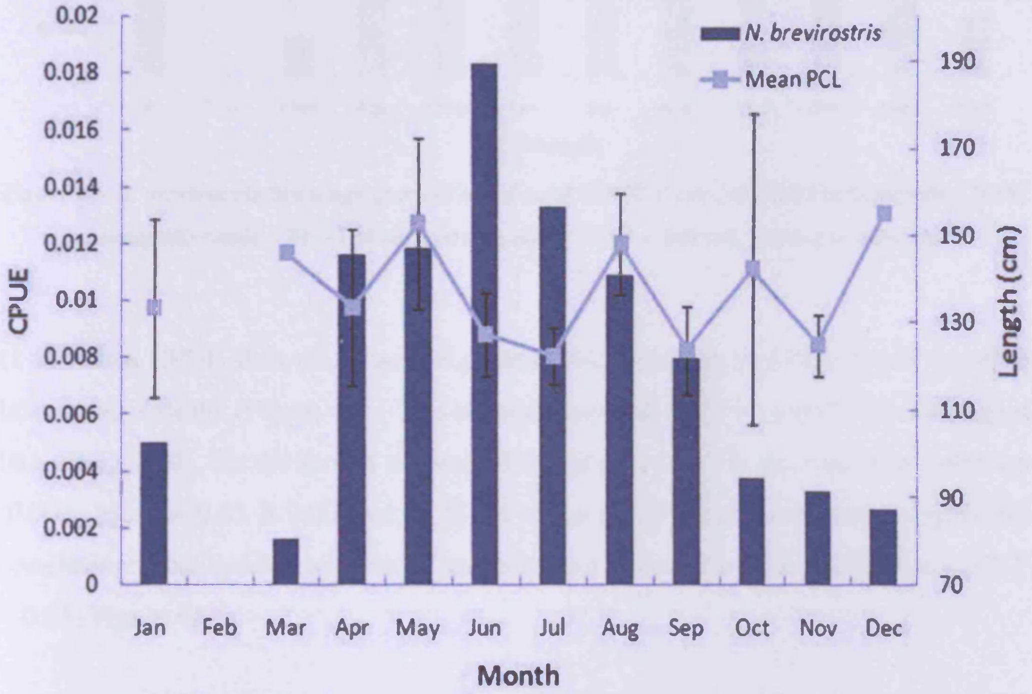


Figure 62. *N. brevirostris* monthly CPUE and mean PCL from July 2003 to September 2008

N. brevirostris life-stage proportions varied between months (Figure 62), with no juveniles sampled throughout the 2003 – 2008 research campaign. The highest value of young sub-adults was for June (0.01), old sub-adults was for July (0.006) and matures for May (0.005). Only old sub-adults were recorded for the months of March and December. No young sub-adults were recorded in the months of February, March and December. No old sub-adults were recorded in the months of February, May and October. No matures were recorded in the months February, March, July, September, November and December.

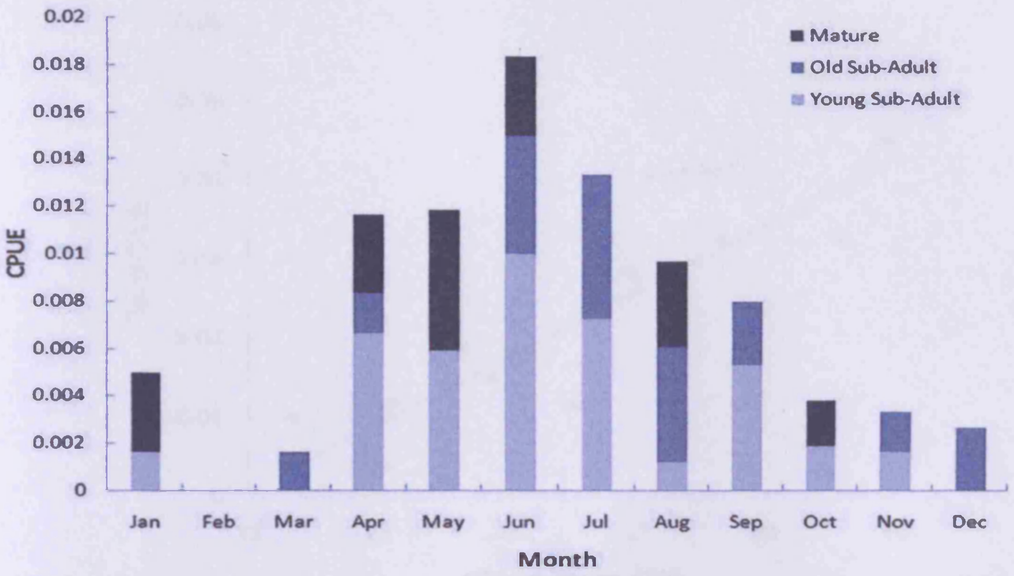


Figure 63. ***N. brevirostris*** **life-stage proportion of total CPUE from July 2003 to September 2008; young sub-adult = 81 – 124 cm, old sub-adult = 125 – 166 cm, mature = 166+ cm**

G. cirratum CPUE showed a seasonal pattern, with the highest CPUE levels recorded in summer months (Figure 64). The highest seasonal *G. cirratum* CPUE was, again like total CPUE, for the month of June (0.05) and lowest for the month of February (0.004; mean = 0.02 ± 0.004 s.e.). *G. cirratum* CPUE showed the most significant correlation of all species with mean monthly water temperature ($r = 0.865$, $n = 12$, $P < 0.05$; Figure 65).

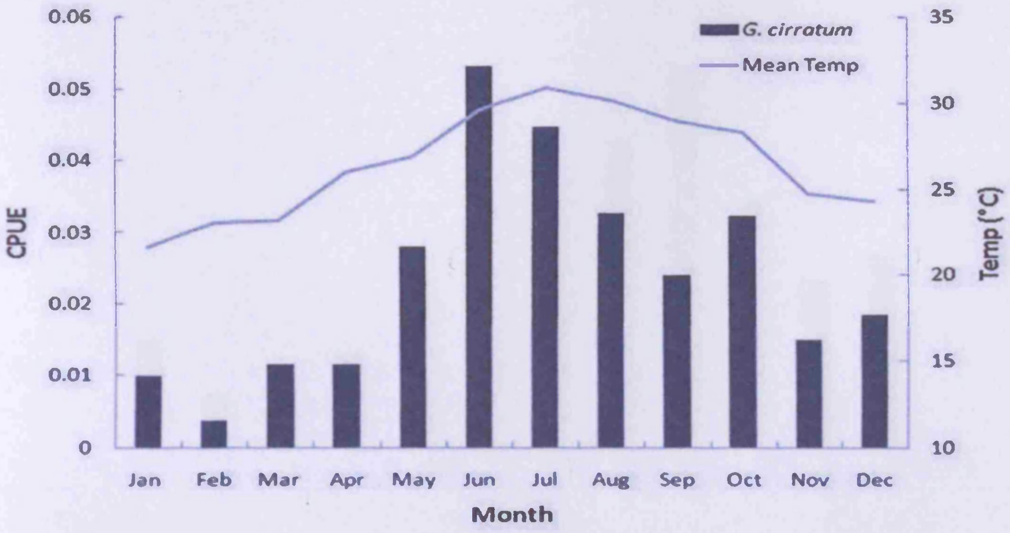


Figure 64. Seasonal *G. cirratum* CPUE and mean temperature from July 2003 to September 2006

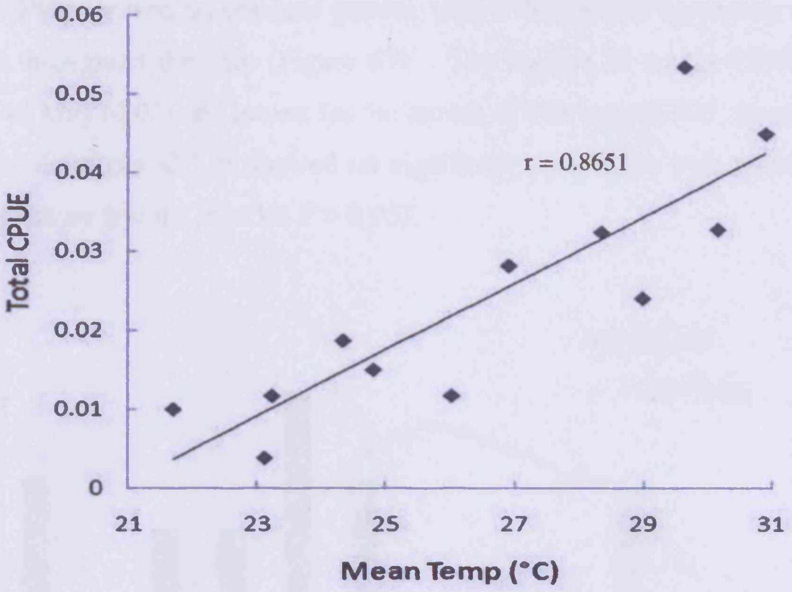


Figure 65. ***G. cirratum*** **monthly CPUE vs mean temperature from July 2003 to September 2008**

C. limbatus CPUE showed a seasonal pattern, with the highest levels offset from the summer months towards the end of the year (Figure 66). The highest seasonal *C. limbatus* CPUE was for the month of September (0.05), with mature females regularly noted to have had fresh mating scars at this time of year, and lowest for the month of February (0.006; mean = 0.02 ± 0.004 s.e.). *C. limbatus* CPUE showed no significant correlation with mean monthly water temperature (r = 0.512, n = 12, P > 0.05).

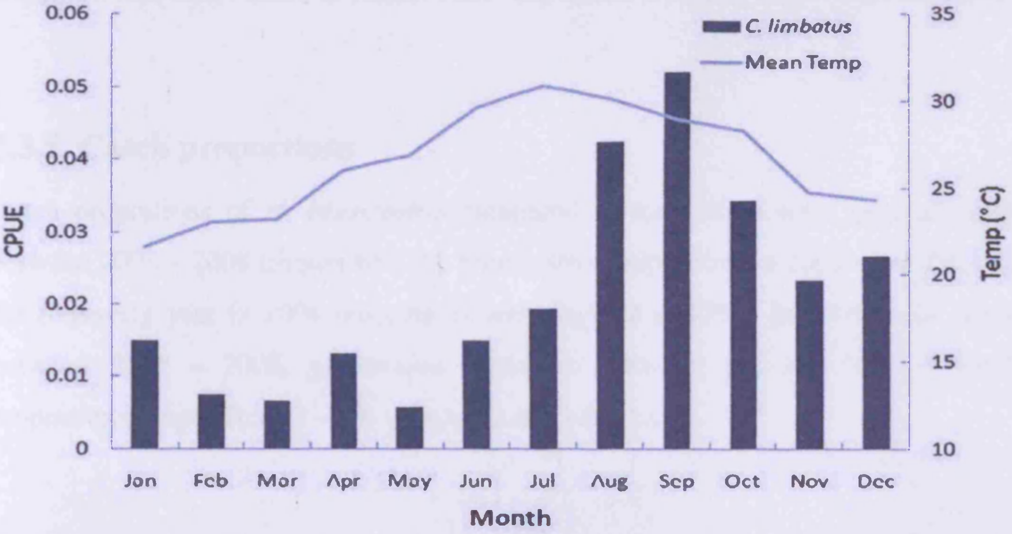


Figure 66. Seasonal ***C. limbatus*** **CPUE and mean temperature from July 2003 to September 2006**

G. cuvier CPUE showed no seasonal pattern, with CPUE levels apparently randomly distributed throughout the year (Figure 67). The highest *G. cuvier* CPUE was for the month of May (0.03) and lowest for the month of February (0.007; mean = 0.02 ± 0.002 s.e.). *G. cuvier* CPUE showed no significant correlation with mean monthly water temperature ($r = 0.1$, $n = 12$, $P > 0.05$).

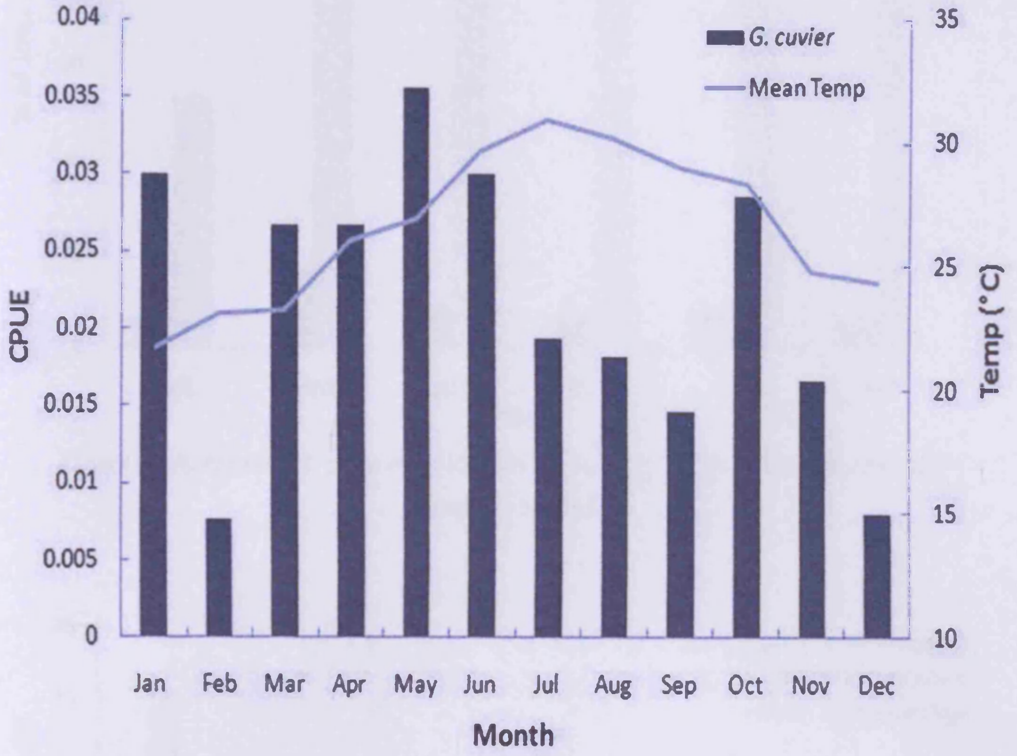


Figure 67. Seasonal *G. cuvier* CPUE and mean temperature from July 2003 to September 2006

3.3.5. Catch proportions

Catch proportions of *N. brevirostris* compared to total catch were generally low between 2003 – 2008 (Figure 68). *N. brevirostris* proportions in 2003 were 7%, and the following year in 2004 proportions were highest at 17%. In subsequent years, between 2005 – 2008, proportions alternated between 9% and 7%. Overall proportions ranged from 7 – 9% (mean = 9.4 ± 1.6% s.e.).

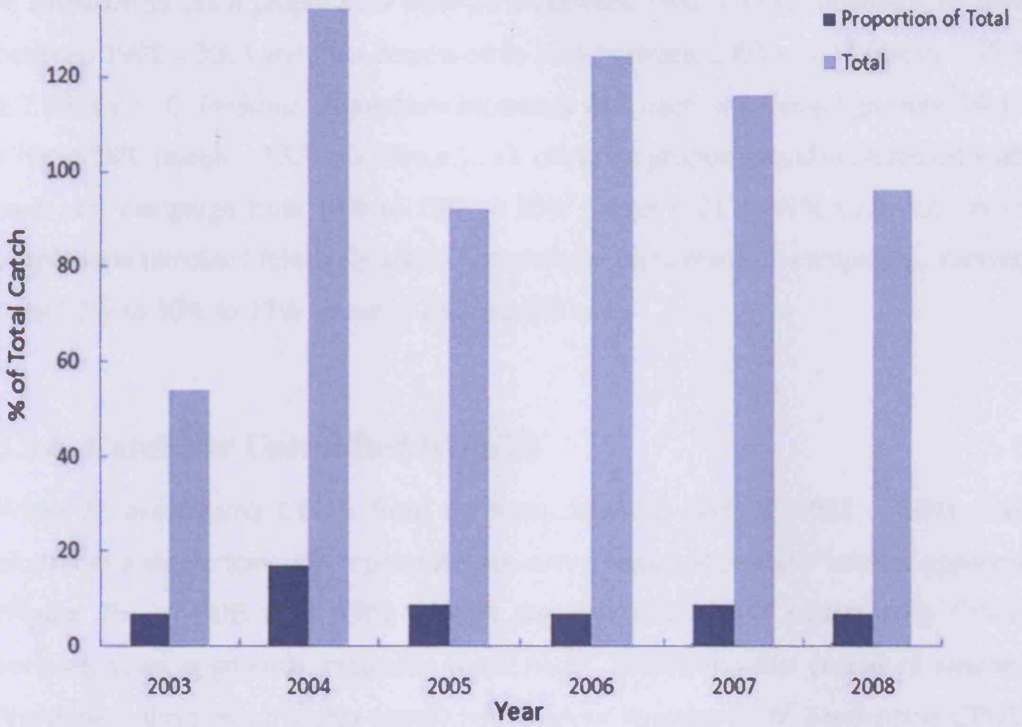


Figure 68. *N. brevirostris* proportion of total shark catch, by year between July 2003 - September 2008

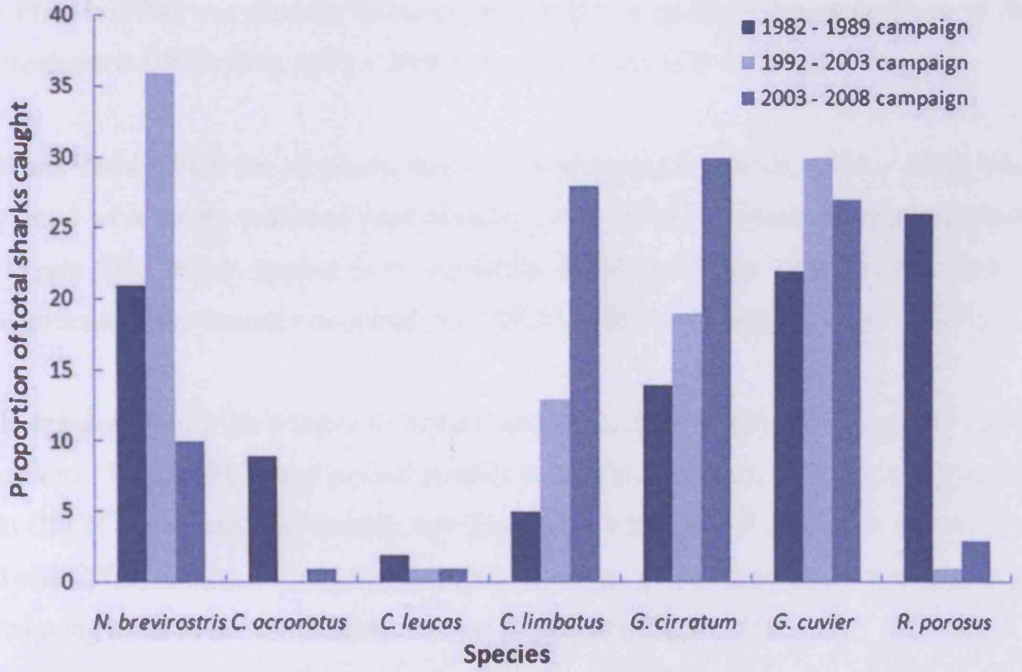


Figure 69. Species proportion of total shark catch by research campaign

N. brevirostris catch proportions were 21% between 1982 – 1989, increased to 36% between 1992 – 2003 and then decreased to 10% between 2003 – 2008 (mean = 22.3 ± 7.5% s.e.). *C. limbatus* proportions increased with each new campaign from 5% to 13% to 28% (mean = 15.3 ± 6.7% s.e.). *G. cirratum* proportions also increased with each new campaign from 14% to 19% to 30% (mean = 21 ± 4.7% s.e.). *G. cuvier* proportions remained relatively stable between the three research campaigns, varying from 22% to 30% to 27% (mean = 26.3 ± 2.3% s.e.).

3.3.6. Catch Per Unit Effort (CPUE)

When *N. brevirostris* CPUE from all three research periods, 1982 – 2003, was plotted as a single temporal representation, some temporal patterns became apparent (Figure 70). CPUE from 1982 – 1989 showed no temporal pattern with CPUE between years apparently randomly distributed. Following this period of random distribution there was a highly significant temporal increase in *N. brevirostris* CPUE from 1992 – 2000 ($r = 0.8508$, $n = 9$, $P < 0.01$), with the lowest value for the entire research efforts recorded in 1993 (0) and the highest in 2000 (0.026; mean = 0.014 ± 0.0015 s.e.). The highly significant linear increase from 1992 – 2000 and peak in CPUE in 2000 was directly followed by a highly significant linear decrease in *N. brevirostris* CPUE from 2000 – 2008 ($r = -0.9237$, $n = 9$, $P < 0.001$).

When Total CPUE for all sharks from all three research periods, 1984 – 2003, was plotted as a single temporal representation, two distinct periods became apparent (Figure 71). Points appear to be randomly distributed from 1984 – 1993, then a significant linear increase occurred from 1995 – 2008 ($r = 0.6668$, $n = 14$, $P < 0.05$).

N. brevirostris CPUE relative to latitude showed a distinct increasing south to north pattern. When CPUE was plotted relative to longline latitude, a significant increase in CPUE with increasing latitude was found ($r = 0.872$, $n = 6$, $P < 0.05$; Figure 72). Total CPUE relative to latitude shows higher values at the upper and lower latitudes, reducing towards the mid-latitudes of the target area (Figure 73).

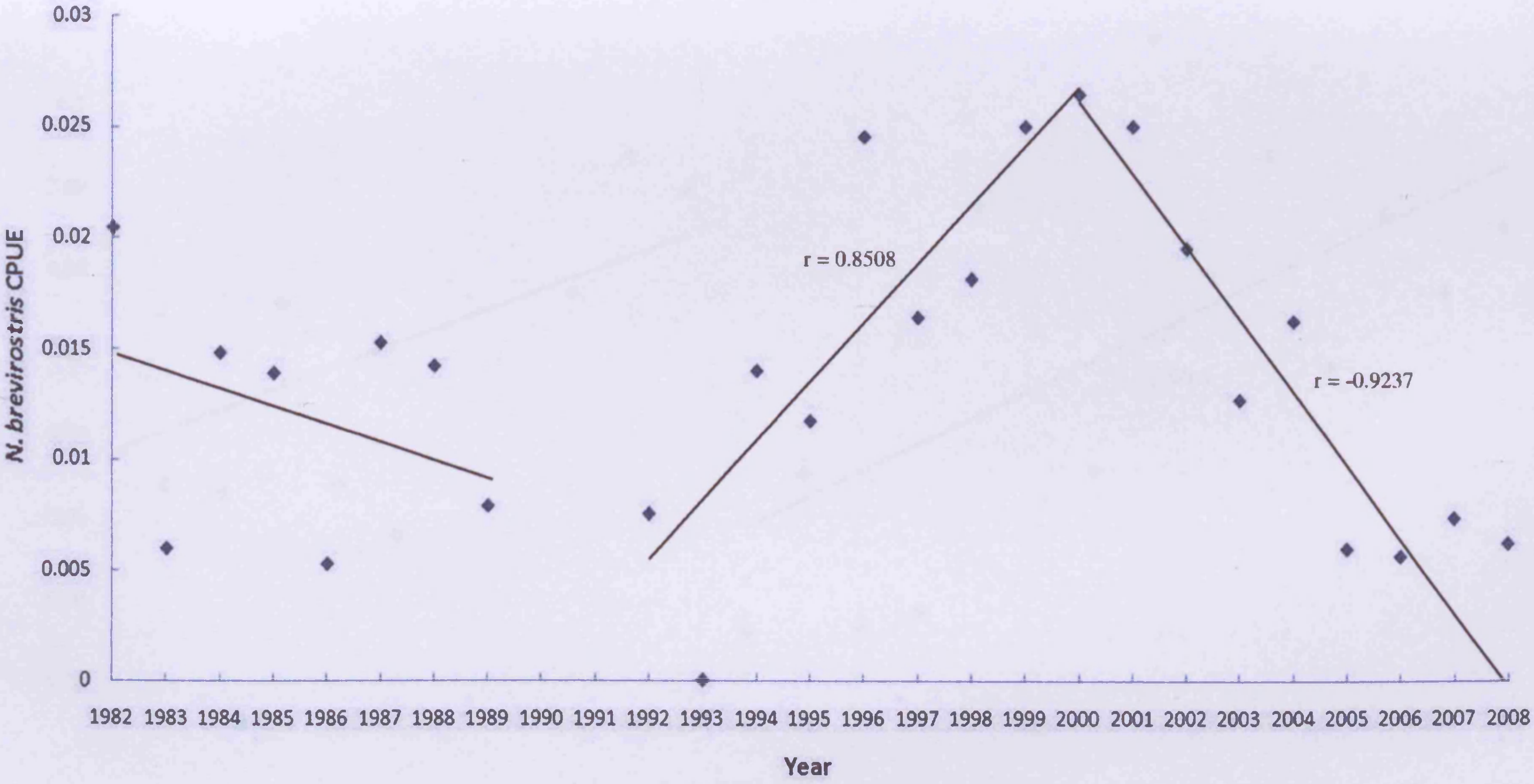


Figure 70. ***N. brevirostris*** **CPUE by year from 1982 - 2008**

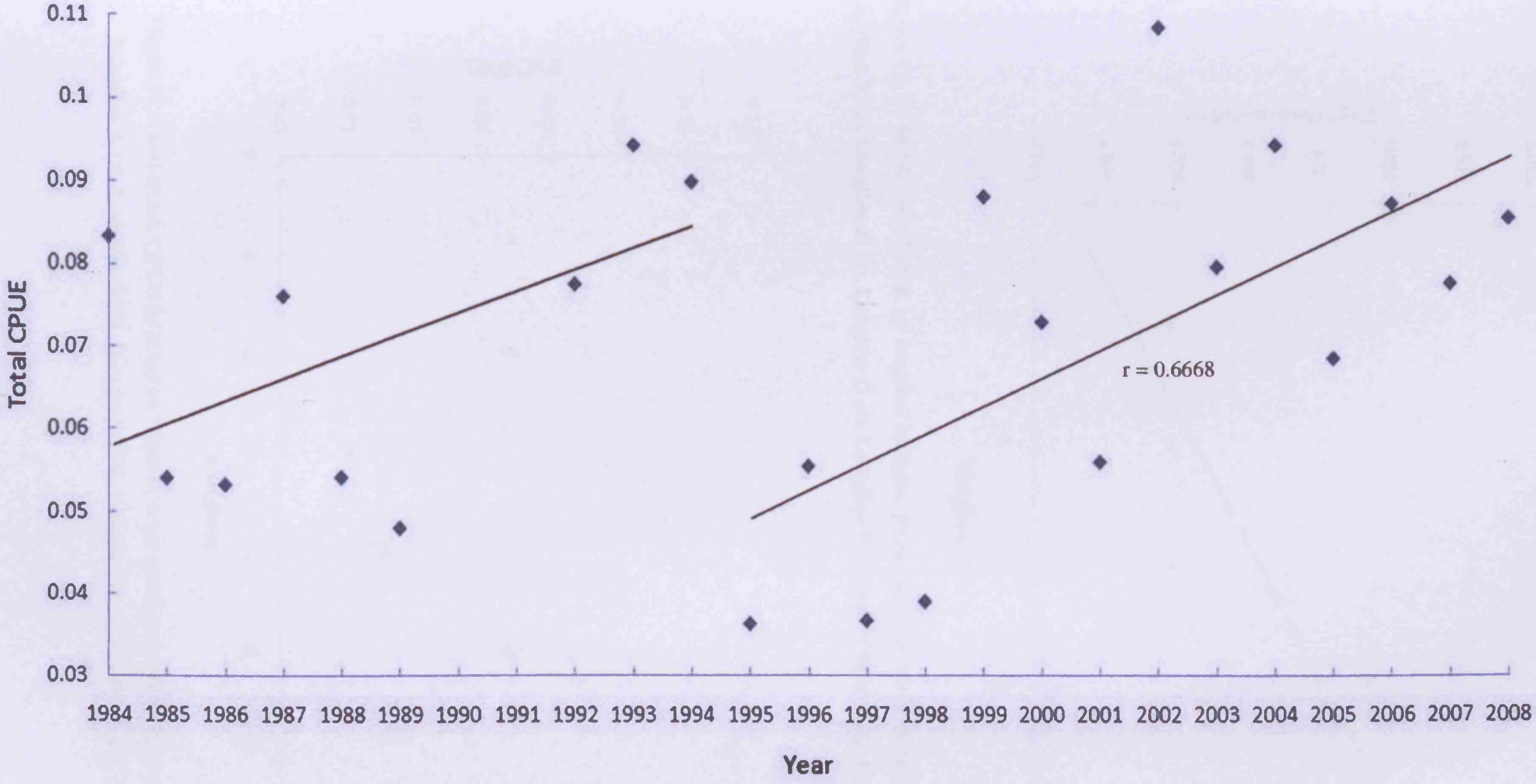


Figure 71. Total shark CPUE by year from 1982 - 2008

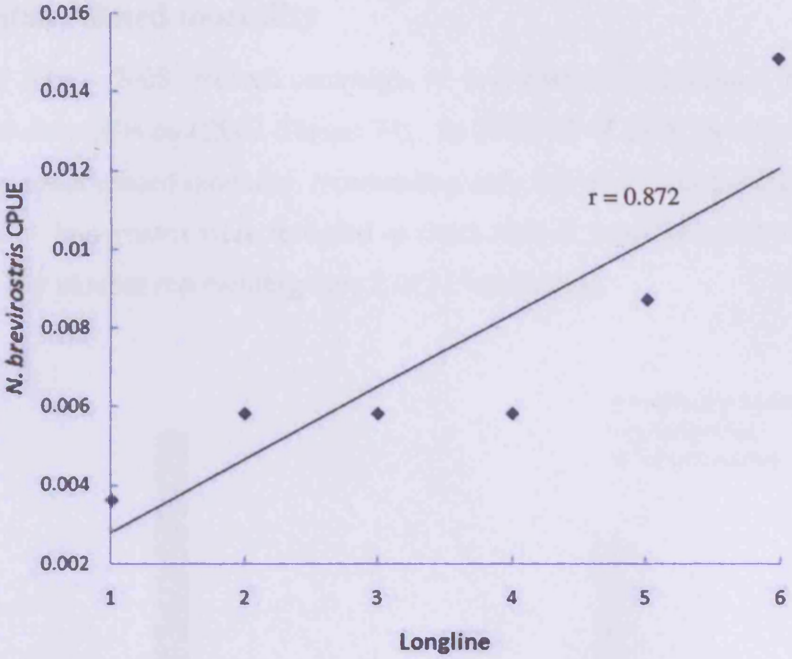


Figure 72. ***N. brevirostris*** **CPUE by longline latitude, from south to north Wildcard South (1), Longline A (2), Longline B (3), Longline C (4), Longline D (5) and Wildcard North (6)**

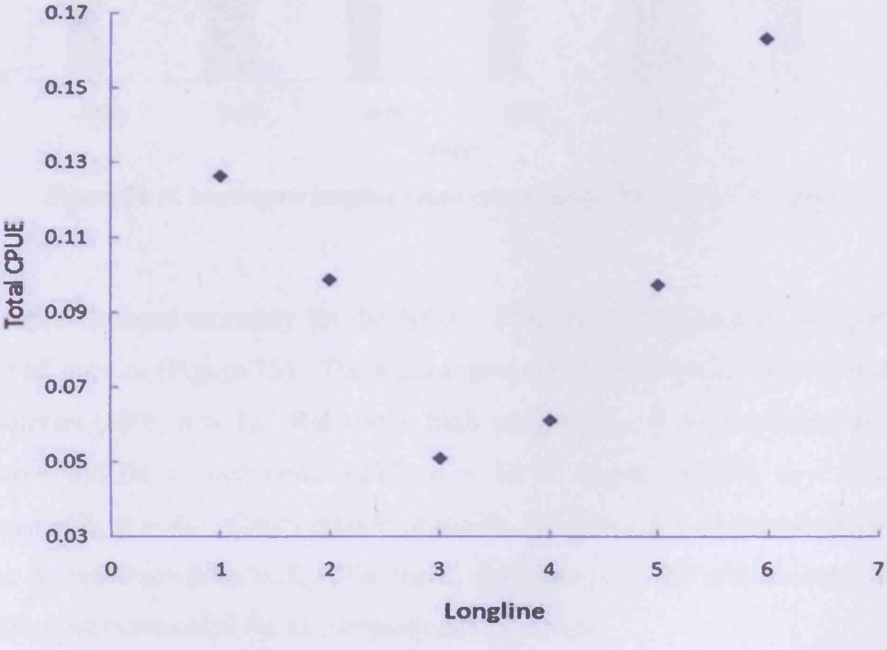


Figure 73. Total shark CPUE by longline latitude, from south to north Wildcard South (1), Longline A (2), Longline B (3), Longline C (4), Longline D (5) and Wildcard North (6)

3.3.7. Catch related mortality

During the 2003 – 2008 research campaign, *N. brevirostris* catch related mortalities only occurred in 2004 and 2007 (Figure 74). In 2004 4% of all *N. brevirostris* were recorded as catch related mortality, representing only one of 23 individuals. In 2007 18% of all *N. brevirostris* were recorded as catch related mortalities, but once again this was a low number representing only 2 of 11 individuals.

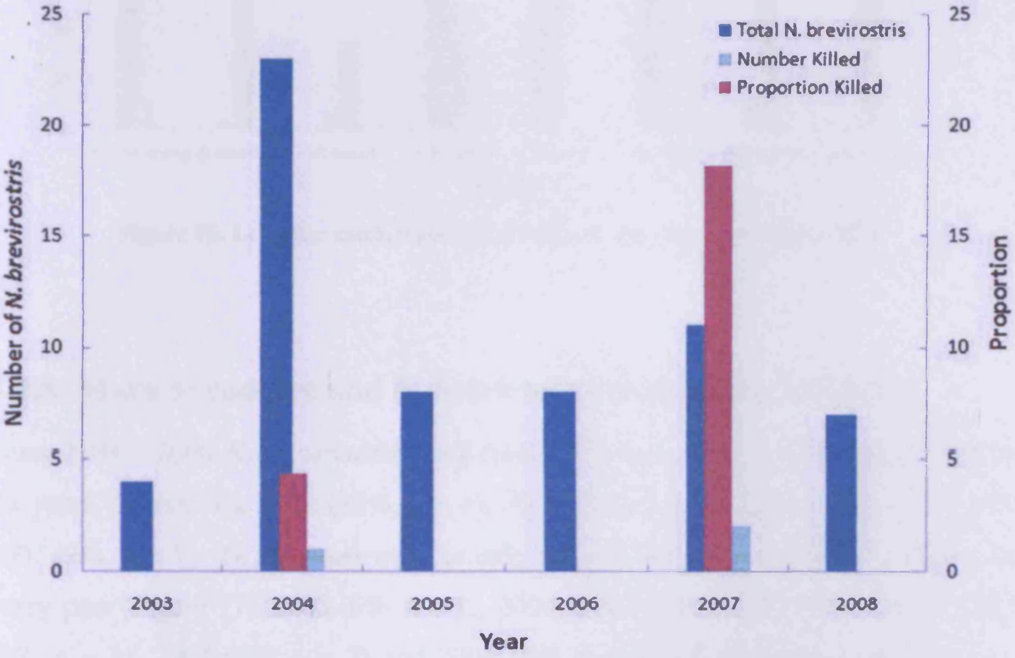


Figure 74. ***N. brevirostris*** **longline catch related mortality from 2003 – 2008**

Total capture related mortality for the 2003 – 2008 research campaign was generally low for all species (Figure 75). The highest proportion of mortality was recorded for *S. mokarran* (50%, n = 1). Relatively high proportions of catch related mortality were recorded for *C. acronotus* (25%, n = 1), *C. leucas* (12.5%, n = 1) and *R. porosus* (24%, n = 4). Catch related mortality for four most abundant species was 5% for *N. brevirostris* (n = 3), 17% for *C. limbatus* (n = 30) and no catch related mortalities were recorded for *G. cirratum* and *G. cuvier*.

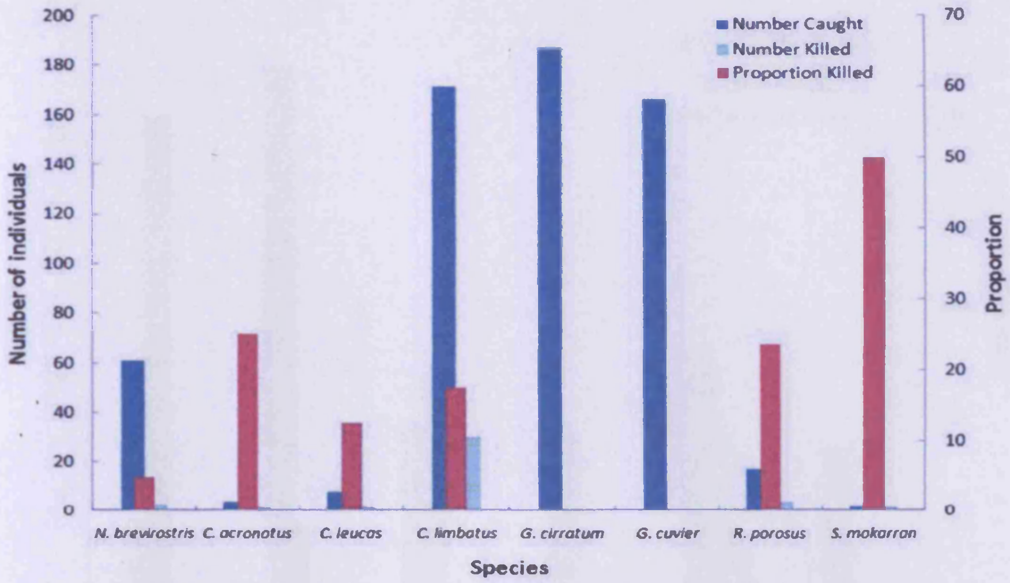


Figure 75. Longline catch related mortality by species from 2003 – 2008

3.3.8. Mark-recapture and *N. brevirostris* population estimates

From 2003 – 2008 *N. brevirostris* mark-recaptures (n = 4) were recorded in four of six years (Figure 76), 2003 (25%, n = 1), 2004 (4%, n = 1), 2005 (13%, n = 1) and 2007 (9%, n = 1). *G. cirratum* was the only species that showed mark-recaptures in every year (Figure 77), 2003 (6%, n = 1), 2004 (10%, n = 4), 2005 (6%, n = 2), 2006 (6%, n = 3), 2007 (9%, n = 2) and 2008 (8%, n = 2). *C. limbatus* showed mark-recaptures only in the two final years (Figure 78), 2007 (2%, n = 1) and 2008 (8%, n = 2). *G. cuvier* showed mark-recaptures in four of the six research years (Figure 79), 2004 (3%, n = 1), 2006 (10%, n = 3), 2007 (16%, n = 6) and 2008 (3%, n = 1). Of the other species *C. leucas* was the only species that showed a mark recapture, just in the year 2005 (25%, n = 1).

The results of the adapted Lincoln-Petersen model gave three *N. brevirostris* mean population estimates based on the longline captures for three progressive longer time periods (Table 4). Overall the *N. brevirostris* population at the Bimini islands was estimated to be a mean of 158 individuals (± 33 s.e.).

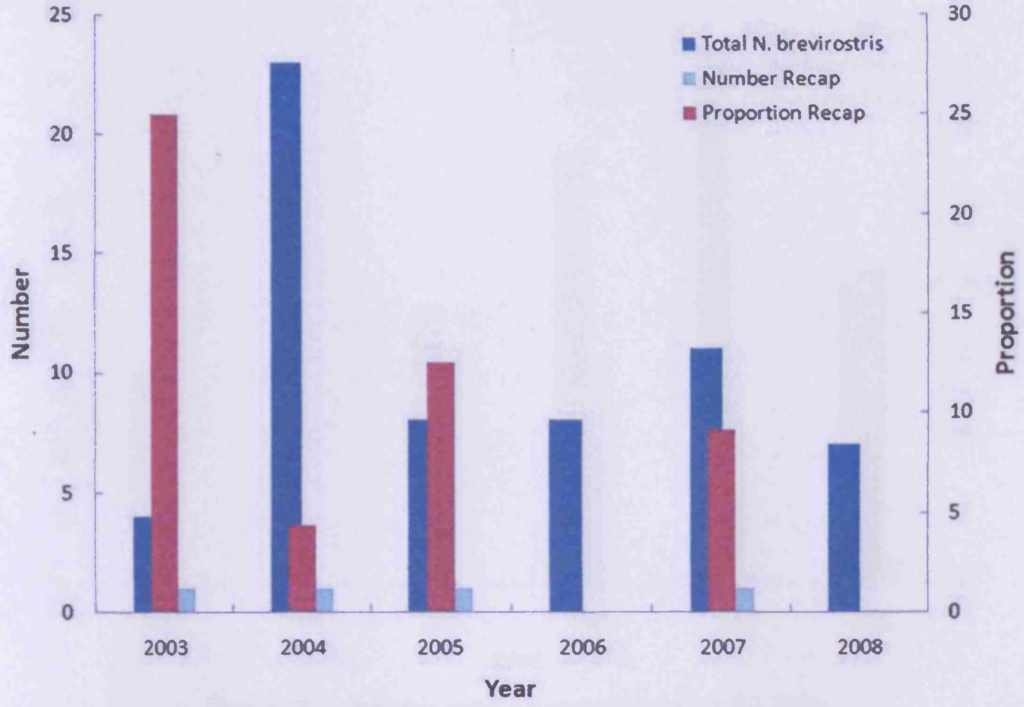


Figure 76. *N. brevirostris* mark-recaptures from 2003 – 2008

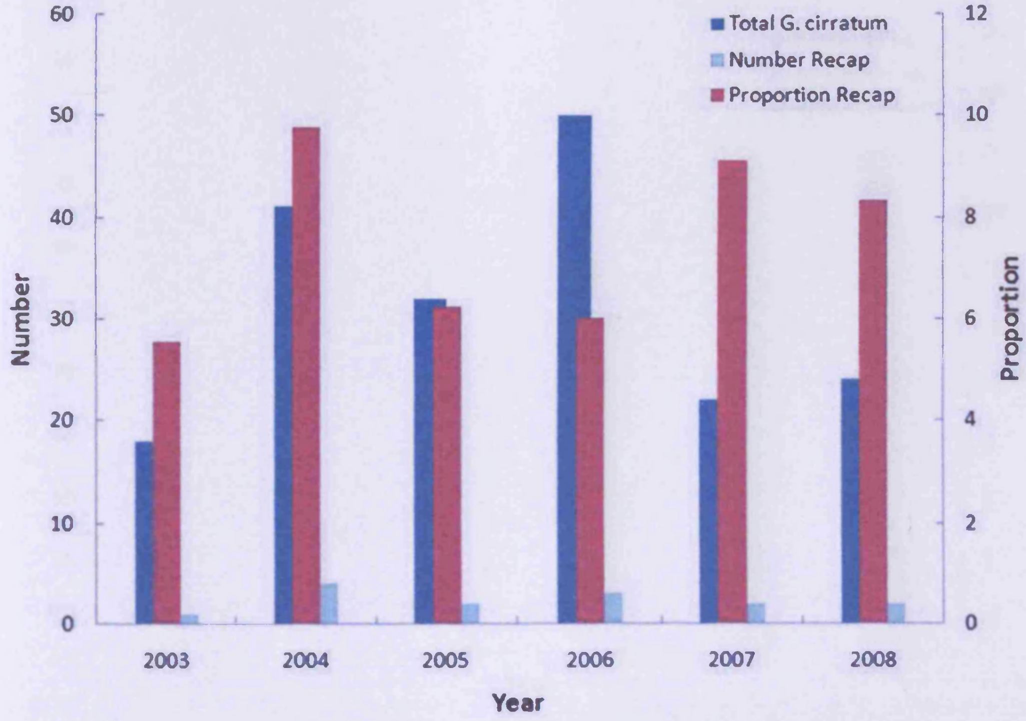


Figure 77. *G. cirratum* mark-recaptures from 2003 – 2008

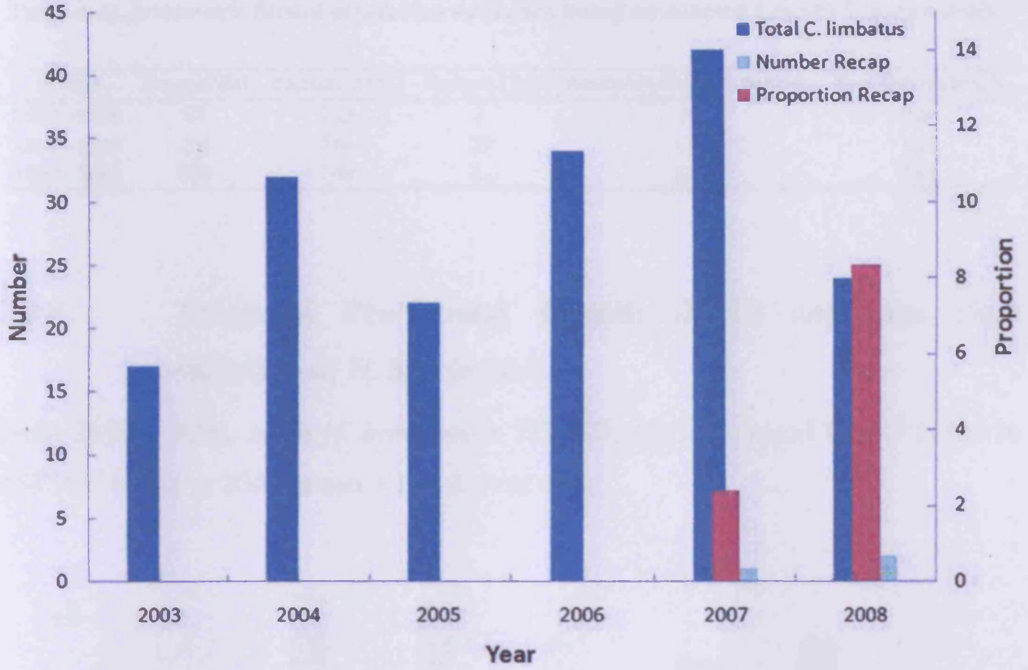


Figure 78. ***C. limbatus*** **mark-recaptures from 2003 – 2008**

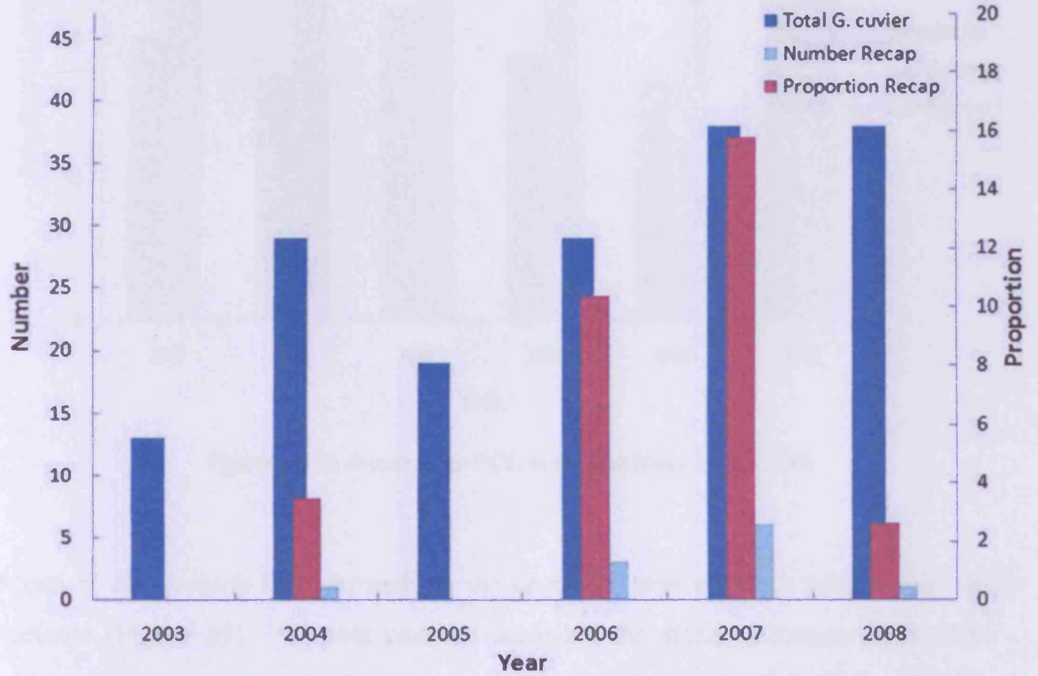


Figure 79. ***G. cuvier*** **mark-recaptures from 2003 – 2008**

Table 4. ***N. brevirostris*** **Bimini population estimates, based on adapted Lincoln-Petersen model**

Period	Tagged (M)	Captured (C)	Recaps (R)	Research Years in Period	Pop. Estimate (N)
1982 - 1989	97	113	7	8	224
1982 - 1999	204	244	27	16	115
1982 - 2008	331	366	37	24	136

3.3.9. Temporal Pre-Caudal Length (PCL) and size class variation of *N. brevirostris*

From 2003 – 2008, mean *N. brevirostris* PCL (Figure 80) ranged from 123 cm in 2003 to 160 cm in 2006 (mean = 138 ± 6 cm s.e.).

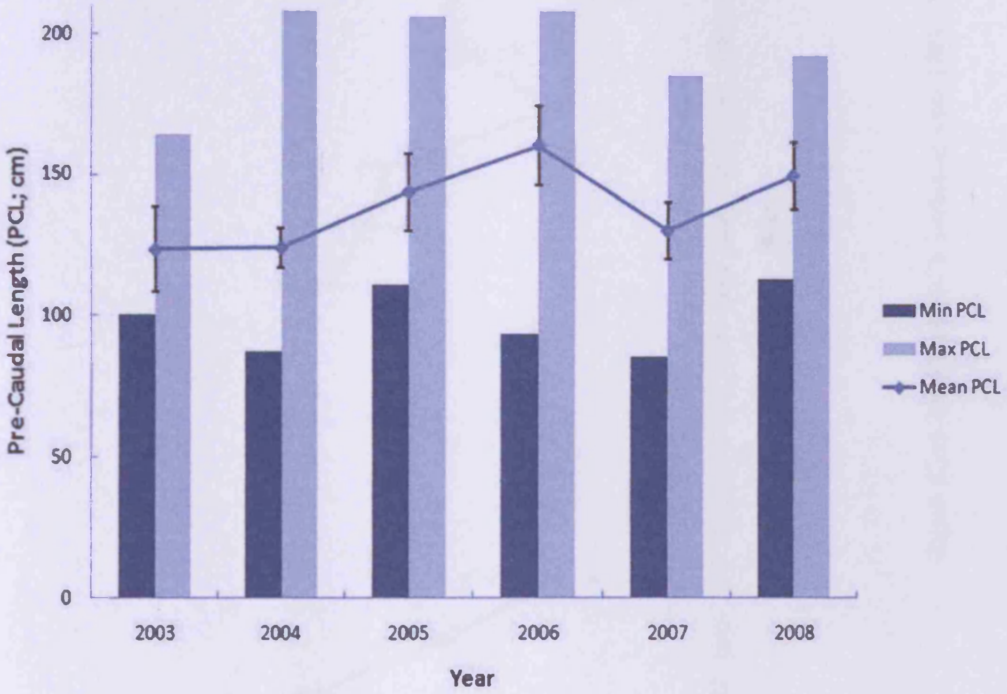


Figure 80. ***N. brevirostris*** **PCL variation from 2003 - 2008**

Mean *N. brevirostris* PCL throughout the entire 27 year research period was highly variable (Figure 81). Notable patterns included the steady decrease from 1986 – 1989; the absence of multiple (n > 1) catches, as the result of limited effort, from 1990 – 1993; the general decline from 1994 – 2001; and the repeating cycle of troughs and peaks from 1997 – 2007.

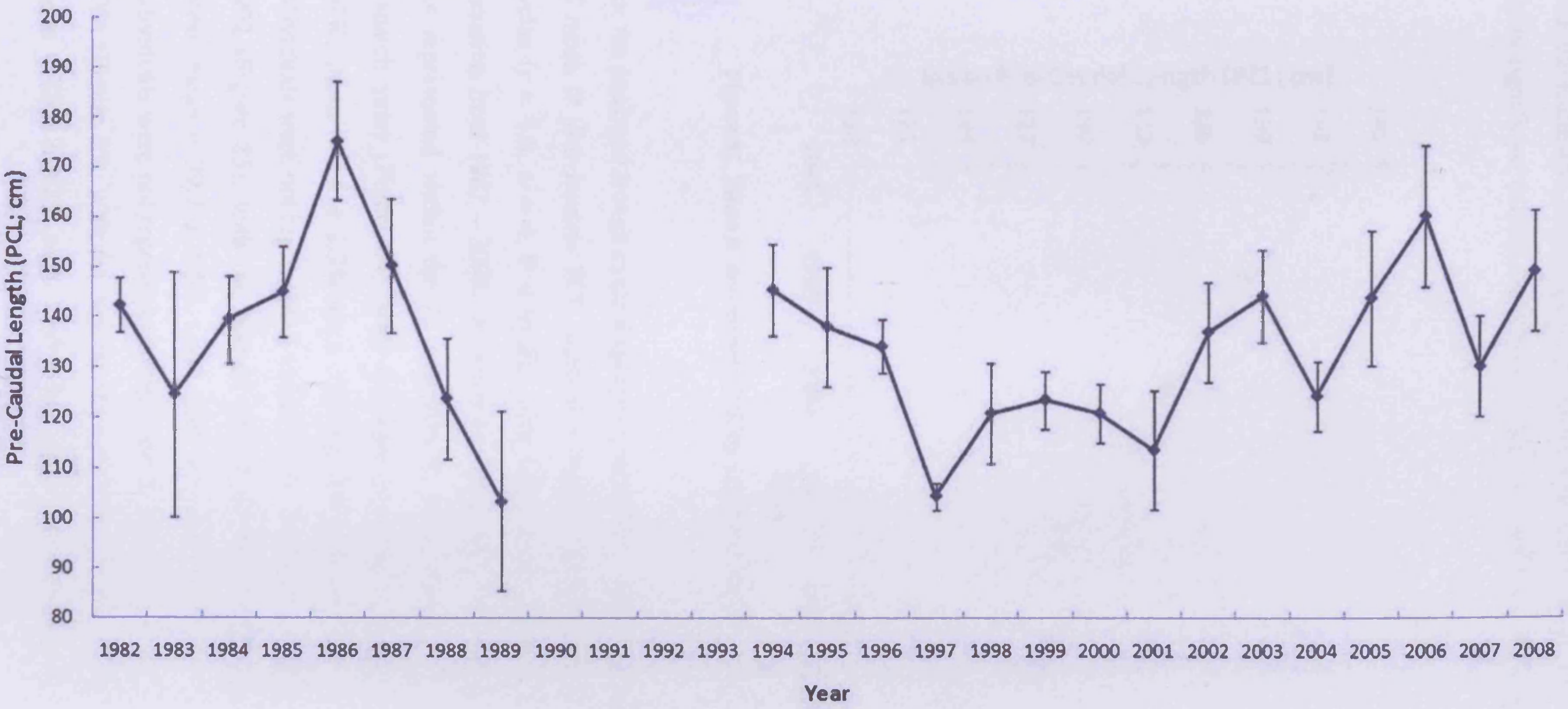


Figure 81. *N. brevirostris* **PCL variation from 1982 - 2008**

With the exclusion of the high recruitment year 1997, *N. brevirostris* PCL showed a highly significant decline from 1994 – 2001 (r = 0.95, n = 6, P <0.01; Figure 82).

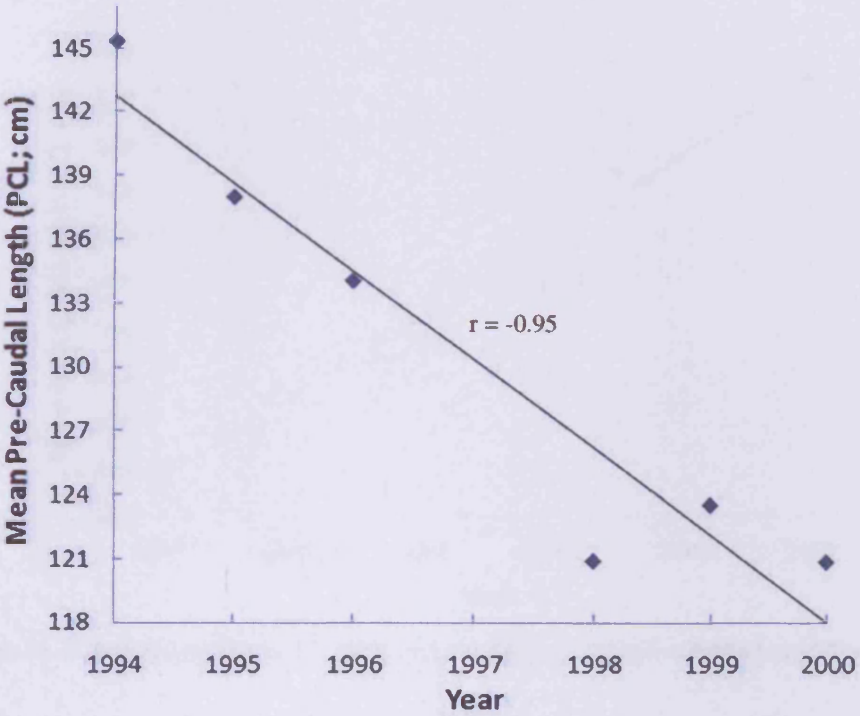


Figure 82. Mean *N. brevirostris* PCL by year from 1994 – 2000, excluding 1997

For the peak and trough cycle displayed from 1997 – 2007 (Figure 83), trough values of mean *N. brevirostris* PCL showed a highly significant linear increase between cycles (r = 1.0, n = 4, P < 0.05). Size class proportions showed a high level of variation from 1982 – 2008. Juvenile life-stage (45 – 80 cm PCL) individuals were not represented within the *N. brevirostris* catch records in 17 of the 25 active research years (Figure 84), with the highest juvenile proportion recorded in 1989 (57%; mean = 4.4 ± 2.3% s.e.). Young sub-adult life-stage (81 – 124 cm PCL) individuals were not represented within the *N. brevirostris* catch records in 1986 and 1992 (Figure 85), with the highest young sub-adult proportion recorded in 2001 (89%; mean = 39.7 ± 4.5% s.e.). Old sub-adult life-stage (125 – 165 cm PCL) individuals were not represented within the *N. brevirostris* catch records in 1992 and 2001 (Figure 85), with the highest old sub-adult proportion recorded in 2007 (55%; mean = 25.5 ± 3.2% s.e.). Adult life-stage (166+ cm PCL) individuals were not represented within the *N. brevirostris* catch records in 1997 and 1999 (Figure 86), with the highest young sub-adult proportion, for years with multiple *N. brevirostris* catches recorded in 2007 (80%; mean = 27.4 ± 5.0% s.e.).

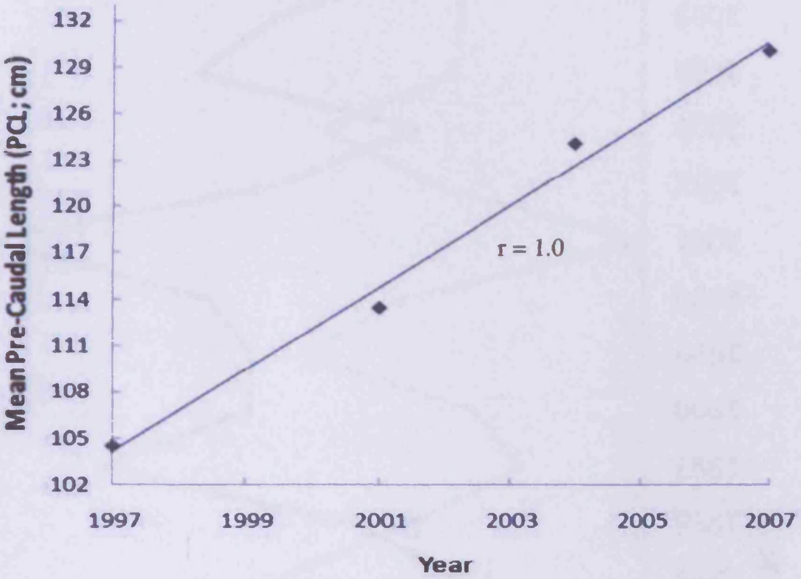


Figure 83. *N. brevirostris* mean PCL high recruitment year trough values from 1997 – 2007

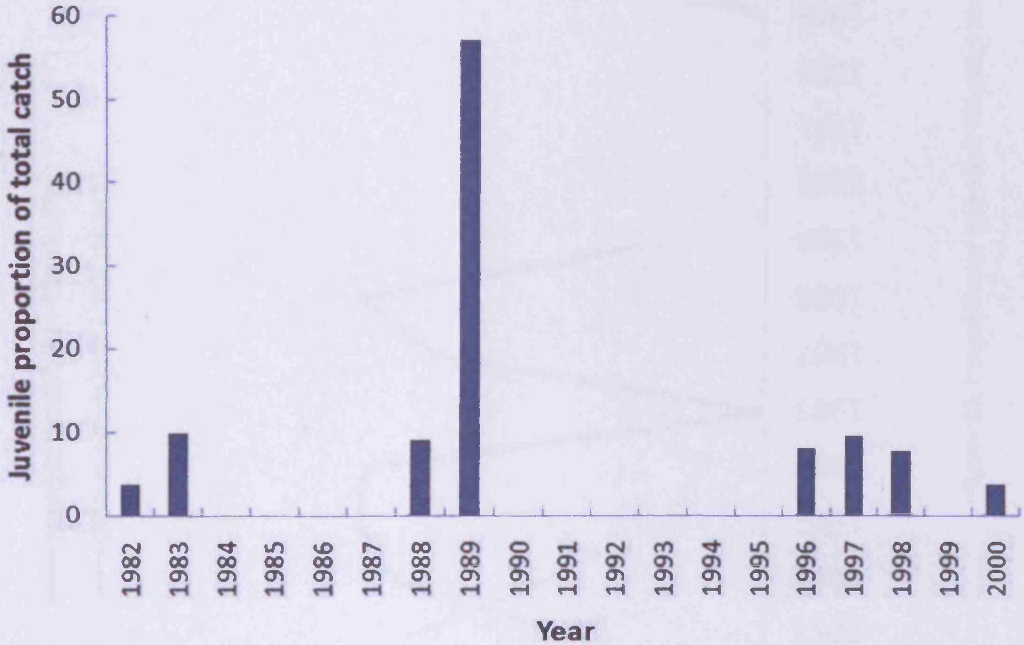


Figure 84. Proportion of juvenile life-stage (45 – 80 cm PCL) individuals within the total annual *N. brevirostris* catches – no juveniles were captured on the longlines after 2000

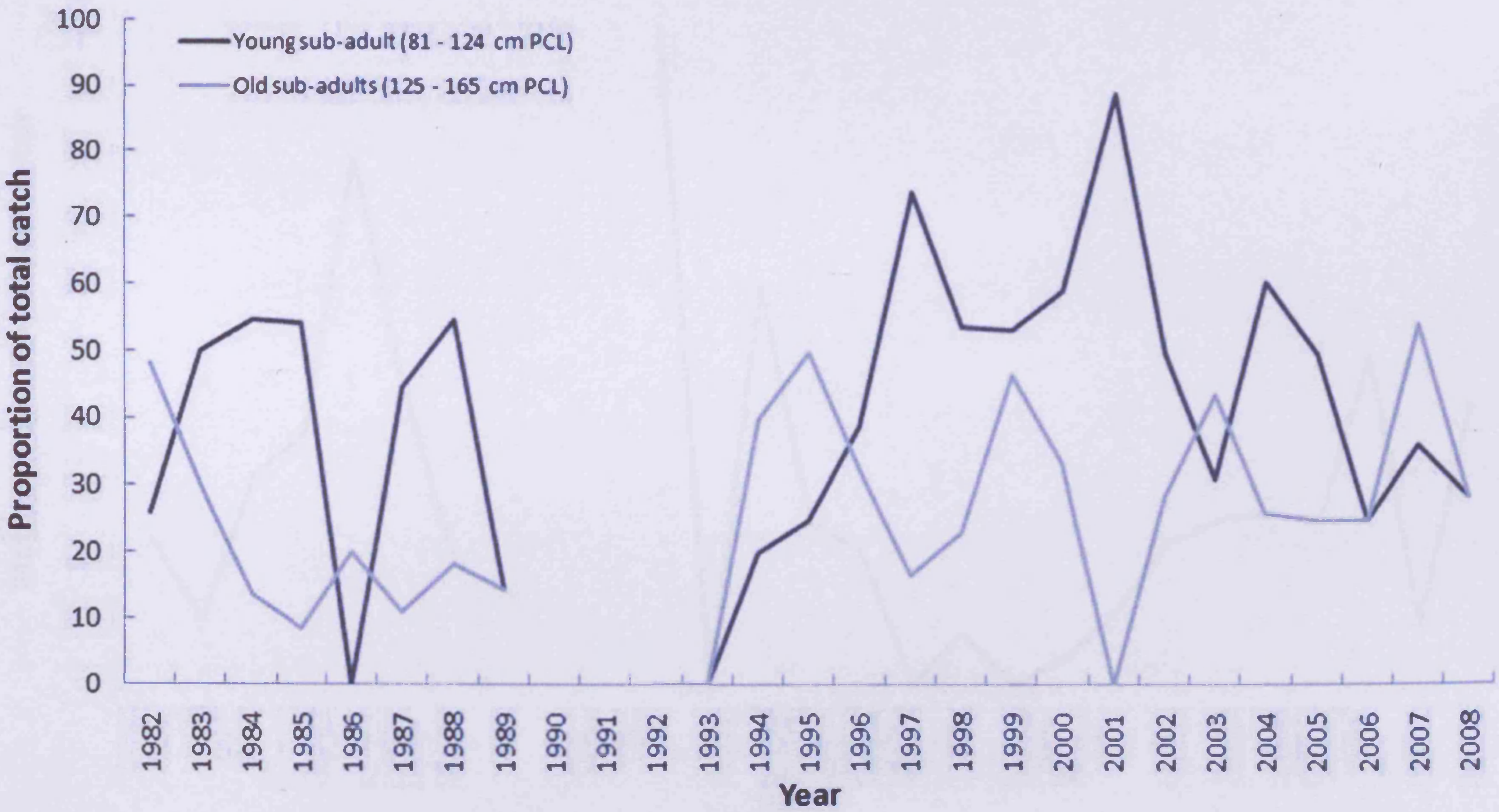


Figure 85. Proportion of sub-adult life-stage individuals within the total annual *N. brevirostris* catches

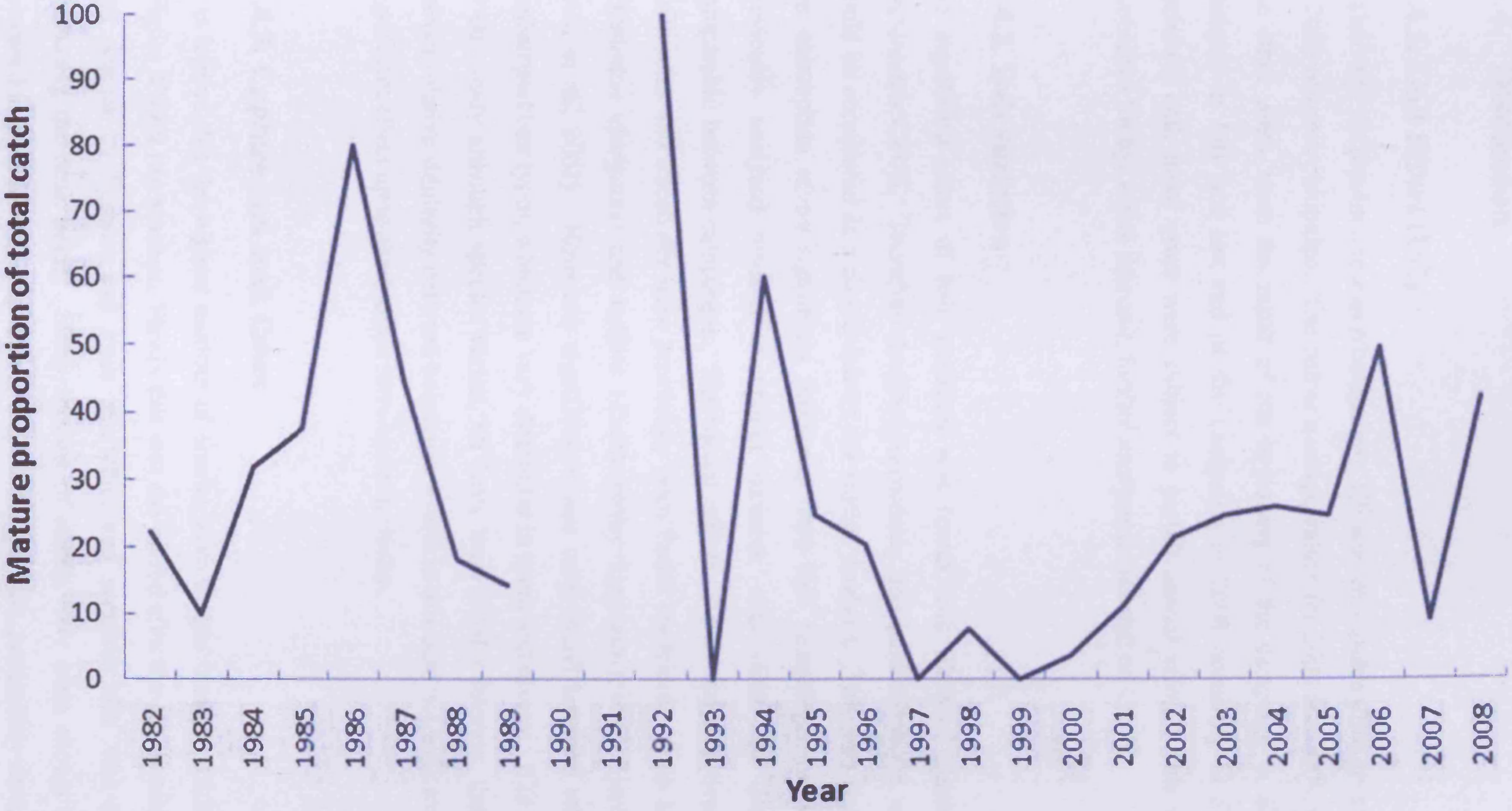


Figure 86. Proportion of adult life-stage (166+ cm PCL) individuals within the total annual *N. brevirostris* catches

3.4. Discussion

3.4.1. Unit Effort (UE)

Relative to the previous research campaigns, UE was very stable throughout the 2003 – 2008 research campaign. The below average values for 2003 and 2008, relative to the other years, were the result of the beginning of the campaign in 2003 being initiated in July and the end of the campaign in 2008 occurring in September, therefore both these years were subject to partial annual effort. This was again accounted for by, where relevant, further analysis conducted on CPUE.

3.4.2. Bait variation

No significant effect of bait variation was found both for total sharks and *N. brevirostris* CPUE. Therefore despite unavoidable bait inconsistencies, all catches could be considered as a single dataset for further analysis. This also suggests that the assumption of no significant influence from bait inconsistencies, within the previously analysed research campaign datasets, was valid and datasets are comparable between campaigns. Significant effects of bait variation over longline catch rates and selectivity have previously been found for teleosts, such as ling cod (*Ophiodon elongatus*) and halibut (*Reinhardtius hippoglossoides*; Bjordal, 1983, Woll et al., 2001). However, significance was only found between teleosts and cephalopod bait types, which are very dissimilar in scent and texture. It is likely that in this study although species varied, all baits were similar teleosts, therefore the greater relative similarity between bait types would in this case not have resulted in a significant effect upon shark catch rates and selectivity.

3.4.3. Capture and soak times

It is logical that the highest number of sharks were caught between 16:31 – 20:30 (Figure 48) for two reasons. Firstly this was the period after the set meaning that the bait was at its freshest and most available, and secondly this was the period containing the dusk hours. Many species of sharks have been shown to display increased activity and feeding during crepuscular periods, particularly dusk (Barry et al., 2008, Dawson and Starr, 2009, Heupel and Bennett, 1998, Johnson et al., 2006, SeguraZarzosa et al., 1997, Ward et al., 2004, Morrissey and Gruber, 1993b), therefore shark catchability would have been highest at this time. The second highest catch rates came in the period directly following this, where effects from the crepuscular period may have carried through and bait was still relatively fresh. The greater fishing power of fresh bait is further supported by high catch rates recorded in the first eight hours of bait soak time (Figure 49). Fresh bait fishes more effectively than old bait (Ward et al., 2004) as, although sharks will scavenge, most rely on hunting live bait for majority of their sustenance (Barry et al., 2008, Cortes and Gruber, 1990, Ellis et al., 1996, Frazzetta, 1994, Hobson, 1963, Kubodera et al., 2007, Lowe et al., 1996, Moss, 1972, Preti et al., 2001, Saidi et al., 2007, SeguraZarzosa et al., 1997, Sims et al., 2006b, Vaske et al., 2009, Wilga et al., 2007), and therefore fresh bait would have been more similar in scent to their favoured living prey state. Fresh bait would have also created a stronger odour corridor (Ward et al., 2004, Lokkeborg and Pina, 1997), drawing in sharks from a wider catchment area relative to older bait towards the end of the set. Thus over the 24 hour fishing period, the longer bait soaks for the less fishing power it has up to a point where most of the scent has leached out and fishing power becomes somewhat even (Ward et al., 2004). It would appear from the results that this was around the 12 hour mark as following this catch rates remained relatively stable. Studies focused on teleosts found no effect of specific soak time over catch rates (Lokkeborg and Pina, 1997). However, many shark species rely more heavily than teleosts on olfaction and the interpretation of olfactory cues in their function of feeding (Gardiner and Atema, 2006, Kajiura et al., 2005, Lisney et al., 2007, Schluessel et al., 2008, Theiss et al., 2009, Tester, 1963, Hodgson and Mathewson, 1978). Therefore shark catch rates at specific soak times would be expected to be more affected by the quantity and strength of olfactants leaching from the bait.

The increase in catches between 12:31 – 16:30 can in part be attributed to early catches on some of the hooks that would have been set prior to 16:30, this would reflect in the high catch rates in the first two hours of soak time. The dawn period is contained within the 04:31 – 08:30 period. The absence of a relatively high catch rate for this period suggests that of the two crepuscular periods, dusk has a greater influence over activity and feeding than dawn, although bait freshness must also be considered.

Catch rates for *N. brevirostris* were surprisingly low during the 16:31 – 20:30 period (Figure 50) and absent for the first 4 h of soak time (Figure 51). The low catches are then followed by the highest catch rates of *N. brevirostris* between 20:31 – 00:30 and at a bait soak time of 4 - 6 h. This could be a product of diel movement patterns that would reduce encounter rates for the first period and increase them during the second. *N. brevirostris* generally cover larger horizontal areas at night (Sundström et al., 2001, Gruber et al., 1988), therefore the chance of longline encounter by the lagoon *N. brevirostris* population is increased at night, and the chance of capture is in turn increased (see section 4.4.2). *N. brevirostris* have also been shown to have increased metabolism at night (Nixon and Gruber, 1988) therefore it is logical that *N. brevirostris* catch rates would be highest in the first period of darkness hours. In past studies, sub-adult *N. brevirostris* caught on bait and thus feeding in the west of the Bimini lagoon were shown to have an east – west diel pattern to their movements, spending the daylight hours in the east of the lagoon and darkness hours in the west of the lagoon where they were presumably feeding (Sundström et al., 2001). Therefore it is logical that the *N. brevirostris* captured by the longlines in the east of the lagoon would spend daylight hours in the west of the lagoon and darkness hours in the east of the lagoon when their metabolic requirements were increased, thus resulting in high night time *N. brevirostris* catches.

From these results *N. brevirostris* appear not to be predominantly crepuscular feeders, although they have been shown at the Juvenile life-stage to display increased activity in crepuscular hours (Morrissey and Gruber, 1993b, Sundström et al., 2001). Potentially, however, the increase in juvenile *N. brevirostris* activity in crepuscular hours could be in response to increased predation risk from other larger sharks in the area that are crepuscular feeders. *N. brevirostris* have been shown to have very good visual systems (Cohen and Gruber, 1977, Gruber, 1977a, Gruber, 1977b, Gruber and Cohen, 1978) and it is possible that *N. brevirostris* can actively avoid longline gear based on aesthetic cues. Thus *N. brevirostris* catch rates would be expected to be higher in hours of darkness when the longline gear would be harder to visually detect. Finally it is possible that *N. brevirostris* were more sensitive to behavioural disruption caused by the setting process. *N. brevirostris* were studied at all life-stages in Bimini since 1982, therefore they may, over the course of their more site-attached life-stages have gained a negative association with vessel activity (Guttridge et al., 2009b). As a consequence, these *N. brevirostris* may have avoided the disrupted area, following the longline set, for a period of behavioural recovery resulting in the absence of any *N. brevirostris* catches in the first four hours of soak time.

Curiously, relatively high *N. brevirostris* catches were recorded during the 12:31 – 16:30 time period between 18 – 22 h of soak time. This could have been the product of non-crepuscular feeding patterns coupled with diel movement patterns (Gruber et al., 1988) resulting in increased encounter rates during this time period, as sub-adults *N. brevirostris* likely to be feeding in the east would not encounter the longlines until their longitudinal shift after daylight hours occurred (Sundström et al., 2001, Nixon and Gruber, 1988). In addition it is possible that, at 18 – 22 h soak time, the bait had reached a stage of maturity that *N. brevirostris* find particularly favourable.

C. limbatus catch rates steadily decreased over the time periods (Figure 52), most likely directly related to bait freshness. This was supported by a temporal decrease in catch rate relative to specific bait soak time (Figure 53). The recorded decrease was probably the result of a combination of a preference to fresh bait (Ward et al., 2004), couple with spatial utilisation and therefore longline encounterability (Cortes et al., 2008, Stoner, 2004, Ward, 2008). The decrease coinciding with a temporal reduction in scent leaching to provide and odour corridor (Ward et al., 2004), would suggest that utilisation of the target area by *C. limbatus* is limited under normal behaviour, therefore an odour corridor is required to draw in *C. limbatus* from the surrounding areas.

G. cirratum displayed high catches during the first time period (Figure 54) and first two hours of soak time (Figure 55), followed by a steady decrease to the lowest catch rates between 04:31 – 08:30 at 12 – 14 h soak time, and then followed by increasing catch rates thereafter. High initial catch rates of *G. cirratum* indicate that *G.*

cirratum are responsive to bait scent and have been shown to rely heavily on olfaction in their predation efforts, locating the scent source more quickly and efficiently by klinotaxis than *N. brevirostris* that employ the less efficient rheotaxis (Hodgson and Mathewson, 1978). With the decreasing scent strength of the odour corridor over time (Ward et al., 2004), decreasing catch rates of *G. cirratum* were recorded. The high catch rate recorded in the first time period could also have been the result of crepuscular feeding that, for *G. cirratum*, would also appear to be stronger at dusk relative to dawn. Following the more standard rate of scent leaching after 12 h, *G. cirratum* catches were likely the result of incidental encounters (Ward, 2008, Stoner, 2004). The low catch between 04:31 – 08:30 and absence of catches from 12 – 14 h soak time could have been the result of daily movement patterns. It is also possible that bait at this stage of maturity was found particularly unfavourable by *G. cirratum*, which then found the bait to become increasingly more favourable with increasing maturity thereafter, accounting for the subsequent temporal increase in catch rates.

G. cuvier catches were highest in the first two time periods (Figure 56) with a lag in soak times the highest catches coming between 4 – 6 h after the set (Figure 57). This suggests that *G. cuvier* abundance was generally lower in the target area and captured individuals were drawn in through the odour corridor (Hodgson and Mathewson, 1978). This is supported by very low incidences of *G. cuvier* sightings in the target area when the longlines were not set (personal observations 2002 - 2008). Later catches, following the temporal reduction in odour corridor strength, are likely the result of reduced incidences of incidental encounter. The second peak in *G. cuvier* catches in the 04:31 – 08:30 time period and between 14 – 16 h soak time coincides with dawn, suggesting that *G. cuvier* are predominately crepuscular feeders.

3.4.4. Seasonal variations

Total CPUE for all shark species showed a highly significant positive correlation with temperature ($r = 0.875$, $n = 12$, $P < 0.01$; Figure 58). This was logical as for ectothermic shark's metabolism, and therefore dietary requirements, increase with increasing water temperature (Miklos et al., 2003, Bernal et al., 2003, Carlson and Parsons, 1999, Dowd et al., 2006b, Dowd et al., 2006a, Tullis and Baillie, 2005). This resulted in a logical seasonal distribution that showed highest CPUE to be recorded in the summer months when water temperatures were highest. It is unclear as to why February showed the lowest CPUE of all the months. This can in part have been attributed to the complete absence of *N. brevirostris* during this month (discussed below; Figure 60). *G. cirratum* were also low in abundance during the winter months (Figure 64) and showed the most significant correlation with CPUE and water temperature (r = 865, n = 12, P < 0.01; Figure 65). The fact that both *N. brevirostris* and *G. cirratum* both showed significant correlation between CPUE and water temperature suggests a further cause for the positive relationship between the two species CPUE (see section 2.3.3.3).

N. brevirostris showed a significant positive correlation with water temperature (r = 0.731, n = 12, P < 0.05; Figure 61). As with other ectothermic species, increased water temperature raised the metabolism of *N. brevirostris* thus requiring an increased food intake for survival and growth during summer months (Nixon and Gruber, 1988). *N. brevirostris* CPUE was highest in the month of June (Figure 60). This can in part have been attributed to the high water temperatures during this month and the positive correlation between water temperature and *N. brevirostris* CPUE. In addition, each year by June the nursery areas were at their highest seasonal capacity, following the mature parturition season in April and May (Sundström et al., 2001, Feldheim et al., 2002a, Jennings et al., 2007). It is likely that this high capacity, and therefore increased competition for prey resources, in the primary nurseries would have acted as a trigger for individuals on the size boundary between juvenile and young sub-adult to leave the nursery ground and join the secondary lagoon population. This was supported by a reduction in mean PCL at this time (Figure 62) and the highest proportion of young sub-adults recorded for all months (Figure 63). *N. brevirostris* CPUE and proportions of young sub-adults remain high while mean PCL remains low until August, which for August showed a decrease in *N. brevirostris* CPUE and proportions of young sub-adults and an increase in mean PCL. It was likely that the temporal changes over the two months following June were the result of predation of smaller individuals and competition for prey resources in the secondary population, following the influx at the lower end of the size classes.

The absence of *N. brevirostris* CPUE in February and low CPUE in March, in addition to the low water temperatures, was likely the result of different causes at the various life-stages. *N. brevirostris* abundance would logically have been at the lowest annual levels as these two months (February and March) directly proceed the parturition season (Feldheim et al., 2002a). Thus the boost in recruitment at the young sub-adult life-stage seen the previous June would have, by February and March, been subject to seven months of predation and natural mortality. Therefore in February and March young sub-adult population levels would have been at their annual low, directly prior to the new influx triggered by the parturition season from April to June (Sundström et al., 2001). The reduced young sub-adult proportion within the overall *N. brevirostris* abundance would have resulted in decreased intraspecific competition for prey resources. The decrease competition, in addition to decreased metabolic requirements with low water temperature, would have resulted in the lowest annual catchability for old sub-adult *N. brevirostris*. Thus a reduction in old sub-adult CPUE would have been expected, as can be seen by a complete absence in February and low CPUE in March for this life-stage (Figure 63).

Finally the absence of mature *N. brevirostris* would have been expected as a function of their breeding biology. *N. brevirostris* have a gestation period of around 13 months (Compagno, 1988, Brown and Gruber, 1988, Gruber et al., 1985). Therefore, given that parturition occurs in April and May, mature *N. brevirostris* would have been courting/mating during the months of February and March. *N. brevirostris* mating has never been reported at the Bimini islands, therefore it is likely that this behaviour takes place elsewhere, resulting in the absence of mature *N. brevirostris* in the target area during February and March each year. This was supported by the high level of mature *N. brevirostris* seasonal activity off the coast of Jupiter, Florida, in what were strongly believed to be courting aggregation, annually during the months of February and March (see section 5.1; Kessel et al., 2009a, Kessel et al., 2008). It must also be noted that matures were also absent for the months of July, September, November and December, therefore their absence in February and March may just be coincidental.

C. limbatus CPUE did not show a significant correlation with water temperature, with the peak in seasonal CPUE offset to highest water temperatures by two months to September (Figure 66). Temperature has been documented as a trigger driving nursery departure for this species (Heupel, 2007), therefore temperature would also be expected to play a role in *C. limbatus* feeding behaviour. It was likely that breeding behaviour dictated *C. limbatus* seasonality as many cases of mature females with fresh mating scars were recorded in the comments section of the catch data during September. It was therefore likely that *C. limbatus* use the waters of, or adjacent to, the target area as mating grounds, causing the increase in September CPUE. *C. limbatus* were recorded only in a small range of life stages, with annual PCL ranging from 80 – 137 cm (mean = 104.6 ± 1.07 cm s.e.), with no neonates or juveniles ever recorded. This suggested that *C. limbatus* nurseries were absent from the island. Therefore mature female *C. limbatus* would have had to depart the island waters for parturition, which could in part explain the low *C. limbatus* CPUE in the earlier months of the year.

G. cuvier CPUE appear randomly distributed throughout the year and showed no seasonal pattern (Figure 67). *G. cuvier* CPUE also showed an insignificant correlation with water temperature. *G. cuvier* CPUE levels appeared to show a largely random distribution, with very little similarity to the other species, bar a seasonal low in February. With the absence of a significant relationship to water temperature, it was likely that the general lack of smaller shark activity in and around the target area during February failed to draw in *G. cuvier*. This suggested that *G. cuvier* abundance was to some extent a product of predation behaviour upon other elasmobranchs (Lowe et al., 1996). Further reasoning for *G. cuvier* random seasonal abundance was the lack of an apparent parturition season, with neonates recorded in the longline catches year round. *G. cuvier* were also recorded in all life stages from neonate to mature, therefore variations in life-stage movements and feeding behaviour (Lowe et al., 1996, Holland et al., 1999) may have inhibited any seasonal patterns to have been apparent.

The significant correlations between *N. brevirostris* and *G. cirratum* CPUE with water temperature appears to have been driving the total CPUE correlation with temperature. Thus *N. brevirostris* and *G. cirratum* CPUE contributed most towards the total CPUE seasonal pattern.

3.4.5. Catch proportions

With the exclusion of 2004 catches, *N. brevirostris* proportions are relatively stable from 2003 – 2008 (Figure 68). It was difficult to take relevance from the 2003 value (7%) as UE does not include the seasonal parturition and recruitment period of April, May and June when *N. brevirostris* was found to be seasonally highest. The disproportionately high value for 2004 (17%) was likely the result of the first full year of intensive twice monthly effort. This resulted in a relatively high *N. brevirostris* catch, thus increasing the proportional longline capture experience within the more resident sub-adult element (87% of *N. brevirostris* catch in 2004; see section 3.3.9; Figure 63) of *N. brevirostris* population. It was possible for this element that capture resulted in a negative association, either visual, olfactory due to the relative bait consistency, or electromagnetic reception, that would have facilitated subsequent gear avoidance (Guttridge et al., 2009b). This in turn would have resulted in a subsequent reduction in resident *N. brevirostris* catchability during the subsequent research years. This theory was supported by the results of the 'acoustic fishing' in section 5.3.2.

Subsequent to the high *N. brevirostris* proportions in 2004, catch proportions alternated between 7% and 9%. This would suggest that *N. brevirostris* proportion variation were, from 2005 – 2008, predominately governed by activities of the mature breeding population. Mature *N. brevirostris* that comprised the breeding population at Bimini display a two year breeding cycle, with mature females returning to the island every two years for parturition (Feldheim et al., 2002a, Feldheim et al., 2004, Sundström et al., 2001). This resulted in two separate breeding groups, with one set displaying philopatry to the island in even years and the other set in odd years. Thus, it would appear that the group displaying philopatry to the island in the years 2005 and 2007 was larger than the group that returned in 2006 and 2008. The theory of the mature breeding population governing the *N. brevirostris* annual catch proportions is supported by the proportions of mature individuals in the annual *N. brevirostris* catch size proportions (Figure 86; section 3.3.9). The influence of the adult population also supported the theory of learned avoidance by the resident sub-adult population, as the adult individuals have much larger home ranges and are present in the target area only intermittently throughout the year (section 3.3.4; Sundström et al., 2001). Therefore they would have been subject to much less annual Bimini longline exposure than the sub-adults, providing less potential for learned avoidance by the adult population. It would therefore be logical that during this research period mature individuals would have had a greater catchability, thus resulting in greater influence over the catch proportions between odd and even years.

The results of the 2003 – 2008 research campaign once again found *N. brevirostris* (10%), *C. limbatus* (28%), *G. cirratum* (30%) and *G. cuvier* (27%) to have dominated the shark community structure in the longline target area (Figure 69). The greatest temporal change however was in the proportion of *N. brevirostris*, as proportions showed a large increase in abundance between 1982 – 1989 and 1992 – 2003, then a large decrease between 1992 – 2003 and 2003 – 2008. These changes were the result of temporal patterns in the *N. brevirostris* abundance (see section 3.3.6). In contrast *C. limbatus* and *G. cirratum* showed increased abundance between all research periods and *G. cuvier* abundance remained relatively stable throughout. This suggests that *C. limbatus*, *G. cirratum* and *G. cuvier* were not negatively affected by the influences that were driving the changes in *N. brevirostris* abundance. In turn, this suggested that the *N. brevirostris*, in support of the recent study by Cortes et al. (2008), were more sensitive and vulnerable to these external influences than the other three species, therefore would require a greater level of management consideration to ensure stock stability.

3.4.6. Catch Per Unit Effort (CPUE)

The absence of a temporal pattern in *N. brevirostris* CPUE, throughout the 1980s (Figure 70), was largely attributed to the research related mortality. U.S. east coast and Gulf fisheries landings throughout the period (NOAA/NMFS, 2006) may have influenced the *N. brevirostris* population, however with the more direct anthropogenic influence of the research sacrifices that occurred it was not possible to find a clear and significant relationship. The research sacrifices that occurred were predominately focussed on larger individuals, with a cumulative effect throughout the 1980s research period. This was reflected in the steady decrease in mean PCL towards the end of the 1980s (Figure 81). Recruitment at the base level of the lagoon population was, however, strong at the end of the 1980s (Figure 84). No considerable local anthropogenic influences were reported in the Bimini *N. brevirostris* nursery areas at the end of the 1980s, therefore it would be expected that the juvenile nursery bound population would have been relatively healthy and high in abundance (personal communications Gruber 2009). Therefore the supply of maturing juvenile *N. brevirostris* for recruitment was not limited at this time. In addition, the reduction in the larger individuals within the *N. brevirostris* population would have resulted in a reduction in conspecific predation pressure, thus reduced predation risk on the smaller individuals (Webster, 2004). This would not only result in an increase in the proportion of smaller individuals within the population, but would also have led to an increase in the home-ranges of these smaller individuals as the result of decreased predation risk (Webster, 2004). This is reflected in the temporal size class proportion, by juveniles comprising the majority of the *N. brevirostris* longline CPUE, and highest juvenile proportions throughout the entirety of the 27 years of research effort, at the end of the 1980s (Figure 84; section 3.3.9).

Based on the longline catches, it would appear that the *N. brevirostris* population at the end of the 1980s was perfectly structured for an increase in abundances throughout the following 1990s research period, which resulted in the highly significant increase in *N. brevirostris* CPUE recorded from 1992 – 2000 (Figure 70). Continued high levels of recruitment at the base level were coupled with reduced predation risk, which allowed the relative large number of smaller individuals to mature at a similar rate across the period, maintaining low predation risk for this group. This resulted in a progressively larger number of young and old sub-adults available for capture on the longlines, with increasingly large home-ranges (Morrissey and Gruber, 1993b, Sundström et al., 2001, Franks and Gruber, 2007) making longline encounter increasingly more likely. In addition, the large number of recruited individuals at the base level, at an estimated age of three years (Brown and Gruber, 1988, Sundström et al., 2001), would have not matured until the age of 12 years (Sundström et al., 2001, Brown and Gruber, 1988), thus the majority would have remained resident to the lagoon area until the end of the 1990s (Sundström et al., 2001, Chapman et al., 2009). Environmentally, the increase was facilitated by low incidences of negative anthropogenic activities throughout the period. Locally scientific related mortalities were extremely low (see section 3.3.7), and effects of the Bimini Bay Development would have not been reflected in the juvenile *N. brevirostris* population abundance until the beginning of the decade (Jennings et al., 2007). On a broader scale, a consistent reduction throughout the 1990s in the U.S. east coast and Gulf fisheries landing of Large Coastal Sharks (LCS; see section 2.4.3.9; NOAA/NMFS, 2006) would have resulted in decreasing mortality risk from the mature proportion of the *N. brevirostris* CPUE. In combination, all the previously stated elements would have allowed for, and even magnified, the potential for the observed highly significant linear CPUE increase ($r = 0.8508$, $n = 9$, $P < 0.01$) throughout the 1990s.

In contrast to the state of the population at the beginning of the 1990s, the state of the population in the year 2000 would have been perfectly poised for a temporal decrease. *N. brevirostris* abundance was at its highest levels for the entire 27 year research period, and due to the reduced predation risk experienced by the large maturing group that entered the population at the beginning of the 1990s, it is likely that the *N. brevirostris* population abundance was in excess of the available resources. This could have resulted in an increase in natural mortality and conspecific predation on smaller individuals (Webster, 2004), coupled with egress of larger individuals away from the target area in search of resources (Chapman et al., 2009). All of which could have contributed to the highly significant reduction in *N. brevirostris* CPUE throughout the 2000s ($r = 0.9237$, $n = 9$, $P < 0.01$).

With reduced recruitment at the base level as the result of the effects of the Bimini Bay Development decreasing juvenile survival rates in the nursery areas (Jennings et al., 2007), the lagoon *N. brevirostris* would have caused a shift in size class proportions toward larger individuals in the 2000s (Figures 85 and 86; section 3.3.9). Regardless of available prey resources, this would have resulted in increased predation risk on smaller *N. brevirostris* within the lagoon population, thus magnifying the shift towards a population dominated by larger individuals. Temporally more of these larger individuals would have reached maturity (Figure 85; see section 3.3.9) and left the lagoon population having increased their home-ranges far beyond the target area (Sundström et al., 2001), thus reducing *N. brevirostris* encounters with the longline gear. Finally it is possible that the potential increased active avoidance of the longline gear by more resident individuals may have magnified the extent of this highly significant linear decrease.

Total CPUE for all shark species showed no temporal pattern from 1984 – 1994, with points appearing to have been randomly distributed throughout (Figure 71). It is therefore impossible to make any comparisons with factors that may have potentially influenced the total shark population dynamics over this period. The increasing seasonal distribution of effort following the initiation of BBFS based longlining in 1992, and particularly thorough seasonal sampling regime following 2003, is likely the cause for the significant liner increase ($r = 0.6668$, $n = 14$, $P < 0.05$) in Total CPUE from 1995 - 2008. The increasing seasonal distribution of efforts would have more effectively sampled different species during their times of highest seasonal abundance (see section 3.3.4), therefore, annually Total CPUE would have increased. The dissimilarity between the *N. brevirostris* CPUE temporal patterns and the Total CPUE temporal patterns, suggested that *N. brevirostris* CPUE was affected by the identified driving influences independent of total shark CPUE. Thus the *N. brevirostris* population is not governed directly by the total shark population, and *N. brevirostris* are more vulnerable to anthropogenic influences than the other species.

N. brevirostris CPUE increased significantly relative to increasing longline latitude ($r = 0.872$, $n = 6$, $P < 0.05$; Figure 72). This suggests an uneven *N. brevirostris* lagoon population distribution across the target area. The longlines set to the south of the target area are somewhat more exposed to the surrounding waters of the Great Bahama Bank and Gulf Stream than the longlines to the north. Also the longlines to the south are in further proximity to the mouth of the central lagoon (Figure 89). This would result in increased predation risk to the south and therefore decreased utilisation of the southern part of the target area by *N. brevirostris*, in turn resulting in decreased CPUE. The three more central longlines, A, B and C, all display similar proximity to the mouth of the central lagoon and all displayed equal CPUE (0.006). Longlines D and WN also displayed a similar proximity to the mouth of the central lagoon compared to the three central longlines, yet received higher *N. brevirostris* CPUE. This suggests that either physical habitat differences of greater spatial *N. brevirostris* abundance were responsible for the higher levels of CPUE (see Chapter 4).

Total shark CPUE relative to longline latitude showed higher CPUE to the north and south, with reducing CPUE towards the middle of the target area (Figure 73). This suggests that sharks generally approached the target area from the north and south, encountering the longlines to the top and bottom of the target area first where they became captured. Clearly the *N. brevirostris* population does not predominately approach the target area from the south in this fashion.

3.4.7. Capture related mortality

Year-on-year capture related mortality was very low for *N. brevirostris* from 2003 – 2008 (Figure 74). Of the three total *N. brevirostris* recorded as catch related mortalities, all were recorded as Dead On Arrival (DOA), two as unavoidable stress related mortalities and the third as the result of predation by a larger shark on the captured individual. The three *N. brevirostris* comprised only 5% of the total 61 *N. brevirostris* captured during this research campaign, which is an expected and acceptable level for capture related mortality for the longlining research technique (Abel et al., 2007, Cortes, 1995, Grubbs and Musick, 2007, NOAA, 2003, Prosser and Abel, 2004). Longline related mortality based on mean abundance estimates (f = 0.06) was considerably less than *N. brevirostris* r-intrinsic estimates (0.2 – 0.6; Gedamke et al., 2007, Cortes, 2000), thus the observed significant decline in *N.*

brevirostris CPUE cannot be attributed to research related mortalities (see section 2.3.3.4; Gedamke et al., 2007).

Catch related mortalities by species, for the whole research campaign 2003 – 2008, varied greatly (Figure 75). The highest proportion of mortality was recorded for *S. mokarran* (50%), however, this represented only one of two individuals, thus would not have affected the overall CPUE. Relatively high proportions of catch related mortality were recorded for *C. acronotus* (25%), *C. leucas* (12.5%) and *R. porosus* (24%), however, again this only represented a small number of individuals (n = 1, n = 1 and n = 4 respectively), therefore would have been unlikely to have affected overall shark abundance. The highest number of catch related mortalities for a species was 30 individuals (18%) for *C. limbatus*. This again highlights the low stress tolerance of *C. limbatus* in relation to longline capture (Cortes et al., 2008). Yet, despite high *C. limbatus* catch related mortalities recorded for all three periods (Figure 19, 42 and 75), *C. limbatus* proportions within the shark population increased between each research campaign (Figure 69). Therefore it would appear that longline catch related mortalities in the target area have not negatively impacted upon the *C. limbatus* population. This also adds further weight to the theory of low site attachment for *C. limbatus* as it would be expected that a more resident population would decline under these levels of anthropogenically influenced mortalities. Despite the capture of high numbers, both *G. cirratum* and *G. cuvier* were not subject to any catch related mortality as the result of the longline activities, again highlighting a low vulnerability to longline activity (Cortes et al., 2008, Holland et al., 1999).

3.4.8. Mark-recapture

The low number of *N. brevirostris* mark-recaptures (n = 4; Figure76) from 2003 – 2008 support two previously stated theories. Firstly, this was the lowest proportion of mark recapture of all three research periods; 6% relative to 13% from 1992 – 2003 and 10% from 1982 – 1989. This supports the theory of a population decline from 2003 - 2008, relative to the previous research campaign, based on the CPUE records. The occurrence of the lowest mark-recaptures rates in the research period that exhibited the most regular and consistent distribution of UE throughout the campaign, supports the theory of active gear avoidance by the resident *N. brevirostris* (Guttridge et al., 2009b). Support came as avoidance through negative association would result in a reduction in catchability, of previously captured individuals relative to previously un-capture individuals (see section 5.4.5.2). Thus a reduction in mark-recaptures was recorded for this period despite, as the result of cumulative tagging efforts from 1982 onwards, the greatest number of tagged individuals potentially available for recapture in this period.

High and consistent mark-recapture rates for *G. cirratum*, from 2003 – 2008 (Figure 77), again suggested that *G. cirratum* was one of the more site-attached of the species recorded in the longline research campaigns (Pratt and Carrier, 2007). In addition it appears that *G. cirratum* did not show the same levels of active avoidance of the longline gear as suggested for *N. brevirostris*. This would be logical, as low capture related mortalities for *G. cirratum* across all three research periods suggests that this species did not suffer from high levels of capture induced stress (Cortes et al., 2008). Therefore *G. cirratum* would have gained less negative association towards the longline gear, as the result of capture, than *N. brevirostris*, and would be less inclined to actively avoid it. In addition, as *G. cirratum* tend to rely less on vision and more on olfaction (Hodgson and Mathewson, 1978, Gruber, 1977a, Kajiura et al., 2003) than *N. brevirostris* it may have been harder for *G. cirratum* to detect the longline gear before hooking occurred.

The increased levels of *C. limbatus* and *G. cuvier* mark-recaptures from 2003 – 2008 (Figures 78 and 79) relative to the previous research campaigns (Figure 44), were likely the result of the increased regularity of longlining efforts in this period. Though both species appear to have little site attachment to the area, twice monthly longlining could have resulted in individuals becoming recaptured before they moved significantly outside of the catchment area within the course of a year. Also with the greatest number of tagged individuals for both species in this period, as the result of cumulative tagging efforts, higher incidences of mark-recaptures for both *C. limbatus* and *G. cuvier* may have been somewhat subjective.

Population estimates, based on the adapted Lincoln-Petersen model (section 3.3.8) were found to be a mean of 158 (± 33 s.e.) individuals comprising the Bimini lagoon *N. brevirostris* population in any given year from 1982 – 2008. Based on personal observations during tenor at the BBFS from 2003 – 2008, this would seem to be a reasonable estimated value. These longline based population estimates were truthed against population estimates devised for aerial surveys in section 4.3.3 and found to be reasonable.

3.4.9. Temporal Pre-Caudal Length (PCL) and size class variation of *N. brevirostris*

Mean *N. brevirostris* PCL appeared relatively stable from 2003 – 2008, but when considered continuously across the entire 27 year research campaign, temporal patterns became apparent (Figure 81). Firstly the only steady year-on-year decline occurred from 1986 – 1989. The decline at the end of the 1980s was most likely the result of consistent scientific *N. brevirostris* sacrifices, predominately of larger individuals for the age and growth study (Brown and Gruber, 1988). The decline resulted in the *N. brevirostris* mean PCL reaching its lowest value for the entire campaign, and abundance temporally low, leaving the lagoon population in the perfect situation, low abundance and a lack of predation risk from larger individuals, for the apparent population increase that followed throughout the 1990s (see section 3.3.4; Webster, 2004). This was increased by a large recruitment of juveniles at this time (Figure 84). The absence of results from 1990 – 1993 was the result of very limited longline efforts during this period resulting in no multiple catches.

From 1994 – 2000 there was an apparent temporal decline in mean *N. brevirostris* PCL, with an unusually low value in 1997 (Figure 81). When the period from 1997 – 2008 was considered, it became apparent that the unusually low value in 1997 was part of a pattern on troughs and peaks in mean *N. brevirostris* PCL, and represented a year of high recruitment (see below). This is verified by a peak in juvenile *N. brevirostris* catch proportions in 1997, resulting in the highest proportion for this period (Figure 84). With the removal of this unrepresentative year, a highly significant decrease in *N. brevirostris* mean PCL ($r = -0.95$, $n = 6$, $P < 0.01$) was found from 1994 – 2000 (Figure 82). This suggested that the steady and highly significant increase in *N. brevirostris* CPUE from 1992 – 2000 ($r = 0.8508$, $n = 9$, $P < 0.01$) was largely driven by a steady influx, bar the disproportionately large influx in 2002, of juveniles at the base level of the lagoon population.

By 2000, *N. brevirostris* CPUE was at its highest (Figure 70), while mean PCL was low (Figure 81). This suggested a large lagoon *N. brevirostris* population dominated by smaller individuals, as supported by the relative life-stage catch proportions at the beginning of the 2000s (Figures 84 – 86). Mean *N. brevirostris* PCL from 1997 – 2008 showed a sequence of peaks and troughs separated at 3 – 4 year intervals. The sequence, based on the regularity of sample regime at this time would appear to relate to the natural cycle of recruitment at the population base level, relative to ontogenetic departure at the top level of the population. Therefore trough years would represent years of high recruitment at the base level of the lagoon population. When only trough years, 1997, 2001, 2004 and 2007 are considered, a significant temporal increase in mean *N. brevirostris* PCL ($r = 1.0$, $n = 4$, $P < 0.05$) for the period was found (Figure 83). The temporal increase, from 1997 – 2008, in mean PCL at the recruitment level of the population suggests that it was a decline in the juvenile and young sub-adult life stages that was driving the observed highly significant CPUE decline ($r = 0.9237$, $n = 9$, $P < 0.001$) through the final research period from 2000 - 2008. The likely causes of the decline in the lower *N. brevirostris* life stages would have been the decrease in recruitment as the result of decreased nursery survival rates post 2001, driven by the impacts of the Bimini Bay Development (Jennings et al., 2007). In addition, and in combination with the decrease in recruitment, there would have been an increase in conspecific predation of smaller individuals within the lagoon population by the increase in larger individuals (Webster, 2004) maturing from the large recruitment levels at the beginning of the 2000s (Figure 84).

3.5. Conclusion

Form 1982 – 2003, the average Bimini lagoon *N. brevirostris* population was estimated to consist of around 158 individuals present in any given year. This was by no means a large population relative to the recorded declines. Given the life-history of *N. brevirostris*, even a relatively small decline in numbers as the result of anthropogenic activities could result in considerable disruption to any natural temporal patterns that may have otherwise been in effect. From 1982 – 1989 it would appear that instability within the population was the result of both anthropogenic influences and artefacts of research design. From 1982 – 1989, the greatest anthropogenic influence came as the result of sacrificial research techniques associated with the various *N. brevirostris* focused studies conducted during this research period. Sacrifices tended to be focused on larger individuals within the population, resulting in imbalance within the population's size classes and the resultant alteration to subsequent population dynamics. This was coupled by inconsistency of the sampling regime, leading to seasonal variations in *N. brevirostris* abundance distorting any potential to reveal temporal population patterns.

Throughout the 1990s period there was minimal anthropogenic disturbance to the lagoon *N. brevirostris* population. The absence of sacrificial research techniques, in addition, to minimal habitat disruption throughout the majority of the period, resulted in a significant population increase from 1992 – 2000. The main anthropogenic disturbance came from the initiation of the Bimini Bay Development activities in 1997. This appeared to cause instant and direct disruption to the lagoon *N. brevirostris* population, in relation to CPUE and size class proportions within the population, repeated again in 2001 in response to the most intensive sub-tidal development activities to date. The sacrificial research activities of the previous campaign in addition to the disruptive influence of the development activities may have also resulted in a lagoon population increase at a rate beyond the resources of the habitat, as the result of imbalance between *N. brevirostris* size classes.

Following the observed increase from 1992 – 2000, the lagoon population experienced a highly significant decline over the subsequent research period from

2000 - 2002. This can be largely attributed to the population disruptions that preceded it in addition to a reduction of recruitment at the population base level. It has been documented that through dredging activities and nursery habitat removal, of fringing mangrove populations, the Bimini Bay Development activities have resulted in a reduction of *N. brevirostris* nursery survival rates (Jennings et al., 2007, Feldheim and Edren, 2002). This resulted in a reduction in the number of individuals available for recruitment into the lagoon *N. brevirostris* population in conjunction with increased predation risks as the result of the previous population disruptions. Collectively these influences resulted in a population decline, possibly magnified in the data by potentially increasing longline avoidance by site attached *N. brevirostris*. From 1992 – 2000, with the absence of any size class influence from the sacrifices of larger individuals, mean PCL declined relative to increasing CPUE and mean PCL then increased relative to decreasing CPUE. This suggests that it was the smaller individuals at the lower life-stages within the lagoon *N. brevirostris* population that were producing the greatest influence over CPUE. Thus the reduction in recruitment as the result of decreased survival rates post 2001 would likely be the most considerable cause for the significant decrease in CPUE from 2000 – 2008.

It is possible that the population *N. brevirostris* increase followed by population decrease, is representative of a natural population pattern at this location for this species. However, should this have been the case it is highly unlikely that all the previously identified factors would not have greatly magnified these patterns to the detriment of this vulnerable species. Of most concern were the apparent effects of the Bimini Bay Development activities. These were evident through all forms and avenues of analysis (CPUE, catch proportions, mean PCL variations and size class proportions) providing very strong evidence of negative impacts not only as identified for the nursery bound juvenile population, but also to the secondary lagoon sub-adult and adult *N. brevirostris* population. This is of great concern as the identified disruptions to the *N. brevirostris* population were only in response to the first stage of the planned Bimini Bay Development. Should the proposed development plans receive full approval from the Bahamian government, the latter stages would produce considerably greater disruption and habitat loss/alteration, with plans in place for the complete removal of all North Sound *N. brevirostris* nursery fringing mangroves and a nine-hole golf course. Given the previously identified negative effects of the development activities and the life-history traits of *N. brevirostris* that make population recovery difficult for this species, further planned development of the Bimini islands could have catastrophic implications for the Bimini *N. brevirostris* populations.

4. Shark longline catchability and encounterability

4.1. Chapter Introduction

Many factors can influence longline Catch Per Unit Effort (CPUE: Ward, 2008, Stoner, 2004), a number of which are outlined in section 2.3.2.5.2. However, the majority of factors that do influence catches are assumed to have no effect over CPUE in the analyses of longline data (Ward, 2008, Ward et al., 2004, Stoner, 2004). Actively assessing the effects of all potential influencing factors is an unfeasible undertaking and would eventually become counterproductive given the amount of time and resources that would be required. Due to the long-term nature of research activities conducted on the shark populations at Bimini, Bahamas, it has been possible to investigate some of these specific potential influences in relation to shark longline CPUE. For the Bimini longline dataset, the affects of lunar variations and hook type were addressed in Chapter 2 and the effects of diel variation, soak time and bait type were addressed in Chapter 3.

The assessment of the previously stated variables proved extremely useful for the results interpretation for the longline data analysis in Chapters 2 and 3. However, some of the variables that may have had significant influence over the longline CPUE results are yet to be addressed. In this Chapter, through a combination of additional available historical data belonging to the Bimini Biological Field Station (BBFS) research group, and some focused research approaches, it was possible to assess the potential effects of more of these important variables. The aims of this chapter were to a) assess influence of hooking success and multiple shark presence over catchability for *N. brevirostris*, *C. limbatus* and *G. cirratum*; b) assess the influence of encounterability and monthly abundance variation over CPUE for *N. brevirostris*; and c) assess the current state of abundance relative to the historical records for *N. brevirostris*. The aims were achieved by video surveillance of baited hooks, the truthing of historical tracking data with focused aerial surveys, the determination of *N. brevirostris* abundance distribution around the Bimini lagoon, abundance estimates based on aerial survey counts, and the extrapolation of historical abundance estimates from the CPUE records and the truthing of the extrapolated estimates with mark-recapture data.

With fishing gears requiring self-hooking, such as longlines, manipulation of the baited hook by the target species has great influence over hooking success and therefore CPUE (Huse and Ferno, 1990), therefore interspecies variation in catchability on self-hooking longline gear could have greatly influenced the historical Bimini longline CPUE results. Interspecies variations in longline catchability have been previously documented for teleost species (Ferno and Huse, 1983, Huse and Ferno, 1990, Olla and Samet, 1974, Ryer and Olla, 1991, Stoner and Ottmar, 2004). Sharks species have been shown to possess different feeding behaviours/techniques and differences in bait manipulation (Frazzetta, 1994, Hobson, 1963, Moss, 1972, Preti et al., 2001, Wilga et al., 2006, Wilga et al., 2007) that may make them more or less susceptible to capture on longline hooks. In addition, other behavioural factors may also influence a particular individual's catchability in a particular moment in time (Stoner and Ottmar, 2004, Stoner, 2004). Specifically, the presence of multiple sharks in the target area may lead to the alteration of a given individual's feeding behaviour, and bait manipulation, as the result of increased resource competition (Stoner, 2004, Stoner and Ottmar, 2004).

This could lead to species that tend to display group behaviour having a higher catchability than species that tend to be more solitary (Davis and Olla, 1992, Olla and Samet, 1974, Ryer and Olla, 1991, Ryer and Olla, 1992, Stoner and Ottmar, 2004, Hobson, 1963). Such variations could lead to certain species being over-represented in the CPUE records, relative to others that may be under-represented. Locally this could affect the understanding of the Bimini longline CPUE dataset, thus reducing confidence in the results. On a broader scale this could have considerable implications for elasmobranch stock assessments – the basis for state and federal elasmobranch regulations in the U.S. Additionally, results could provide further insight into the validity of some highly disputed issues within the reports of mass global shark population declines (Baum et al., 2003, Burgess et al., 2005a, Burgess et al., 2005b, Baum et al., 2005, Baum and Myers, 2004).

4.2. Methodologies

4.2.1. Baited hook video surveillance

Video surveillance has previously been employed as a tool to assess such variations in teleost species (Huse and Ferno, 1990, Shardlow, 1993, Stoner and Ottmar, 2004) and crustaceans (Jury et al., 2001). For sharks, video surveillance has recently been employed to assess population structure and species abundance (Meekan et al., 2006). In this study, video surveillance technology was used to assess influence of potential interspecies variables on catchability, with specific attention on species hooking success and the influence on multiple shark presence on bait attempts and hooking success.

The baited hook video surveillance equipment (Figure 87) was set up as follows to replicate a single gangion section of a real longline. First the 30 m mock section of main longline was secured in place with the use of a concrete block and Danforth® anchor at each end. The gangion was then clipped to the centre of the line by tuna clip. The underwater video camera was positioned 5 m up current of the gangion. The camera was connected to a recording unit and monitor on a vessel anchored 30 m up current by a long cable, to allow for real-time underwater observations to be made. While the submerged equipment was being assembled, cloud cover, wind strength/ direction and surface conditions were recorded onboard the vessel. Following the placement of the camera, visibility was recorded from a secchi disk. Finally the chum cage, containing 1/3 of a standard chum block (1.6 kg), was located 3 m up current of the gangion and the bait placed on the hook. Bait consisted of a pre-cut *S. barracuda* steak of 4 cm width. The time at which the hook was baited was recorded as the trial start time.

The field team consisted of 4 members, one to monitor the video screen, two to make surface observations and one to record data. Any shark presence or behaviour documented on either the video monitor or from surface observations was entered in the data-book as a data record. A data record consisted of the time of observation, species (if identifiable), a behaviour code and detailed description of the observed behaviour. Behaviours documented relative to this research project were: 'Bait

Attempt' – the shark makes a directed effort to manipulate the bait with its mouth; 'Successful Hooking' – as the result of a bait attempt the shark became captured on the hook and remains captured for a period of at least 3 minutes, 'Multiple Shark Presence' – more than one shark was observed in the target area, either on the video monitor or from the surface, at the same moment in time. The trial end time was recorded when a shark became successfully hooked, or when the bait was removed from the water. If a shark became successfully hooked it was processed by the methodology described in section 3.2.3. On returning to the research base, the video was digitally rendered onto a computer and then reviewed to create a comprehensive video data log.

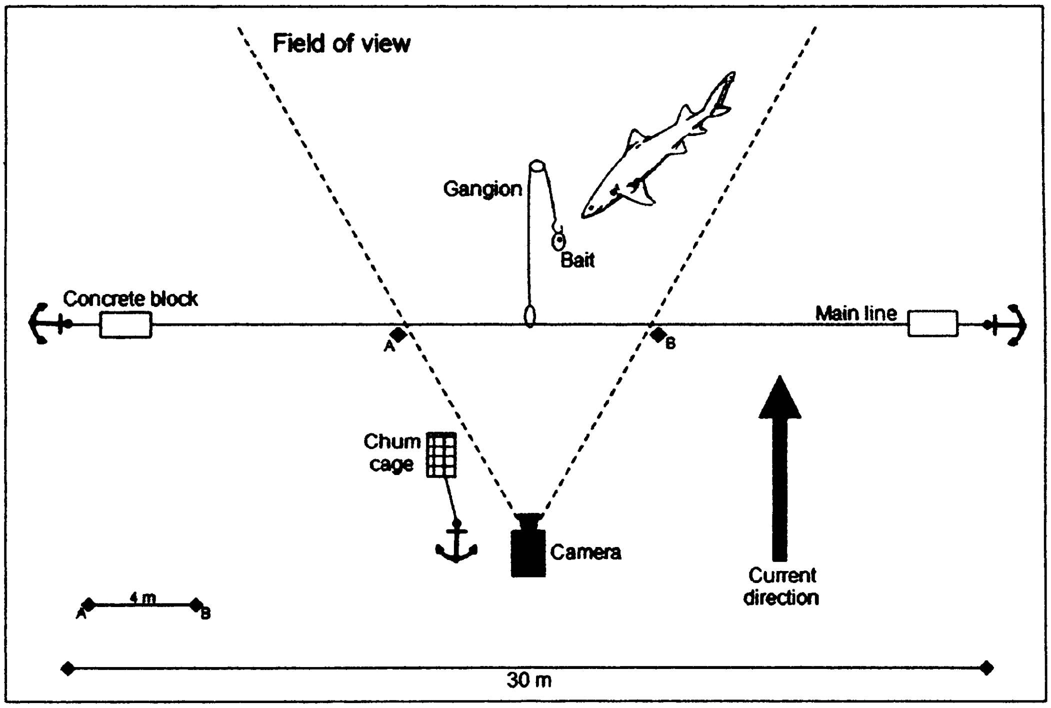


Figure 87. Baited hook video surveillance equipment set-up – A and B represent knots in the main line to restrict the lateral movement of the gangion

4.2.2. Acoustic tracking

Acoustic tracking has been widely utilised for many years in definition of shark home-range and spatial utilisation (Andrews et al., 2007, Cartamil et al., 2003, Heupel and Simpfendorfer, 2008, Heupel et al., 2006, Ortega et al., 2009, Ubeda et al., 2009, Brunnschweiler, 2009, Nelson et al., 1997, Holland et al., 1992, Carlisle and Starr, 2009, Sundström et al., 2001). Fortunately, the BBFS has a long history of acoustic telemetry utilisation that has not only resulted in a very large dataset, but also provided the basis for a good understanding of *N. brevirostris* home-ranges and habitat utilisation in the Bimini Lagoon (Morrissey and Gruber, 1993a, Morrissey and Gruber, 1993b, Sundström et al., 2001, Sundstrom and Gruber, 2002, Sundstrom and Gruber, 1998, Franks and Gruber, 2007). A proportion of these studies, particularly in recent years, have focused on the juvenile life stage of the Bimini N. brevirostris. However, after the establishment of the BBFS in 1990, telemetry studies have consistently focused on the sub-adult *N. brevirostris* that comprise the majority of the Bimini lagoon population. Permission of access was granted to the entire Bimini sub-adult tracking database (Gruber personal communications 2007) for further analysis specific to the aims of this project. It was therefore possible to gain a comprehensive insight of Bimini sub-adult *N. brevirostris* abundance distribution for comparison to the longline CPUE results.

Acoustic tracking of sub-adult *N. brevirostris* at the Bimini islands was conducted from November 1992 – January 2008. Specimens were issued with acoustic transmitters by either external attachment with a stainless steel dart, or by internal implantation into the peritoneal cavity, as detailed in section 5.2.2. Specimens were allowed a minimum of 24 hours to recover and return to their normal behaviour before active tracking was initiated. Active tracking involved following the acoustic signal from specimens issued with acoustic tags in a flat bottom skiff. The transmitted acoustic signal was detected with the use of an underwater hydrophone and onboard acoustic receiver. Each transmitter had a given frequency between 60 and 80 KHz and a unique coded transmission sequence to allow for individual specimen identification. A minimum distance of 30 m was maintained from the study specimen, whenever possible, to minimise the potential of disturbance to the sharks natural behaviour. Vessel GPS position, in decimal degrees, compass bearing and estimated distance to the study specimen, based on acoustic signal strength, were recorded at five minute intervals. Vessel track GPS points were subsequently converted into study specimen locations using the Bearing, NewPosLat, NewPosLong, and Posdist spherical geometry functions in Excel® (Laake, 2001).

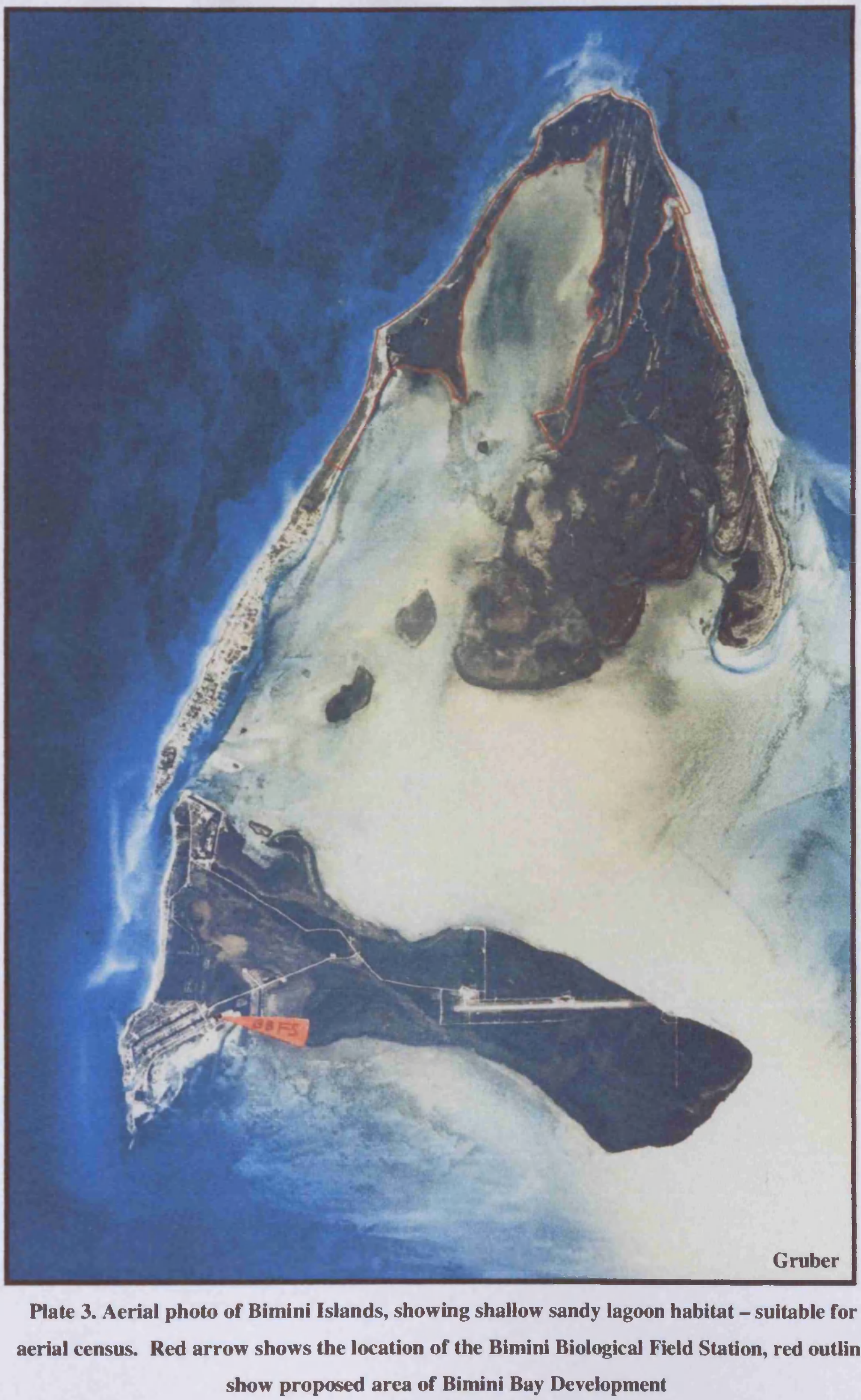
Study specimens were located by acoustically searching the target area with vessel transects conducted at idle speed. Once located, the study specimen was tracked continuously for as long as possible, changing crews at eight hour intervals if necessary, until the signal was lost consistently for in excess of one hour. Continuous tracks were conducted, on the same individual, for up to and above 72 hours. In total, 21,562 tracking points, produced by 47 individuals were obtained from over 15 years of acoustic tracking activities.

4.2.3. Aerial Survey

Aerial survey is a technique that has been widely used for many years to assess species population abundance for both terrestrial and marine vertebrates (Marsh and Saalfeld, 1989, Slooten et al., 2004, Marsh and Sinclair, 1989, Edwards et al., 2004, Miller et al., 2005, Fewster and Pople, 2008). For marine species, employment of aerial survey census techniques has mainly focused on marine mammals and reptiles (Cardona et al., 2005, Craig and Reynolds, 2004, Edwards et al., 2007, Pollock et al., 2006, Roos et al., 2005, Salberg et al., 2009, Slooten et al., 2004, Witt et al., 2009). Marine mammals and reptiles are suitable for census from the air in that all need to regularly breathe and are therefore are regularly visible at the surface. To date, employment of aerial census for sharks has been limited in the literature to whale sharks (*Rhincodon typus*; Rowat et al., 2009, Cliff et al., 2007, Sleeman et al., 2007) and basking sharks (*Cetorhinus maximus*) as these species both spend long periods filter feeding at the surface (Sims et al., 2005, Wilson, 2004) and are therefore suited to aerial based census techniques. Most shark species however spend relatively little time at the surface and costal Carcharhinidae species tend to spend the majority of their time near the sea bed (Sundström et al., 2001). This makes Carcharhinidae species generally unsuitable for aerial census techniques, and resultantly the only literature with aerial census used to survey a Carcharhinidae species relates to experimental surveys of the Bimini lagoon *N. brevirostris* population (Gruber et al., 1988).

The Bimini lagoon *N. brevirostris* population however provided a very good opportunity to revisit the employment aerial census for *N. brevirostris* abundance, as previously utilised by Gruber et al. (1988) to identify activity patterns and spatial utilisation. A number of factors combined to make this particular population of sharks suitable; firstly although *N. brevirostris*, like other coastal Carcharhinidae, spend the majority of their time near the sea bed, the Bimini population display high site attachment to the central lagoon area (Sundström et al., 2001, Gruber et al., 1988). The central lagoon area is shallow throughout (< 4 m deep; Plate 3), consists predominately of sandy light substrata (Hussey, 2003), and water clarity is usually high (personal observations 2002 – 2008). Therefore even when at the very bottom of the water column, *N. brevirostris* were still highly visible from the air (Rowat et al., 2009). The combination of the *N. brevirostris* population and habitat properties provided the perfect opportunity to re-employ the aerial census technique for this species in this location.

The aerial survey team consisted of four members: a pilot, two observers and a survey monitor. The first observer was located in the co-pilot seat at the front right of the cockpit, with the second observer located directly behind the first in the right hand side passenger seat. Both observers looked out of the right side of the aircraft, therefore covering the same area, and recorded *N. brevirostris* sightings in tally form on a pre-prepared survey sheet. Following the completion of the survey, sheets were cross referenced to produce a combined final sheet with the maximum count for each zone, i.e. the largest number for each zone recorded by either observer. By covering the same area with two observers, the chance of a given *N. brevirostris* being missed was halved and the assessment of observer variation could be used to calculate the Perception Correction Factor (PCF; see below). The survey monitor was located directly behind the pilot, and was charged with the task of recording all the flight parameters, mainly time of takeoff and landing, and start and end time of each survey transect. Pilots provided their time and aircraft on a volunteer basis, therefore a combination of four different aircraft were utilised throughout the duration of the research project. The fixed-wing aircraft utilised were a Cessna 172, a Beechcraft 35 Bonanza, a Piper Pa-28 Archer and a Piper PA-31-350 Navajo Chieftain. The pilot's sole responsibility was to fly the predetermined flight path with the aid of a map, onboard GPS unit and instructions issued in the pre-flight briefing. An altitude of 100 m and a groundspeed of 185 km/h were maintained for each transect.



Gruber

Plate 3. Aerial photo of Bimini Islands, showing shallow sandy lagoon habitat – suitable for aerial census. Red arrow shows the location of the Bimini Biological Field Station, red outline show proposed area of Bimini Bay Development

The survey design was based on existing aerial survey protocols (Marsh and Saalfeld, 1989, Marsh and Sinclair, 1989, Shelden and Laake, 2002, McDaniel et al., 2000, Rowat et al., 2009), using a stratified block sampling protocol (Figure 88). The target area was divided into logical zones and the area of each zone calculated. The area sampled within each zone was then derived from each strip transect, with the visual sample width previously established (see below). For each survey, a total of 10 transects were flown, providing two passes for each zone, one on the western edge travelling north and one on the eastern edge travelling south (Figure 88). From start to finish all 10 transects took 30 – 40 minutes to complete. For maximum sighting potential, aerial surveys were only conducted within the following environmental conditions. To minimise the potential for poor surface conditions and turbid waters, which could obscure the view of the submerged sharks, surveys were only conducted in wind conditions below Beaufort scale 3 (Rowat et al., 2009, Marsh and Sinclair, 1989, Shelden and Laake, 2002, Edwards et al., 2007). To ensure sufficient light for visual identification was available and to minimise the effects of surface glare, aerial surveys were only conducted when cloud cover was < 30% and from two hours prior and two hours after 12:00, when the sun was highest in the sky.

4.2.4. Analytical methodology

Unless otherwise stated, or specifically being investigated in the section, all variables stated in section 3.2.4.2 are assumed to have had no effect on the results. For all tidal based group analysis, high-tide was defined as 3 hours prior to and 3 hours after dead high-tide, and low-tide was defined as 3 hours prior to and 3 hours after dead low-tide.

4.2.4.1. Interspecies hooking success

From the footage review records of the baited hook video surveillance trials, bait attempts were calculated for each species that had displayed multiple behaviours, *N. brevirostris*, *C. limbatus* and *G. cirratum*. For each species the proportion of bait attempts that resulted in a successful hooking were calculated. Differences between species were compared.

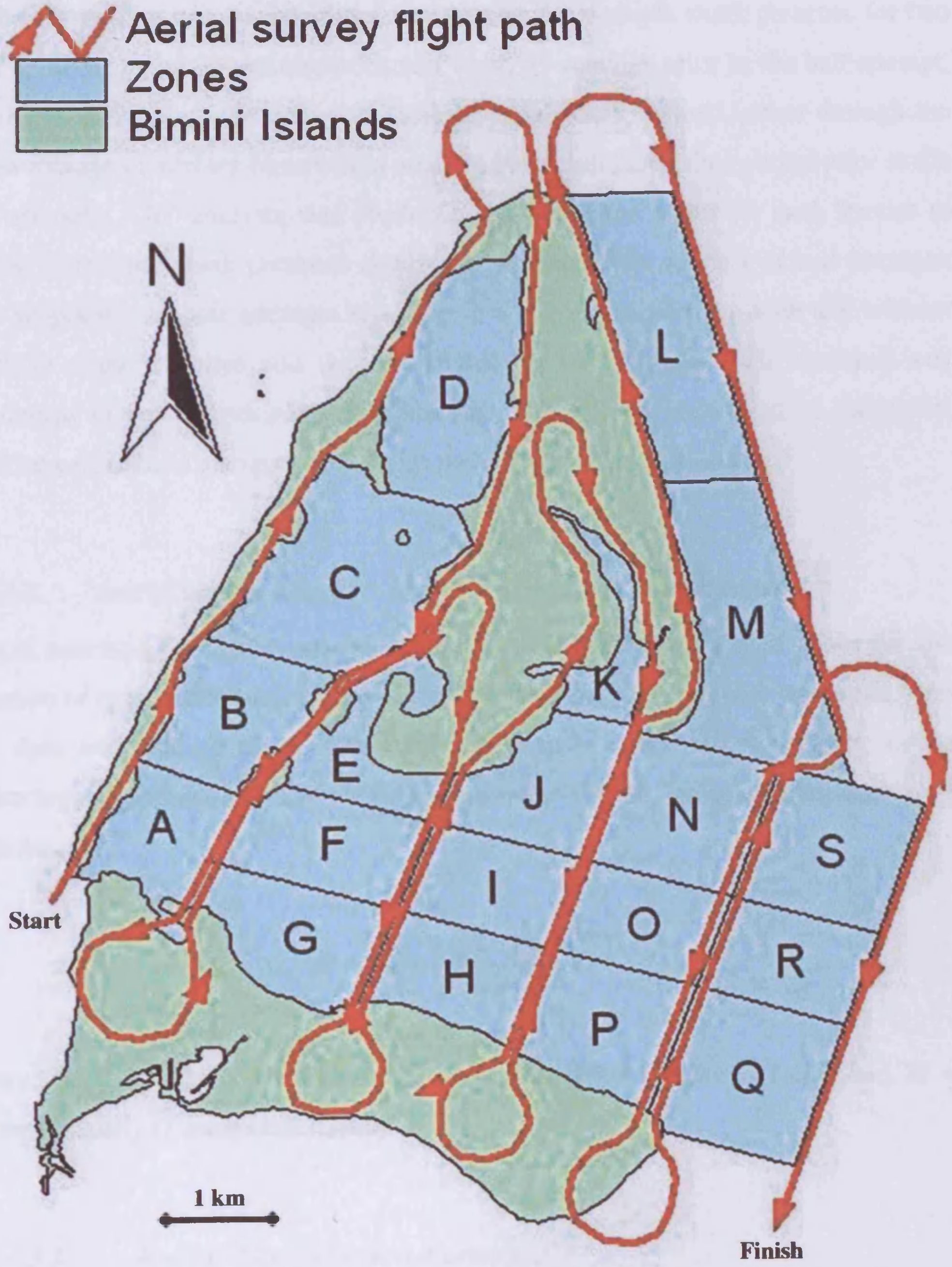


Figure 88. Aerial survey transect flight path and stratified block sampling zones

4.2.4.2. Effects of multiple shark presence on bait attempts and hooking success

Each bait attempt was issued with a 1 or 0 value for multiple shark presence for two time periods: up to 30 minutes prior and up to 15 minutes prior to the bait attempt. 'Multiple shark presence' refers to more than one shark sighted, either through the video footage or surface observation notes, within each given time period prior to the bait attempt. Chi^2 analysis was conducted for both time scales for each species to assess if multiple shark presence significantly affected the number of bait attempts. The proportion of bait attempts resulting in a successful hooking with and without multiple shark presence was then calculated for each species. Chi^2 analysis was conducted to see if multiple shark presence affected the proportion of successful hookings relative to attempts made with no multiple shark presence.

4.2.4.3. Aerial survey based *N. brevirostris* abundance estimates

It was assumed that there was no transition of individuals between zones for the duration of each aerial survey. For each zone an abundance estimate was made from raw data, and then all zones were combined to give an abundance estimate for the entire lagoon population. The abundance estimate (*N*) was calculated for each zone as follows:-

$$N = \frac{(C \times ACF \times PCF)}{SI}$$

where: C = *N. brevirostris* count, ACF = availability correction factor and SI = survey intensity (Rowat et al., 2009).

4.2.4.3.1. Availability Correction Factor (ACF)

ACF accounts for individuals within the population not visibly available for counting during the survey. For aerial surveys of the marine environment this usually is a product of water turbidity, depth and diving behaviour (Cliff et al., 2007, Marsh and Saalfeld, 1989, Marsh and Sinclair, 1989, Rowat et al., 2009, Slooten et al., 2004). In Bimini the maximum water depth within the survey area was 5 m, thus water depth and diving behaviour were not considered to be variables effecting *N. brevirostris* visual detection. Also, surveys were only conducted in calm conditions with little to no turbidity; therefore turbidity was also not considered a variable. Availability of *N. brevirostris* within the target area, during the aerial surveys, could however have been affected by *N. brevirostris* local movements. The area to the south of the island was not considered for the aerial survey census due to unfavourable substrate (dense seagrass beds) for identifying sharks against. Figure 89 shows that sub-adult *N. brevirostris* do travel outside of the survey target area; therefore individuals residing outside of the perimeter during the execution of the survey would not have been considered for counting. Therefore, ACF, in the case of the Bimini aerial surveys, related to local movements.

In order to calculate ACF it was necessary to calculate an estimate for the proportion of *N. brevirostris* movements, from 21,562 tracking points, that were outside of the aerial survey target area. This was achieved using ArcGIS® 9.2 software to isolate all *N. brevirostris* tracking points outside of the target area. The tracking points outside of the aerial survey area were then calculated as a proportion total tracking points, giving an estimate for the proportion of time spent by Bimini *N. brevirostris* outside of the aerial survey target area of 14%. Thus an ACF of 1.14 was applied for *N. brevirostris* abundance estimates.

4.2.4.3.2. Perception Correction Factor (PCF)

PCF accounts for individuals missed by the observer and can be the result of a number of factors (Marsh and Sinclair, 1989). For a survey of this nature, the two greatest potential sources for *N. brevirostris* to be missed by the observer were a) altitude and b) individuals simply not visually detected by the observer. From a given altitude, it may not be possible to see an individual of a given size, with increasing altitude decreasing the ability to identify a small individual. During their comparative studies, Marsh and Sinclair (1989a,b) found that a ratio of 274:1 (altitude: minimum animal size) was sufficient for accurate detection. With a maintained altitude of 100 m and a minimum animal target size of 1 m a ratio of 100:1 was obtained, well within the limits of accurate detection. Therefore it was not necessary to employ a PCF for survey altitude.

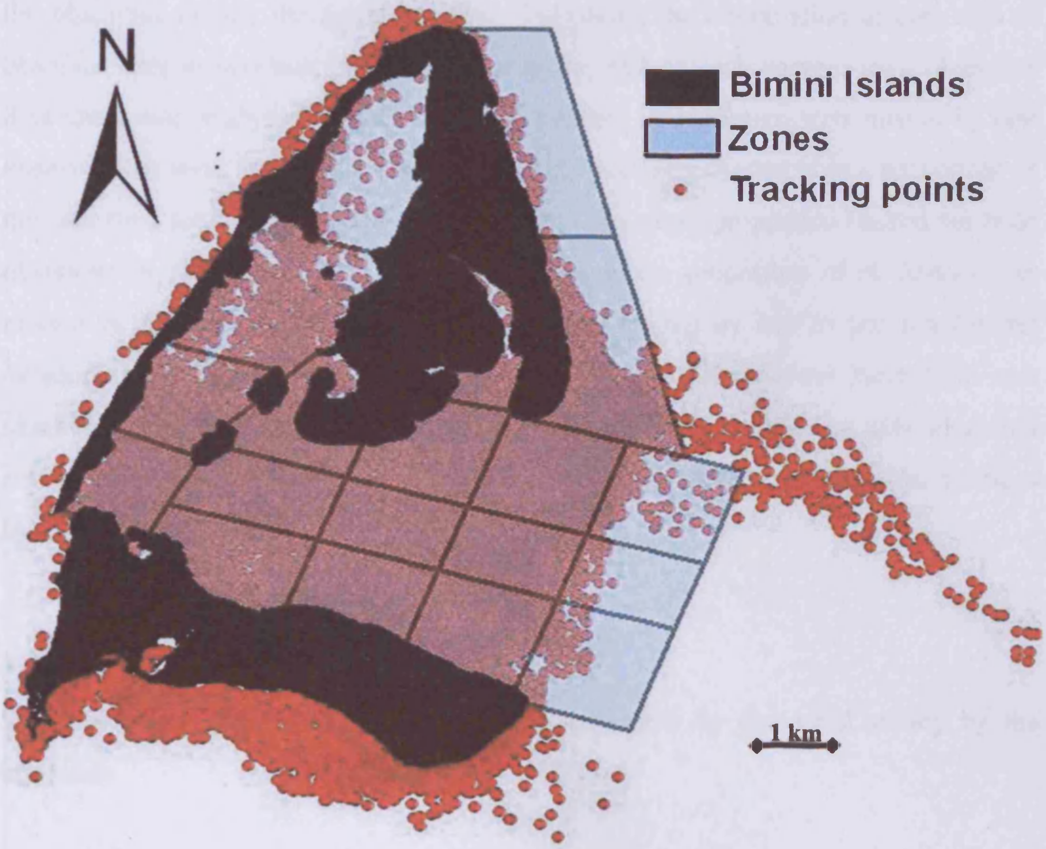


Figure 89. Historical tracking point locations relative to aerial survey zones as used to calculate Availability Correction Factor (ACF) – i.e. individuals exhibiting movements outside of aerial survey zones would not be recorded during the aerial survey

Observers may simply miss or fail to identify *N. brevirostris* within the survey area for a number of reasons, including glare, fatigue or inattention (Slooten et al., 2004). This can vary between observers and is usually accounted for by the modified Peterson estimate as defined by Marsh and Sinclair (1989). However, the same observers were used for all surveys therefore the employment of this method was not necessary as individual perception error remained constant. It was thus possible to devise a value for PCF based on the number of individual *N. brevirostris* missed by the observers during the aerial surveys. Following the culmination of both sets of observer data to produce the final count at the end of each survey, each observers data sheet was analysed to calculated the number of *N. brevirostris* missed by one observer that were recorded by the other. This was then converted to a proportion of the observed total for each observer, and then the mean proportion missed for both observers in that survey was calculated. The mean proportion of *N. brevirostris* missed in all surveys was calculated and then divided by two to account for the reduced chance of missing an individual, as in any given survey there were two observers. The final mean proportion of *N. brevirostris* missed by an individual in a survey was found to be 36% (± 2.7 s.e.), thus when halved became 18%, giving a PCF for all surveys of 1.18.

4.2.4.3.3. Survey Intensity (SI)

SI accounts for proportion of the total area sampled by the aerial survey by the equation:

$$SI = \frac{area\ of\ coverage}{area\ of\ zone}$$

It was therefore necessary to calculate these values for each zone using ArcGIS® 9.2. Individual polygons were created for each of the aerial survey zones allowing the area of the marine habitat contained within each to be obtained, providing for each the *area of zone*. The effective visual transect width was truthed for standard survey altitude and speed (100 m and 185 km/h respectively) using submerged markers and found to be 350 m. *Area of coverage* was then obtained by the union of the zone polygons with the 350 m buffer of the plotted line transects. By the union process each zone polygon was divided into three subsequent polygons; two of which represented the area of coverage for the north and south line transects in each survey zone. The combined areas of the two isolated coverage polygons thus provided the *area of coverage*.

4.2.4.4. *N. brevirostris* zone density

Estimated zone abundance was divided by zone area to give a value for estimated *N. brevirostris* zone density as a value of *N. brevirostris* (NB) per km^2 (NB/km^2). Values for all surveys were combined for each zone and then divided by the number of surveys conducted to give a mean *N. brevirostris* density for each zone. Surveys were then divided into low and high-tide counts and the process repeated, resulting in three mean density values, total, high and low-tide, for each zone. The produced density values were then attributed to the respective zones in ArcGIS 9.2® to produce a zone density distribution map for each set of values (total, high and low-tide). The produced zone density maps were subsequently used to truth the acoustic tracking data. Additionally the longline set locations were plotted over the top of the total zone densities to allow for comparison between set location and zone densities.

4.2.4.5. Distribution truthing

It is possible that the devised *N. brevirostris* abundance distribution plots were the result of spatial bias in acoustic tracking focus. The shallow nature of the Bimini lagoon habitat meant that certain areas are extremely shallow, if not dry, around low-tide. Due to the difficulties associated with acoustic tracking and vessel manoeuvring in very shallow areas, it is possible that tracking crews may have avoided, or had less tracking success, in very shallow areas. Therefore tracking based *N. brevirostris* abundance distribution plots may show bias in having higher densities in deeper areas of the lagoon. Of particular concern was the dramatic variation between low and high plots in the area of the lagoon that corresponded to aerial survey zones I and J (Figure 88). This area is the shallowest in the lagoon and, depending on tide height, at low-tide becomes extremely shallow or dry. Logically *N. brevirostris* would move away from this area at low-tide, however *N. brevirostris* have been documented to regularly inhabit areas of extremely low water depth, to the point where a large proportion of their body can be exposed above water (Reyier et al., 2008). Since the aerial survey technique provided standard coverage of all lagoon areas, irrespective of water depth or tide, it was possible to compare the un-bias aerial survey results with the potentially bias acoustic tracking results for truthing purpose.

The produced *N. brevirostris* abundance distribution maps were first truthed visually against the aerial survey zone *N. brevirostris* density maps and assessed for similarity. For quantitative truthing, for both high and low-tide, the number tracking points in each zone (I and J) were obtained using the 'select by theme' tool in Arc GIS 9.2®. The proportion reduction for the two zones from high to low-tide was then calculated for both number of tracking points and estimated *N. brevirostris* abundance, and the results compared.

4.2.4.6. *N. brevirostris* abundance distribution

All 21,562 tracking points were plotted into ArcGIS 9.2®, and then converted to a point density plot, on a 40 x 40 m grid, with each cell representing number of points if extrapolated over a square kilometre. Three plots were produced; one for all tracking data and one each for high and low-tide tracking points. Where exact capture time was available, longline *N. brevirostris* catches were divided into two groups based on high or low-tide at time of capture. *N. brevirostris* low-tide catches were plotted over the low-tide point density plot, and high-tide catches were plotted over the high-tide point density plot. The combined plots allowed comparisons to be made between *N. brevirostris* abundance distribution, assumed to be proportional to encounter probability, and *N. brevirostris* catch locations. Three additional plots were made over the complete tracking point density plot. Firstly line set location was plotted to assess each longlines fishing power relative to encounter probability. Secondly *N. brevirostris* CPUE by specific location, as defined in section 2.3.2.5.5, was plotted to assess the effect of encounter probability on CPUE. Finally the distribution of known shallow seagrass beds were plotted to assess the relationship between available refuge proximity and *N. brevirostris* abundance distribution.

4.2.4.7. Annual *N. brevirostris* abundance estimates

Assuming that CPUE is directly proportional to abundance (Richards and Schnute, 1986), it was possible to extrapolate abundance estimates for each research year back to 1982. For each research year the proportional value of *N. brevirostris* CPUE was calculated relative to 2008 *N. brevirostris* CPUE (0.006). A proportional *N. brevirostris* abundance estimate (*N*) for each year was then calculated from:-

$$N = \left(\frac{AE}{100}\right) \times CP$$

where: AE = mean *N. brevirostris* abundance estimate for 2008 (52 ± 9.2 s.e.), and CP = *N. brevirostris* CPUE proportion of 2008 value (0.006). Finally, from the resultant extrapolated *N. brevirostris* abundance estimates, means were calculated for the periods 1982 – 1989, 1982 – 1999 and 1982 – 2008, for comparison with the mark-recapture abundance estimates obtained in section 3.3.8.

4.3. Results

4.3.1. Hooking susceptibility

4.3.1.1. Interspecies hooking success

All three species, *N. brevirostris* (n = 25), *C. limbatus* (n = 26) and *G. cirratum* (n = 32), made a similar and relatively low number (26, 27 and 32 respectively) of attempts at the bait. Resulting from bait attempts, all three species also showed and extremely similar proportion of successful hookings, with *N. brevirostris* at 24%, *C. limbatus* at 27% and *G. cirratum* at 25%.

4.3.1.2. Effects of multiple-shark presence on bait attempts and hooking success

The affect of multiple shark presence in the target area on bait attempts varied between species (Table 5). For *N. brevirostris*, multiple shark presence up to 30 minutes prior to the bait attempt resulted in a highly significant increase in bait attempt frequency ($\chi^2 = 9.85$, d.f. = 1, $P < 0.01$), and multiple shark presence up to 15 minutes prior to the bait attempt resulted in a significant frequency increase ($\chi^2 = 3.85$, d.f. = 1, $P < 0.05$). For *C. limbatus*, multiple shark presence up to 30 minutes prior to the bait attempt resulted in a highly significant increase in bait attempt frequency ($\chi^2 = 9.85$, d.f. = 1, $P < 0.01$), but multiple shark presence up to 15 minutes prior to the bait attempt did not result in significant frequency increase ($\chi^2 = 2.46$, d.f. = 1, $P > 0.05$). For *G. cirratum*, multiple shark presence both up to 30 and 15 minutes prior to the bait attempt did not result in significant frequency increase ($\chi^2 = 0.03$, d.f. = 1, $P > 0.05$ and $\chi^2 = 0.76$, d.f. = 1, $P > 0.05$).

Table 5. Number of bait attempts with and without multiple shark presence for 30 and 15 minutes prior to attempt; *NB = N. brevirostris, CLI = C. limbatus* and *GCI = G. cirratum*

Species	Time scale (mins)	Alone	Multiple presence	Chi Sq	d.f.	Significant
NB	30	5	21	9.85	1	P < 0.01
NB	15	8	18	3.85	1	P < 0.05
CLI	30	5	21	9.85	1	P < 0.01
CLI	15	9	17	2.46	1	P > 0.05
GCI	30	16	17	0.03	1	P > 0.05
GCI	15	19	14	0.76	1	P > 0.05

The affect of multiple shark presence in the target area on bait attempt hooking success varied between species (Table 6). For *N. brevirostris*, multiple shark presence up to 30 minutes prior to the bait attempt resulted in a significant decrease in hooking success ($\chi^2 = 3.84$, d.f. = 1, $P < 0.05$), and multiple shark presence up to 15 minutes prior to the bait attempt did not result in any significant hooking success change ($\chi^2 = 0.73$, d.f. = 1, $P > 0.05$). For *C. limbatus*, multiple shark presence up to 30 minutes prior to the bait attempt resulted in no significant change in hooking success ($\chi^2 = 1.52$, d.f. = 1, $P > 0.05$), but multiple shark presence up to 15 minutes prior to the bait attempt did result in a significant increase in hooking success ($\chi^2 = 5.76$, d.f. = 1, $P < 0.05$). For *G. cirratum*, multiple shark presence both up to 30 and 15 minutes prior to the bait attempt did not resulted in and significant change in hooking success ($\chi^2 = 1.46$, d.f. = 1, $P > 0.05$ and $\chi^2 = 0.17$, d.f. = 1, $P > 0.05$).

Table 6. Proportion of bait attempts resulting in successful hooking, alone and with multiple shark presence for 30 and 15 minutes prior to attempt; *NB* = *N. brevirostris*, *CLI* = *C. limbatus* and *GCI* = *G. cirratum*

Species	Time scale (mins)	Prop. Alone (%)	Prop. multiple (%)	Chi Sq	d.f.	Significant
NB	30	40	19	3.84	1	P < 0.05
NB	15	25	22	0.73	1	N.S.
CLI	30	20	24	1.52	1	N.S.
CLI	15	11	29	5.76	1	P < 0.05
GCI	30	31	18	1.46	1	N.S.
GCI	15	26	21	0.17	1	N.S.

4.3.2. Encounterability

4.3.2.1. Distribution truthing

Comparison of figures 90 and 93 shows similar results for estimated *N. brevirostris* density based on aerial survey data relative to tracking point based density, with the central lagoon area containing the highest densities of both methods. Comparison of figures 91 and 92 to 95 and 96 shows a similar density distribution reduction, from high to low-tide, of *N. brevirostris* density relative to tracking point density. The variation of zones I and J, from high to low-tide, showed a 73 % reduction of *N. brevirostris* density based on the aerial survey data, and a 94 % reduction of *N. brevirostris* tracking points. Thus zones I and J were utilised less at low-tide relative to high-tide and the density reduction is true, not simply an artefact of tracking ability.

4.3.2.2. *N. brevirostris* abundance distribution

Results with all aerial surveys showed the area of highest *N. brevirostris* estimated density to be the most central zones E – J and O – P (Figure 90). The highest *N. brevirostris* estimated density was recorded in zone F (6.5 *NB*/km^2) and the lowest in zone Q (0.17; mean = 1.6 ± 0.35 s.e.). Longlines A – D were subject to increasing proximity to the central lagoon area from south to north. The Wildcard South (WS) longline sets were outside of the aerial survey zones, therefore *N. brevirostris* estimates were not present for this set area. The Wildcard North (WN) longline sets were in relative close proximity to the central lagoon area.

N. brevirostris abundance distribution, based on historical tracking data, was again greatest in the central area of the lagoon (Figure 93). Similar to *N. brevirostris* estimated density; longlines A – D were in increased proximity to areas of high abundance distribution from south to north, with longline D consistently set in very close proximity to the area of highest abundance distribution, around the shallow seagrass beds to the northeast of the central lagoon (Figure 94). Abundance distribution varied relative to WS longline set location, with a number located outside of the document habitat utilisation for sub-adult *N. brevirostris*. WN longline set locations were, like longline D sets, in very close proximity to the area of highest abundance distribution. Variation in *N. brevirostris* abundance showed distinctly different distributions between high and low-tide (Figure 94 and 95). At low-tide, relative to high, the area of greatest *N. brevirostris* abundance distribution was considerably displaced to the east and west, which resulted in considerably reduced *N. brevirostris* density in the central lagoon area. The shift in abundance resulted in higher *N. brevirostris* abundance in close proximity to the longline set area (Figure 93) during low-tide relative to high-tide. Thus encounter rates of *N. brevirostris* with the longline gear would have been expected to be greater at low-tide relative to high. The eastern extent of *N. brevirostris* was also greater at low-tide than at high. For the 18 *N. brevirostris* for which exact capture times were available, seven were captured at high-tide and 11 were captured at low-tide.

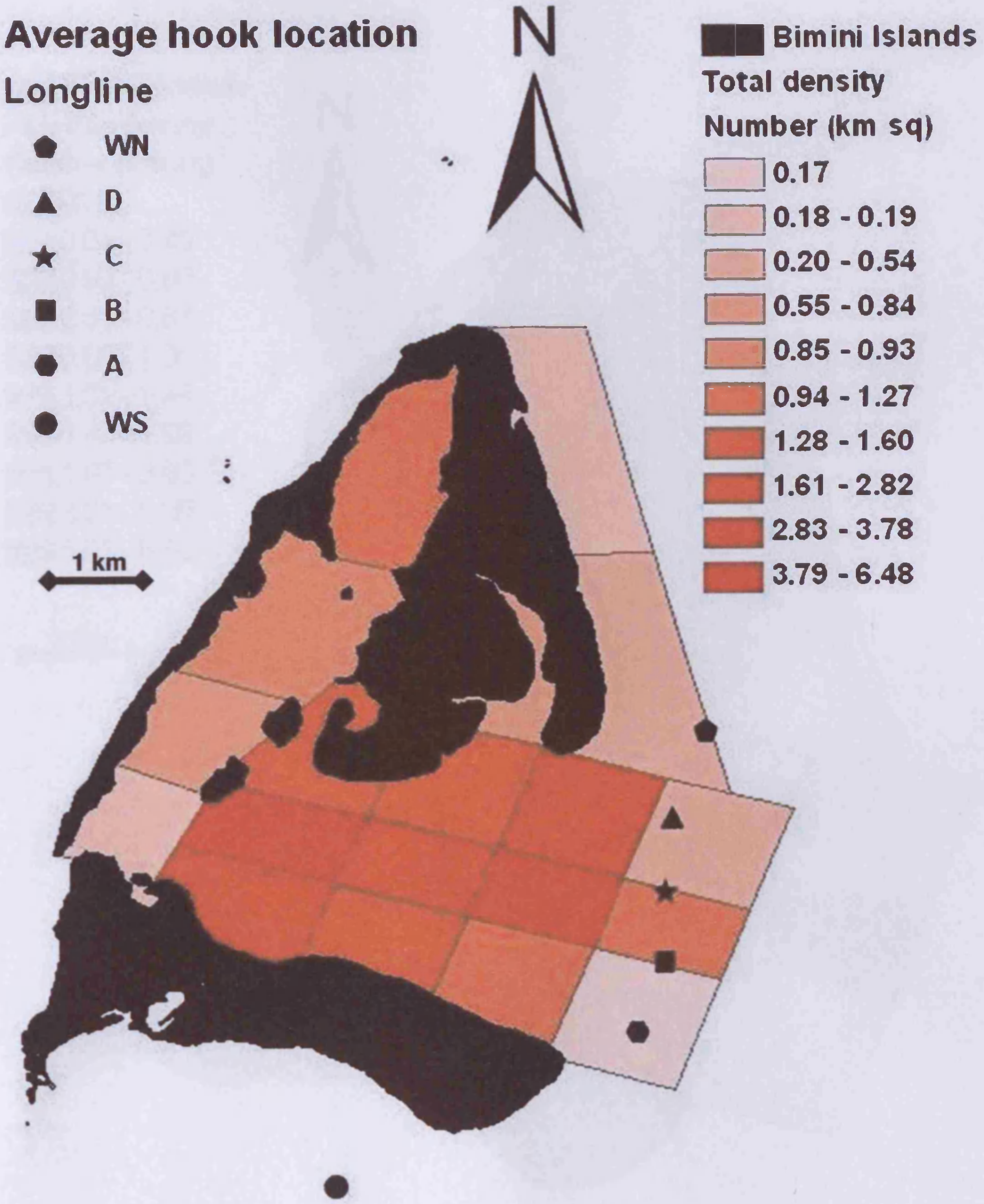


Figure 90. **Longline average hook locations relative to aerial survey data based *N. brevirostris* zone density estimates**

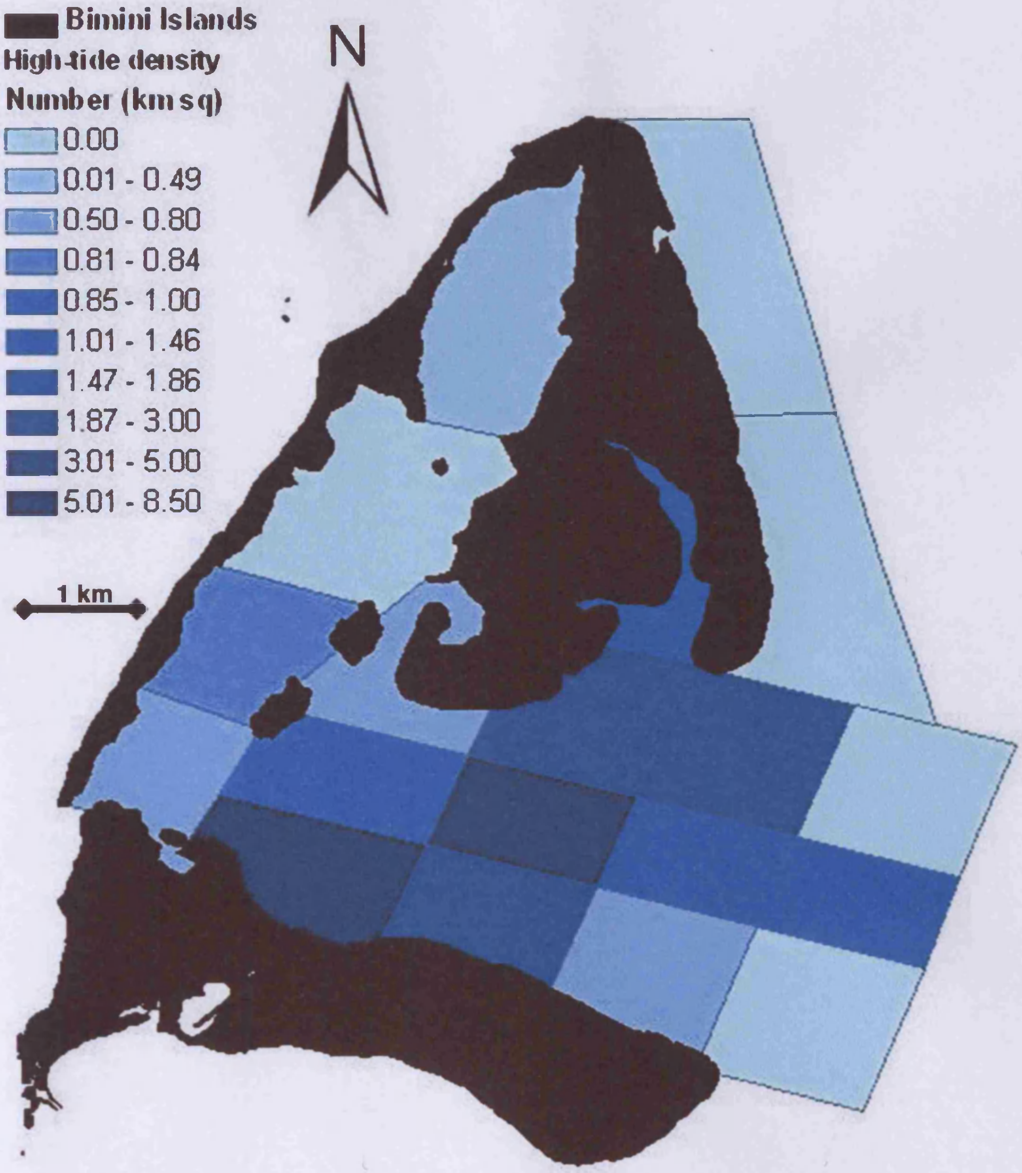


Figure 91. ***N. brevirostris*** **zone density estimates based on data from aerial surveys conducted at high-tide**

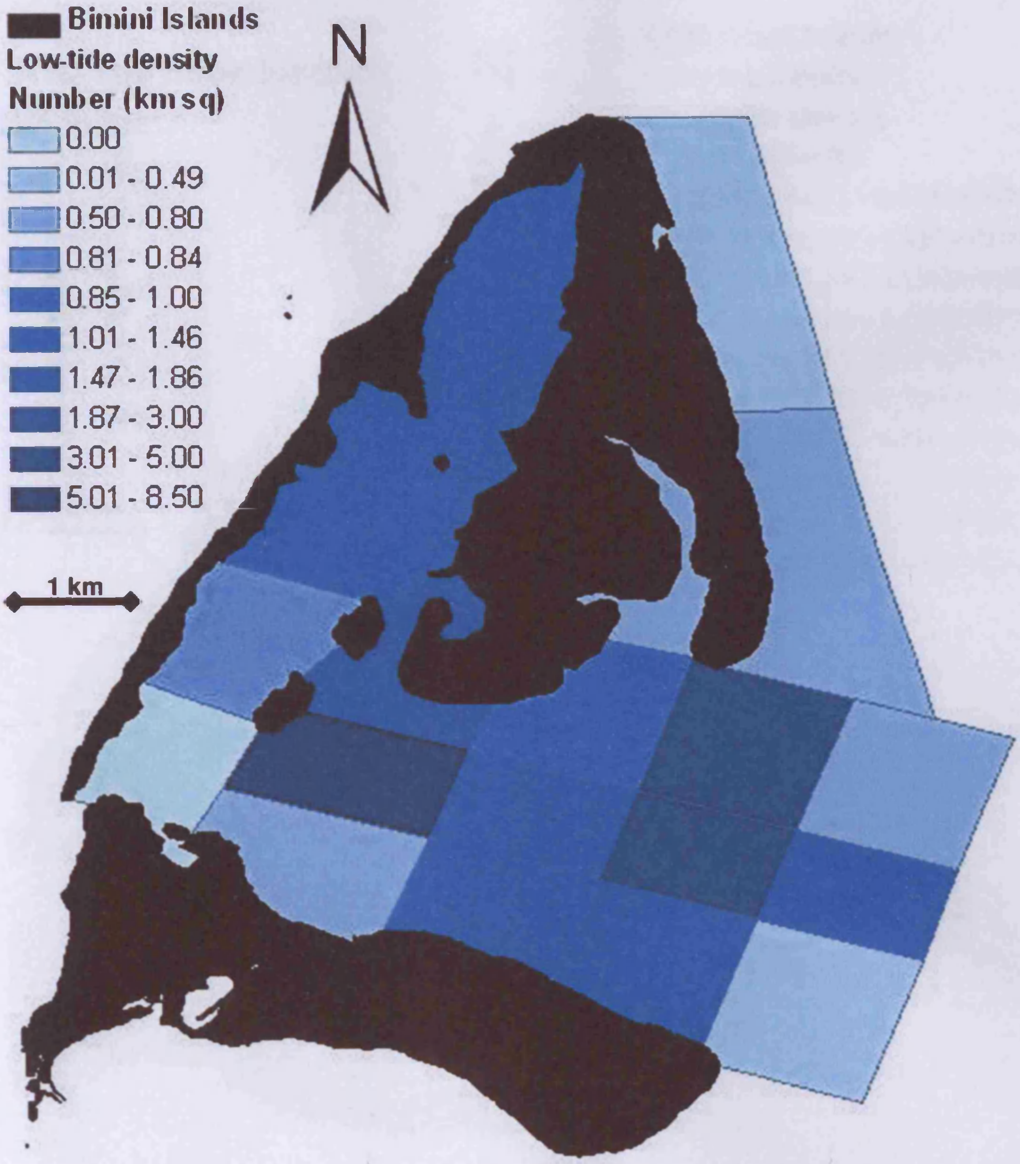


Figure 92. ***N. brevirostris* zone density estimates based on data from aerial surveys conducted at low-tide**

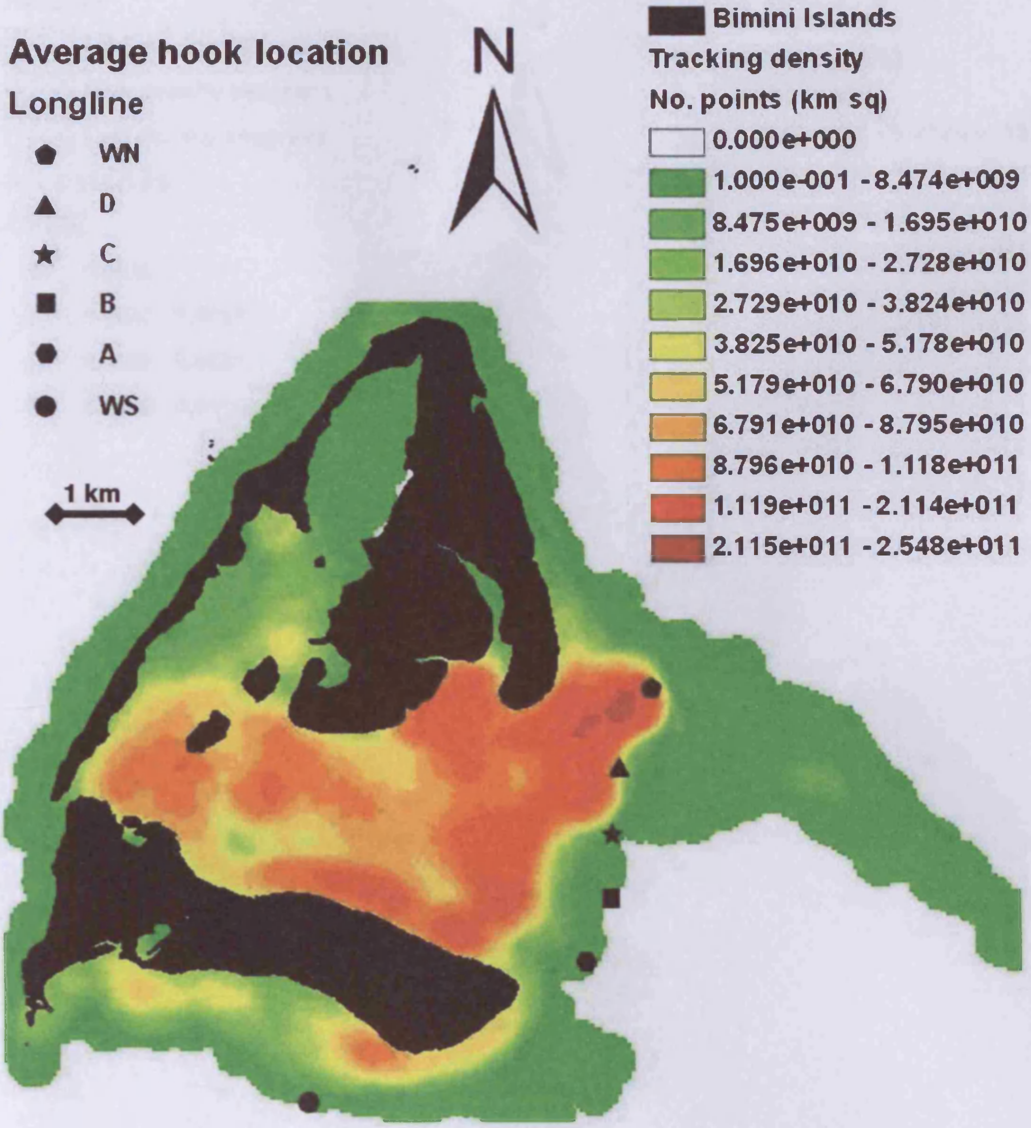


Figure 93. Longline average hook location relative to complete *N. brevirostris* tracking point density plot

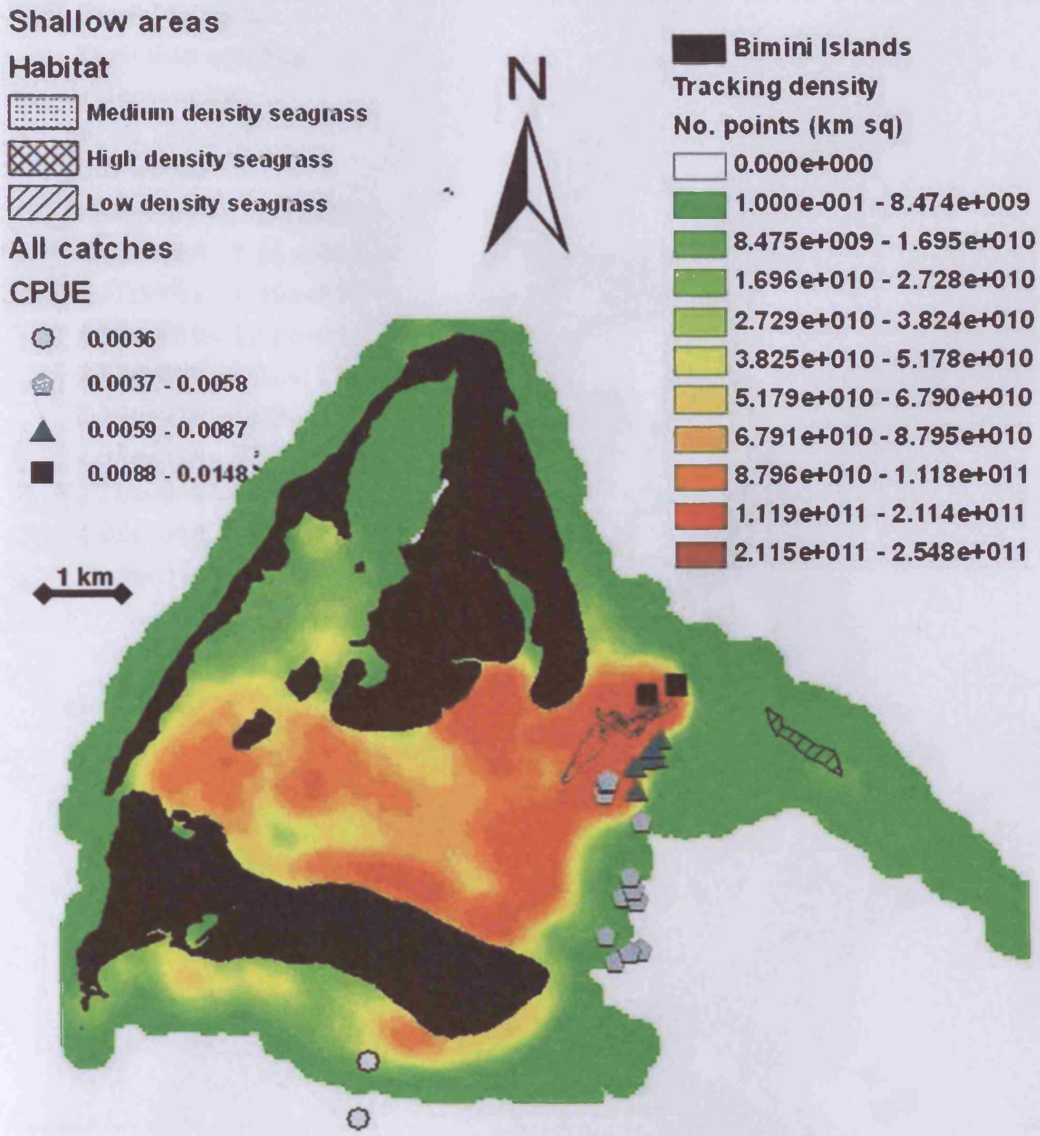


Figure 94. ***N. brevirostris*** **CPUE by specific catch location, and shallow seagrass bed locations (low density = ~50 blades/m^2; medium density = ~75 blades/m^2; high density = ~150 blades/m^2), relative to complete** ***N. brevirostris*** **tracking point density plot**

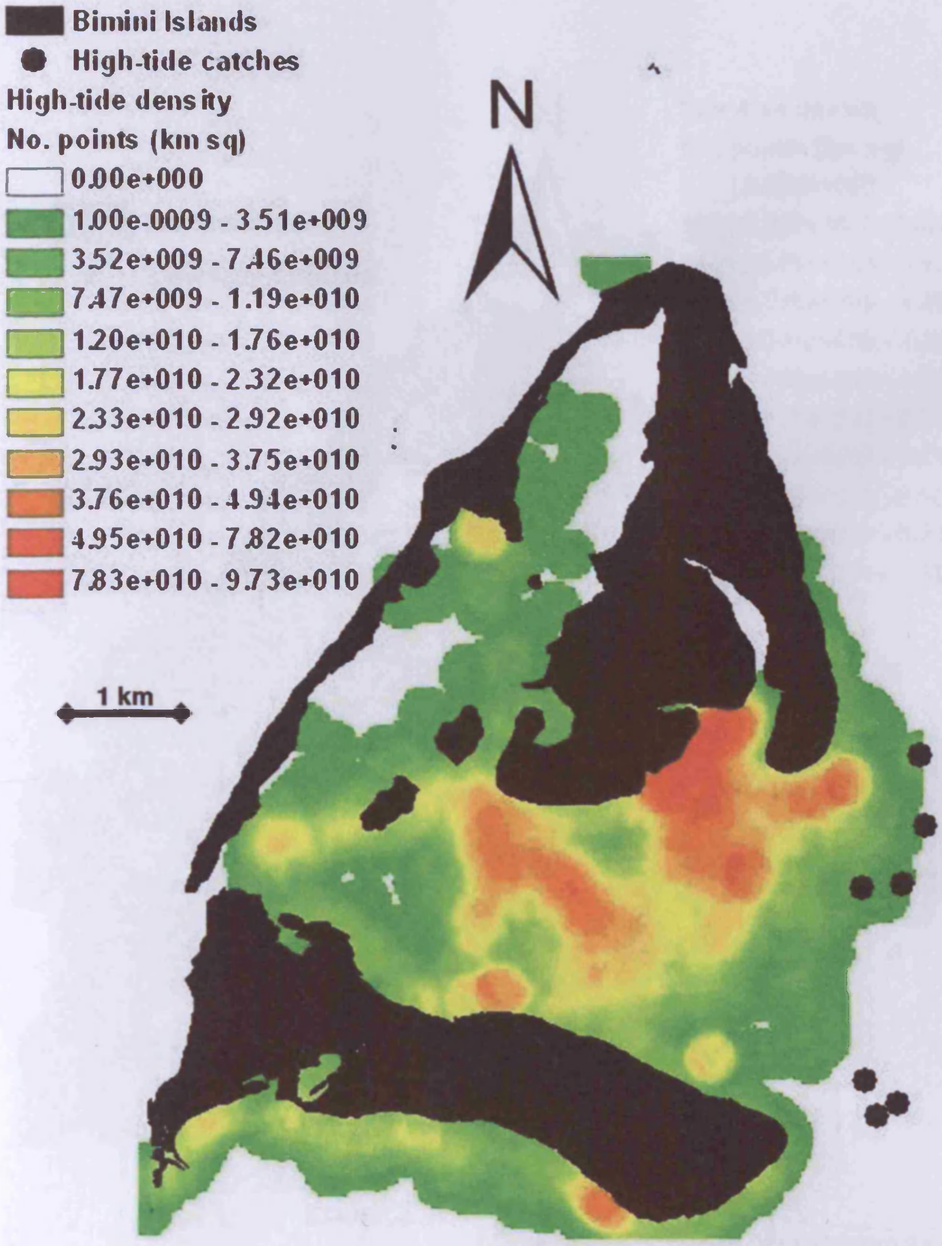


Figure 95. ***N. brevirostris*** **high-tide catch locations relative to high-tide** ***N. brevirostris*** **tracking point density plot**

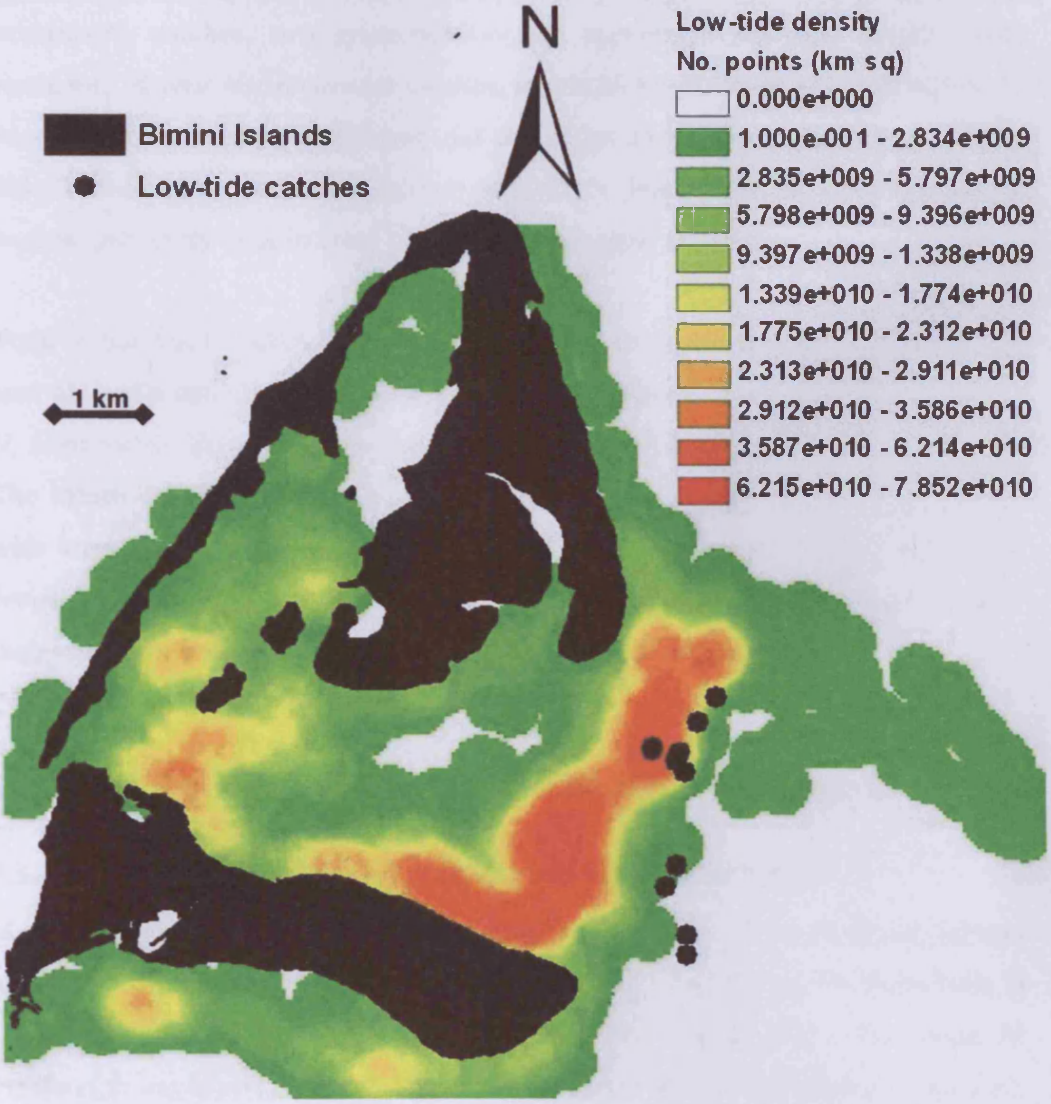


Figure 96. ***N. brevirostris*** **low-tide catch locations relative to low-tide** ***N. brevirostris*** **tracking point density plot**

Of the seven high-tide *N. brevirostris* catches three were distributed to the south of the lagoon mouth, outside of the documented *N. brevirostris* high-tide distribution, and four to the north of the lagoon mouth (Figure 95). The four *N. brevirostris* catches to the north of the lagoon mouth were distributed in relatively similar proximity to the area of higher abundance distribution. Of the 11 low-tide *N. brevirostris* catches, two groupings became apparent. The first to the south, consisting of four *N. brevirostris* catches, two in close proximity to the identified *N. brevirostris* abundance distribution and two in an area of lower abundance (Figure 96). The group to the north consisted of seven *N. brevirostris* catches all occurring in close proximity to or in areas of high *N. brevirostris* abundance.

Total *N. brevirostris* abundance distribution, over all tidal states, showed the broader area utilised within the *N. brevirostris* lagoon population's home-ranges (Figure 94). *N. brevirostris* abundance appeared to be spatially focused in central lagoon area. The identification and plotting of key shallow seagrass beds appeared to coincide with areas of elevated *N. brevirostris* abundance distribution. The plotting of *N. brevirostris* CPUE by specific catch location showed CPUE to increase with increasing proximity to areas of high *N. brevirostris* abundance.

4.3.3. Aerial survey based *N. brevirostris* abundance estimates

4.3.3.1. Monthly *N. brevirostris* abundance estimate variations

N. brevirostris population estimates, based on the results of eight aerial surveys conducted from September 2007 – September 2008, varied from 16 individuals in March 2008 to 88 individuals in September 2008 (Figure 97). The mean *N. brevirostris* abundance estimate for the entire period was 52 individuals (± 9.2 s.e.). When considered by month from September 2007 – July 2008 (Figure 98), population estimates appeared to vary in accordance to mean water temperature. A significant correlation between all eight survey *N. brevirostris* abundance estimates and mean monthly temperature was observed ($r = 0.78$, $n = 8$, $P < 0.05$; Figure 99). However, there was no significant relationship found for monthly CPUE with monthly population estimates ($r = 0.59$, $n = 8$, $P > 0.05$).

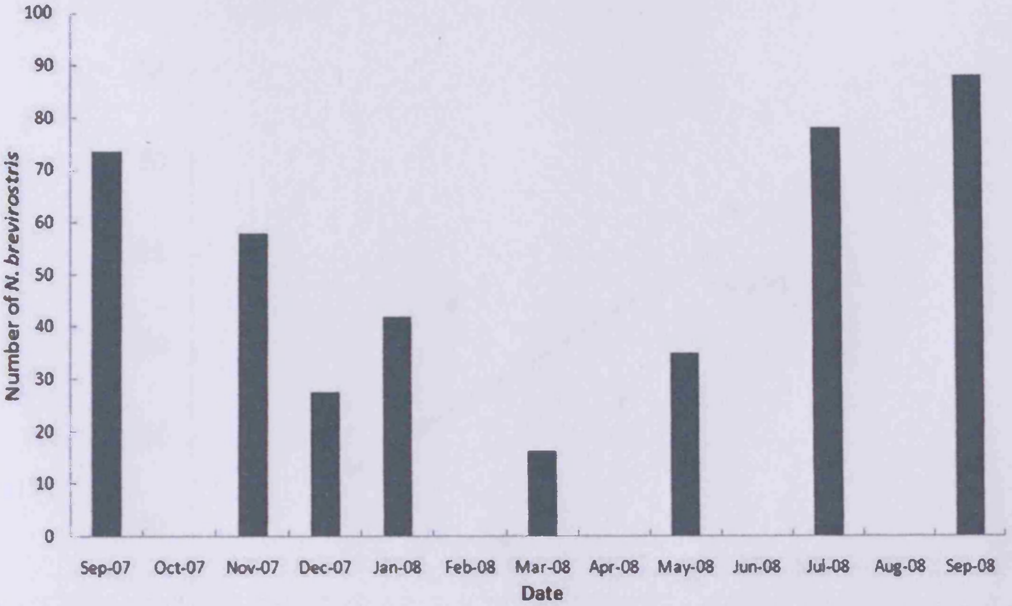


Figure 97. ***N. brevirostris*** **abundance estimates for months aerial surveys were conducted**

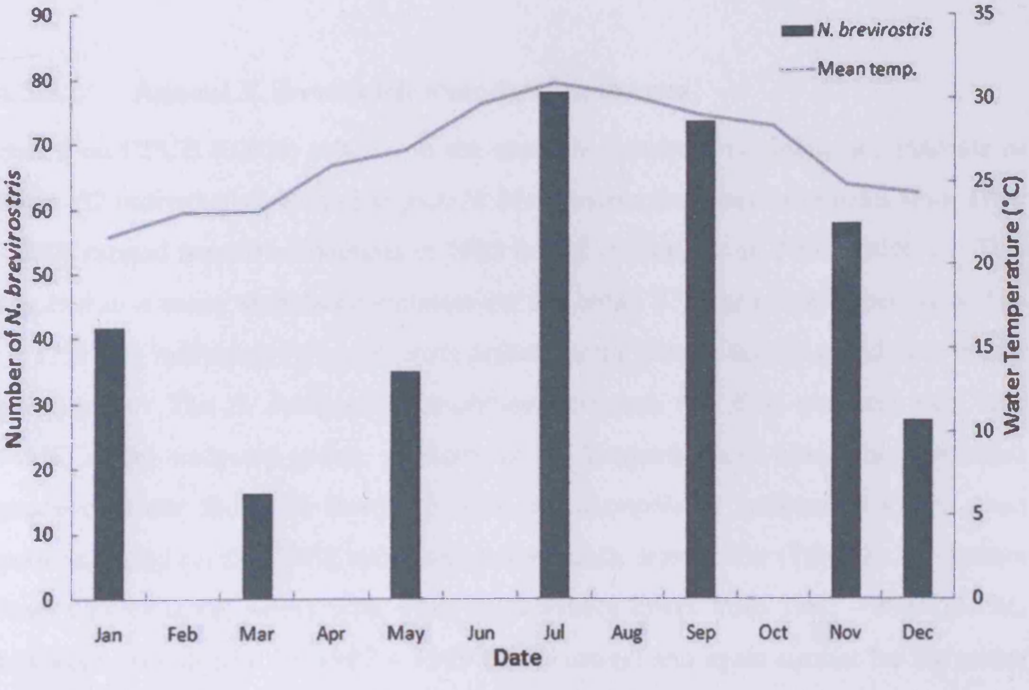


Figure 98. ***N. brevirostris*** **abundance estimates with mean water temperature by month**

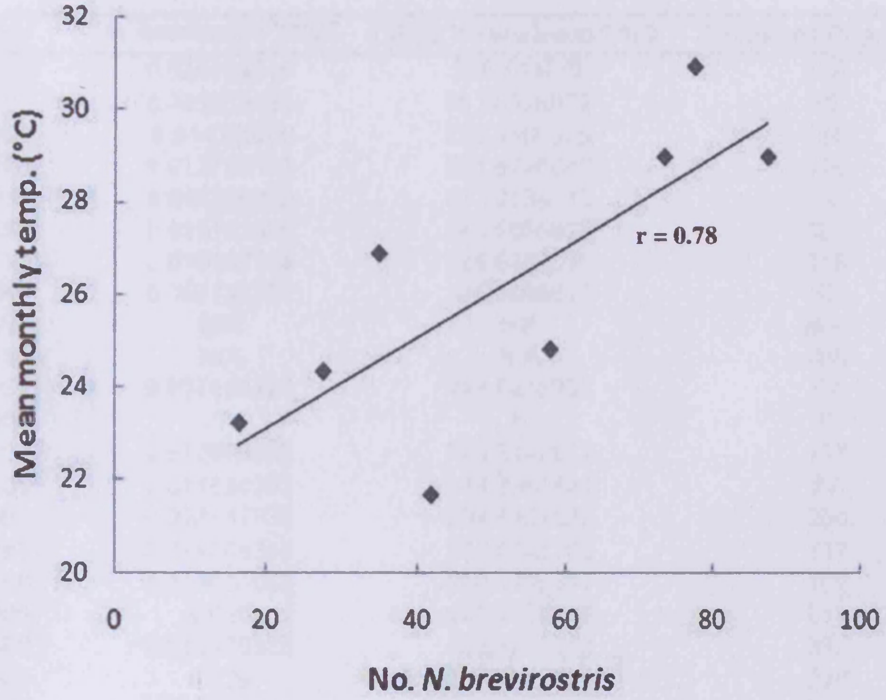


Figure 99. Mean monthly water temperature vs *N. brevirostris* abundance estimate

4.3.3.2. Annual *N. brevirostris* abundance estimates

Based on CPUE (0.006) relative to the mean *N. brevirostris* abundance estimate in 2008 (52 individuals), Bimini lagoon *N. brevirostris* abundance estimates from 1982 - 2008 ranged from 0 individuals in 1993 to 222 individuals in 2000 (Table 7). This resulted in a mean abundance estimate for the entire 27 year research period of 114 (± 12.2 s.e.) individual *N. brevirostris* present in the Bimini lagoon population in any given year. The *N. brevirostris* abundance estimate for 2008 was less than half (46%) of the temporal mean. Relative to the temporal mean abundance estimates produced from the mark-recapture data, all extrapolated estimates for the same periods, based on the CPUE and aerial survey data, were lower (Table 8). Estimates from CPUE/Aerial survey data were considerably lower from 1982 – 1989 (55%), but were very similar for 1982 – 1999 (2.6% lower) and again similar for the entire period from 1982 – 1989 (16% lower).

Table 7. Extrapolated annual *N. brevirostris* abundance estimates based on CPUE

Year	*N. brevirostris* CPUE	CPUE % relative to 2008	Predicted Pop. Est.
1982	0.020454545	328.733778	172
1983	0.005952381	95.66326872	50
1984	0.01474359	236.9505579	124
1985	0.013793103	221.6748848	116
1986	0.005208333	83.70536013	44
1987	0.015151515	243.5065022	127
1988	0.014102564	226.6483597	118
1989	0.007777778	125.0000045	65
1990	N/A	N/A	N/A
1991	N/A	N/A	N/A
1992	0.007407407	119.0476233	62
1993	0	0	0
1994	0.013888889	223.2142937	117
1995	0.011594203	186.3354104	97
1996	0.024537037	394.3452522	206
1997	0.016304348	262.0341708	137
1998	0.018055556	290.1785818	152
1999	0.025	401.7857286	210
2000	0.026470588	425.4201833	222
2001	0.025	401.7857286	210
2002	0.019444444	312.5000112	163
2003	0.01254902	201.6806795	105
2004	0.016140351	259.3985055	136
2005	0.005925926	95.23809864	50
2006	0.005614035	90.22556713	47
2007	0.007333333	117.8571471	62
2008	0.006222222	100	52

Table 8. *N. brevirostris* mark-recapture population estimates relative to aerial survey population estimates

Period	Research years	Mark-recapture pop. est.	Aerial survey pop. est.
1982 - 1989	8	224	102
1982 - 1999	16	115	112
1982 - 2008	24	136	114

4.4. Discussion

4.4.1. Hooking susceptibility

4.4.1.1. Interspecies hooking success

Results indicated that all three species had a similar chance of becoming successfully hooked as the result of a bait attempt. This would imply that for the Bimini longlining campaigns, species CPUE proportions would not have been affected by interspecies variations in bait manipulation behaviour. Similar studies utilising underwater video surveillance to monitor baited hooks (Lokkeborg et al., 1989, Huse and Ferno, 1990) found a considerable effect of bait manipulation over relative hooking success between haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*). With the wide range of bait manipulation described for the target species in this study (Motta et al., 1997, Motta et al., 2008, Wetherbee et al., 1990, Springer, 1961, Moss, 1972, Frazzetta, 1988, Frazzetta, 1994, Frazzetta and Prange, 1987), considerable variation in hooking success was expected. The lack of apparent hooking success variation between species was probably the result of a relatively small dataset for this study. When studying sharks relative to teleosts, the number of expected bait attempts, probable to be captured on video, were considerably less. However it must be noted that relative to the likely number of bait attempts experienced by the longline gear, for the same time period, but with a bait availability increased by a factor of 75, this represented a very low test proportion. Therefore given a larger dataset, any true interspecies variations may have become apparent.

4.4.1.2. Effects of multiple-shark presence on bait attempts and hooking success

For teleost species, video surveillance has revealed fish density can result in increased catchability on baited hooks through social facilitation and resource competition (Davis and Olla, 1992, Olla and Samet, 1974, Ryer and Olla, 1991, Ryer and Olla, 1992, Eklov, 1992). Furthermore, video surveillance by Shardlow (1993) revealed that per capita attacks on trolled lures by salmon increased with abundance. Stoner and Ottmar (Stoner and Ottmar, 2004) demonstrated in laboratory experiments that increased densities of Pacific halibut (*Hippoglossus stenolipus*) resulted in increased per capita bait attack rates, with no overt aggression observed among fish of equal size, and concluded an increased propensity to strike baits in the presence of potential competitors. In this study, the significant increase of bait attempt frequency made by *N. brevirostris*, in response to multiple shark presence up to both 30 and 15 minutes (Table 5), indicated that resource competition reduces caution and drives decisive bait attempts for this species. This would imply that overall hooking success is increased for *N. brevirostris* as bait attempts are the first active stage of the hooking process. However it did not appear that multiple shark presence in turn resulted in increased direct hooking success for *N. brevirostris* when bait attempts were made. The significant reduction in *N. brevirostris* hooking success in response to multiple shark presence 30 minutes prior to bait attempt is curious (Table 6). A reduction in hooking success would be an unlikely product of multiple shark presence, unless it caused rushed snatch attempts at the bait in relation to more definitive unprompted bait manipulation when alone (Stoner and Ottmar, 2004, Motta et al., 1997). However if this was the case, hooking success proportion would be expected to decrease from 30 minute to 15 minutes prior to multiple shark presence. In reality hooking success proportion increased from 30 to 15 minutes, suggesting that more immediate multiple shark presence, and thus increased competition pressure, resulted in higher hooking success.

Though bait attempt frequency was highly significantly increased, no significant influence of multiple shark presence 30 minutes to bait attempt was found for *C. limbatus* hooking success. It is possible that, in these cases, sharks present up to 30 minutes prior may have moved sufficiently away from the target area so as not to present a competition threat, thus no significant influence would have been found. No significant influence of multiple shark presence up to 15 minutes prior to bait attempt was found. However, for bait attempts made within this 15 minute time scale, multiple shark presence would have been likely to exhibit a competition threat (Stoner, 2004). Even if the other individuals had left the target area, the affect of their prior presence on the individual making the bait attempt may not have worn off. Significant influence of multiple shark presence 15 minutes before bait attempt was found for *C. limbatus* (χ^2 = 5.76, d.f. = 1, P < 0.05). This strongly suggests that increased competition from multiple shark presence resulted in increased hooking success for *C. limbatus*. *C. limbatus* are commonly observed in Bimini to display group behaviour, particularly in response to a scent source, and like other *Carcharhinus* species have been documented to show a marked increase in excitement when feeding in numbers (Hobson, 1963), thus *C. limbatus* could be over represented in the Bimini catch records relative to species that exhibit more solitary behaviour (Stoner and Ottmar, 2004, Eklov, 1992, Ryer and Olla, 1991).

G. cirratum showed no significant effect of multiple shark presence on bait attempt frequency or hooking success for both 30 and 15 minute prior time scales. This indicated that social facilitation and resource competition did not affect their feeding behaviour. However, this may be the result of interspecies bait manipulation variations. *G. cirratum* are suction feeders (Motta et al., 2008, Matott et al., 2005, Motta et al., 2002), where as *N. brevirostris* and *C. limbatus* are both ram feeders (Motta et al., 1997, Springer, 1961, Frazzetta, 1988, Frazzetta, 1994, Frazzetta and Prange, 1987, Moss, 1972, Huber et al., 2006). A likely response to resource competition would be to consume the prey item as quickly and as decisively as possible, to guarantee getting the whole meal, and to avoid pursuit from other individuals that may result in leaving any of the prey item exposed in the process of consumption (Stoner, 2004, Stoner and Ottmar, 2004). For ram feeders, such as *N. brevirostris* and *C. limbatus*, this would be achieved by a large jaw gape to engulf the entire piece of bait in one motion (Motta et al., 1997, Frazzetta and Prange, 1987, Moss, 1972). This would usually result in the large 16/0 circle hook contained completely within the mouth cavity and thus increasing the chances of a successful hooking as the gangion is brought under tension (personal observations 2007 - 2008).

For a suction feeder, such as *G. cirratum*, this would be achieved through an increase in suction intensity rather than increased jaw gape (Motta et al., 2008, Matott et al., 2005, Motta et al., 2002). In the case of suction feeding, as the bait enters the mouth, particularly for smaller individuals, there is a high chance that the orientation of the hook may be vertical relative to the jaw. If the hook is longer vertically than the jaw opening this would create pressure between the bait and hook, increased by the increased suction intensity would more likely tear the bait from the hook with the hook still outside of the individual's mouth. This would result in a steal rather than a successful hooking, therefore hooking success would more likely be reduced by this behaviour. Alternatively, *G. cirratum* rely heavily on olfaction for feeding (Demski, 1982, Theiss et al., 2009), whereas *N. brevirostris* and *C. limbatus* tend to rely more on vision (Hobson, 1963, Cohen and Gruber, 1977, Gruber, 1977a, Cohen, 1990, Gruber, 1977b, Gruber, 1982, Kajiura et al., 2003). It is possible that *N. brevirostris* and *C. limbatus* would be more visually aware of surrounding activity than *G. cirratum*, when making a bait attempt; therefore *G. cirratum* would be relatively less influenced by multiple shark presence.

In a review of the effects of fish density over CPUE, Stoner (2004) concluded that fish catchability can be expected to increase with fish density. It would appear from the results of this study that shark catchability can also be expected to increase with shark density, at least for Carcharhinidae species such as *N. brevirostris* and *C. limbatus*. Specific behavioural interactions towards the longline gear only become a variable effecting catch rates when the shark is in close proximity to the longline gear, and therefore is preceded by encounterability as a variable.

4.4.2. Encounterability

Variations in CPUE are driven, at the base level, by species availability to longline gear based on spatial distribution, referred to as 'encounterability' (Stoner, 2004, Ward, 2008, Ward et al., 2004, Engas et al., 1996, Cortes et al., 2008). The following subsections discuss the effect of encounterability to the Bimini longline *N. brevirostris* CPUE.

4.4.2.1. Distribution truthing

Comparison of the results of the aerial survey study (Figures 90 – 92) with the results of the acoustic tracking database (Figures 93 - 96) showed that changes in the distribution of *N. brevirostris* abundance, to and from the central lagoon area, followed a tidally related pattern. The greater proportional reduction of tracking point density relative to the aerial survey estimated *N. brevirostris* abundance density, 94% relative to 73% respectively, is likely to have been the product of the difficulties associated with acoustic tracking in very shallow water. The proportional discontinuity between the two datasets suggested that the aerial survey based tidal abundance distributions were a more accurate representation of *N. brevirostris* density. However both techniques showed a similar pattern, and therefore it was acceptable to compare the more comprehensive tracking data based density plots to the *N. brevirostris* longline catch data.

4.4.2.2. *N. brevirostris* abundance distribution

For the lagoon *N. brevirostris* population density, both abundance estimates and tracking points were found to be highest in the central region (Figures 90 and 93). This was probably the result of predation risk from larger sharks (Sundström et al., 2001, Webster, 2004, Gruber et al., 1988). The central region is the shallowest of the section of the lagoon (personal observations 2002 - 2009), therefore it is the most inaccessible to larger sharks that would pose the greatest risk of predation to the smaller *N. brevirostris* individuals within the population (Webster, 2004). The low-tide abundance distribution shift away from the central lagoon and predominantly to the east (Figures 92 and 96) was probably the result of decreasing water depth. At low-tide much of the central lagoon becomes extremely shallow and in some areas exposed substratum (personal observations 2002 - 2009), becoming unusable for *N. brevirostris*, which are forced into deeper water areas to the west and predominately to the east. *N. brevirostris* will still remain in relatively shallow water as the area to the east would have also reduced in water depth with the falling tide.

Tidal driven movements were logical for this *N. brevirostris* population, as are well documented for sharks inhabiting shallow primary and secondary nurseries in response to predation risk (Carlisle and Starr, 2009, Papastamatiou et al., 2009, Wetherbee et al., 2007, Ortega et al., 2009, Chapman et al., 2009, Franks and Gruber, 2007). It appears that areas of isolated shallow seagrass beds were favoured (Figure 94), probably the result of a combination of increased predator protection, from the shallow areas and slim channels running between them, and the potential increased prey availability provided by the seagrass beds (Valle and Bayle-Sempere, 2009, MacDonald et al., 2009, Kessel, 2004, Jennings et al., 2007, Nagelkerken et al., 2008) and marine life the structural relief attracts (Paramo et al., 2009, Vasquez-Yeomans et al., 2009, Nagelkerken and Faunce, 2008). This theory is supported as the greatest documented excursions away from the central area of the lagoon appeared to be orientated to the most easterly shallow seagrass bed and the direction of the subsequent depth contour in a WNW to ESE orientation.

Catches recorded outside of the defined high-tide *N. brevirostris* home-range were probably the result of olfactory attraction along the odour corridor provided by the longline baits (Figure 95; Hobson, 1963, Tester, 1963). Proportionally increased catches around areas of high *N. brevirostris* abundance displaced to the east at low-tide were likely the result of increased encounterability (Figure 96; Stoner, 2004). Therefore it would appear that *N. brevirostris* longline catches were the result of a combination of both olfactory attraction and incidental encounters. Decreased predator risk in the longline set area at low-tide due to reduced water depths would have increased the potential of encounter by smaller *N. brevirostris* within the lagoon population and thus in turn increased the catchability of these individuals (Webster, 2004, Stoner and Ottmar, 2004).

The identified increase in *N. brevirostris* CPUE, relative to specific catch location (Figure 94), with increasing proximity to areas of high *N. brevirostris* abundance is logical (Stoner and Ottmar, 2004). Not only was there increasing chance of incidental encounter with increasing proximity, but there was also increasing chance of odour corridor detection (Olla and Samet, 1974, Ward, 2008, Tester, 1963, Hobson, 1963). Areas of high *N. brevirostris* abundance may have also signified areas of high prey density, therefore the *N. brevirostris* utilising these areas would likely be seeking a food source (Hobson, 1963, Tester, 1963). When presented with bait at a time of increased feeding motivation, catchability would have increased relative to areas of less utilisation density that may represent times when behaviour was less driven by dietary requirements (Sims et al., 2006a). Also, in contrast to species and life-stages where individuals roam over a large area (Sims et al., 2006b), for the Bimini lagoon *N. brevirostris* that show repeated movement patterns over a relatively small geographical area (Sundström et al., 2001, Gruber et al., 1988), bait presented in an area usually utilised for foraging would appear more natural for consumption relative to bait located in an area usually utilised for other activities such as resting to aid digestion (Sims et al., 2006a). Therefore the bait presented in the foraging area would have had greater fishing power than bait presented in the resting area (Stoner, 2004), carrying bias to the spatial distribution of the observed results.

N. brevirostris catches completely outside of the identified *N. brevirostris* lagoon population home-range (Figure 94) were probably in response to olfactory attraction along the odour corridor, representing motivated movements outside of the *N. brevirostris* natural movement patterns (Sundström et al., 2001, Tester, 1963, Gruber et al., 1988). The limits of the *N. brevirostris* abundance appear driven by predation risk (Sundström et al., 2001, Chapman et al., 2009, Franks and Gruber, 2007, Gruber et al., 1988), therefore predation risk would have increased with increasing longline distance from the normal *N. brevirostris* movement distribution limits. Longlines located in closer proximity to the areas of higher *N. brevirostris* abundance were subject to increased fishing power relative to the other longlines. The significant south to north increase in longline *N. brevirostris* CPUE identified in section 3.3.6 can be largely attributed to increasing longline proximity, from south to north (Figure 93), to areas of high *N. brevirostris* abundance. Collectively the results of this section suggest that for the Bimini lagoon *N. brevirostris* population, the influence of predation risk has considerable effect over catchability, therefore *N. brevirostris* catchability is governed more by longline encounterability in areas of lower predation risk than olfactory attraction. Limited prey availability can greatly increase hunger and lead to increase exposure to predation risk in response to feeding motivation (Stoner, 2004, Lokkeborg et al., 1995, Webster, 2004). The identified pattern between longline encounterability with CPUE would suggest that *N. brevirostris* prey availability was sufficient in the lagoon area to not regularly justify increased exposure to predation risk in response to hunger. Predation risk appears to have been the largest variable driving longline encounterability and therefore fishing power.

4.4.3. Monthly *N. brevirostris* abundance estimate variations

From the aerial survey data based estimates, the lagoon *N. brevirostris* abundance varied between months (Figure 97), with a range of 16 – 88 individuals (mean = 52 ± 9.2 s.e.). A monthly variation in aerial survey abundance results would be logical for a life-stage or species that is known to display large scale seasonal movements (Rowat et al., 2009), but the Bimini lagoon sub-adult *N. brevirostris* have been shown to display year round site attachment (Sundström et al., 2001, Chapman et al., 2009, Gruber et al., 1988). A monthly variation in *N. brevirostris* abundance would partly explain the documented seasonal variation in CPUE (see section 3.3.4), although monthly variations were proportionally different to variation in CPUE and no significant relationship was found between the two. However, a significant relation was found between abundance estimate and mean monthly water temperature ($r = 0.78$, $n = 8$, $P < 0.05$; Figure 99). This suggests that, as documented for other *Carcharhinus* species (Grubbs et al., 2007), water temperature could have been driving seasonal abundance in the Bimini lagoon *N. brevirostris* population.

N. brevirostris temperature preferences may have resulted in seasonal latitudinal migrations, however it is unlikely, based on previously defined home-ranges (Sundström et al., 2001, Gruber et al., 1988, Franks and Gruber, 2007), that the majority of individuals travel far enough at this life-stage to experience a sufficient latitudinal temperature change. Alternatively *N. brevirostris* may have moved to the deeper and warmer waters of the adjacent Gulf Stream, a behaviour exhibited by other ectothermic shark species in response to temperature change (Ortega et al., 2009, Conrath and Musick, 2008). However, this too is an unlikely scenario for the Bimini lagoon *N. brevirostris* as exploratory longline sets conducted on the edge of the Bimini Gulf Stream shelf consistently yielded catches of very large *G. cuvier* (Kessel unpublished 2007 - 2008), a documented predator of smaller elasmobranchs (Lowe et al., 1996). As the defined abundance plots of the Bimini *N. brevirostris* lagoon population showed no such movements to the gulfstream waters, migration to deeper/warmer waters would in this case have been an unlikely response to reduced water temperatures.

A possible explanation for the observed monthly abundance variation was that decreased *N. brevirostris* metabolism in response to decreased water temperatures result in decreased activity (Miklos et al., 2003, Sundstrom and Gruber, 1998, Stoner, 2004, Bigelow et al., 1999, Dowd et al., 2006b, Heupel and Simpfendorfer, 2008, Sims et al., 2006a). *N. brevirostris* individuals were more easily visible when in motion relative to the surrounding habitat (personal observation 2007 - 2008), therefore active individuals were more likely to be recorded during the aerial surveys than resting individuals. In months of lower water temperature the *N. brevirostris* population would have been generally less active (Sims et al., 2006a), therefore less visible, resulting in a larger number of individuals potentially missed through increased perception error by the observers, rather than a true *N. brevirostris* abundance decline (Marsh and Sinclair, 1989). The apparent *N. brevirostris* abundance decline, caused by the increased observer perception error, would have been similarly reflected in the monthly CPUE through reduced dietary requirements in response to temperature lowered *N. brevirostris* metabolisms as discussed in section 2.4.4.5.

It would have been very interesting to compare aerial survey data based *N. brevirostris* abundance estimates with *N. brevirostris* CPUE for the month of February, as no *N. brevirostris* catches were recorded in this month from 2003 – 2008. Unfortunately due to poor weather conditions and limited pilot availability, during February 2008 it was not possible to obtain this data and therefore no comparison could be made

4.4.4. Annual *N. brevirostris* population estimates

Based on CPUE (0.006) relative to the mean *N. brevirostris* abundance estimate in 2008 (52 individuals), annual Bimini lagoon *N. brevirostris* abundance estimates must be considered to have a low level of confidence, as they have been extrapolated from the results of only one out for 25 years (Table 7). For single species analysis, CPUE has been found to be closely proportional to abundance (Richards and Schnute, 1986), but certain driving variables may have greater effect over CPUE than population abundance (Punsly and Nakano, 1992, ArreguinSanchez, 1996, Quinn et al., 1985, Ward, 2008). However the relative standardisation of longline set location and gear set-up throughout the research periods and the similarities to the mark-recapture based abundance estimates (Table 8) indicated a reasonable level of accuracy for these results. The large dissimilarity for the period 1982 – 1989 (55% lower from the aerial survey based estimate) was probably the product of overestimation in the mark-recapture data as the result of scientific sacrifices of captured individuals. This would have reduced the number of tagged *N. brevirostris* available for recapture, thus resulting in a biased overestimation of population size (Simpfendorfer et al., 2000). Once this bias had been diluted by the greater number of records considered in the longer subsequent survey periods, mean abundance estimates based on the mark-recapture data possibly became more accurate. The bias created by the scientific sacrifices explains the large error margins between the aerial survey/CPUE estimates relative to the mark-recapture estimates for the first period from 1982 - 1989. Additionally, the identified *N. brevirostris* diel behaviour variations that may have resulted in underestimates in the 2008 aerial survey based abundance estimates, could have been the cause of the marginally lower temporal abundance estimates relative to the mark-recapture based estimates.

Based on personal observations during tenure at the BBFS from 2002 – 2009 and personal observations made by the director of the BBFS, Dr. Samuel H. Gruber, between 1982 – 2008, the population estimates, extrapolated from the annual CPUE values relative to the 2008 aerial survey based estimates, seem to be reasonable. This indicated that the temporal means produced for comparison to the mark-recapture estimates are probably a good truthing parameter. This would in turn indicate that the latter two mean population estimates from both the mark-recapture and aerial survey data provide a reasonable representation of *N. brevirostris* Bimini lagoon abundance. Therefore, despite the difficulties in providing mark-recapture based abundance estimates in section 3.3.8, the adapted Lincoln-Petersen model provided representative estimates. If the mean annual *N. brevirostris* abundance from 1982 – 2008, based on the mark-recapture data, was estimated as an annual mean of 136, then the aerial survey data based estimated mean for 2008 (52 ± 9.2 s.e.) was considerably less than this (38%). This suggests that the perceived abundance decline, based on CPUE values, from 2000 – 2008 represents a true decline and is not an artefact of active longline gear avoidance by the resident *N. brevirostris* as previously suggested.

4.5. Conclusion

It would appear that for sharks, as previously documented for teleosts (Shardlow, 1993, Stoner and Ottmar, 2004), interspecies behavioural variations significantly influenced longline CPUE. Multiple shark presence significantly altered behaviour towards the longline gear; for *N. brevirostris* bait attempts were significantly increased and *C. limbatus* hooking success was significantly increased, whereas *G. cirratum* displayed no apparent behavioural alterations. This would have resulted in disproportionate interspecies responses to the same variable and therefore different resultant species specific catchability. Catchability governed by multiple shark presence response would be influenced at the base level by species group behaviour, with species that have been shown to exhibit group behaviour, such as *N. brevirostris* (Guttridge et al., 2009a, Gruber et al., 1988), disproportionally susceptible to this influence. Species specific bait manipulations may also have had influence over catchability. It is extremely unlikely therefore, that in relation to these variables, all species display the assumed equal catchability; therefore for a more accurate interpretation of Bimini longline catches it would be necessary to apply species specific weightings. However, considerably more research into shark species specific catchability variation is required before appropriate weightings can be devised.

The truthing, with aerial survey data, of historical *N. brevirostris* tracking data confirmed its validity to assess the influence of encounterability over catchability. Overall abundance distribution results supported the previously stated *N. brevirostris* residence theory, and strongly implied that predation risk has a strong influence over the distribution limits through proximity to water depth based refuges. Predation risk distribution limits were further supported by strong patterns of decreasing *N. brevirostris* CPUE with decreasing longline proximity to abundance distribution as determined in this study. This suggests that predation risk has a strong influence over the Bimini lagoon *N. brevirostris* population dynamics. Longline fishing power, proportional to distance from *N. brevirostris* abundance distribution, should therefore be considered for future Bimini longline data analysis.

Results of the aerial survey estimates suggest that *N. brevirostris* abundance does appear to vary throughout the year, which could explain some of the monthly variations in CPUE. However it must be considered that the monthly variations may be the product of increased observer perception error with decreased *N. brevirostris* activity relative to water temperature. The process of extrapolating historical abundance estimates from CPUE records, relative to aerial survey based data comparisons shows promise, as results were supported by the mark-recapture based estimates. However currently with only one year available for comparison confidence in the estimates are relatively low. Continuation of this research for a minimum of three more years, to triple the available comparison, would provide a better basis for increasing data confidence in application for the extensive Bimini historical longline dataset.

Based on the extrapolated dataset, the apparent temporal abundance decline to a level well below the temporal mean is a cause of great concern. It would be extremely difficult for the *N. brevirostris* population to recover from the identified abundance decline due to the life-history traits identified in section 1.1.3. Recovery would be made additionally difficult due to the reduction in recruitment at the base level as the result of reduced nursery *N. brevirostris* survival rates. This gives further weight to the argument for down-scaling the proposed Bimini Bay Development, to avoid a further reduction in survival rates and in turn assist the Bimini lagoon *N. brevirostris* population recovery before a potential complete population collapse.

5. Adult *Negaprion brevirostris* aggregations off the coast of Jupiter, Florida

5.1. Chapter Introduction

The biggest challenge currently hindering the effective management of elasmobranch stocks is a considerable short fall of available life-history data (Simpfendorfer, 1999, Gruber and Hoenig, 1990, Musick et al., 2000). For many species, including *N. brevirostris*, the lack of life-history data specifically relates to temporal and spatial structure of populations (Cortes, 2004). It is hoped that a proliferation of elasmobranch focused mark-recapture and acoustic telemetry studies in recent years, including the study forming the focus of this Chapter, will fill the lacunae in our understanding of this subject (Cortes, 2004).

The results of Chapters 2 – 4 have provided a comprehensive understanding of the population dynamics of the *N. brevirostris* sub-adult life-stage, at a lagoon based sub-tropical island, but have contributed very little to the understanding of adult *N. brevirostris* life-history. With a substantial existing body of literature, *N. brevirostris* is arguably the most intensively studied of all the shark species, however, the vast majority of this research has focused on the juvenile life-stage (45 to 80 cm PCL; e.g. Ache de Freitas et al., 2009, Barker et al., 1997, Cohen and Gruber, 1977, Cortes and Gruber, 1994, Cortes and Gruber, 1992, Cortes and Gruber, 1990, de Freitas et al., 2009, DeAngelis et al., 2008, Dibattista et al., 2007, Dibattista et al., 2008, Franks and Gruber, 2007, Freitas et al., 2006, Gruber, 1982, Gruber, 1984, Gruber et al., 1985, Guttridge et al., 2009a, Morrissey and Gruber, 1993a, Morrissey and Gruber, 1993b, Newman, 2003, Reeve et al., 2009, Watsky and Gruber, 1990, Wetherbee et al., 1990) and to a much lesser extent the sub-adult life-stage (81 to 165 cm PCL; e.g. Brown and Gruber, 1988, Chapman et al., 2009, Rasmussen and Gruber, 1993, Sundstrom and Gruber, 1998, Sundström et al., 2001). Very little research has focused on *N. brevirostris* adult life-stage (>165 cm PCL; Kessel et al., 2009b), which given the proportion of total *N. brevirostris* life-history it comprises (including the reproductive process), is arguably the most important with respect to management (Gruber and Hoenig, 1990, Kinney and Simpfendorfer, 2009).

Despite the extensive research focused on the immature life-stages, no suitable mature *N. brevirostris* study population had previously been identified. This was until large groups of mature aggregating *N. brevirostris* (up to ~ 100 individuals in an aggregation), off the coast of Jupiter Florida, were reported to the BBFS research group in 2001 by a local sports diver. The aggregations were reported to have occurred consistently over the past two winter seasons from December – April. This provided the first opportunity for a focused research program on wild mature *N. brevirostris* specimens.

Intermittently over the following four winter aggregation seasons, starting in 2002, a pilot study was conducted to assess the feasibility and population suitability for a focused research study. It was concluded that specimens could successfully and reliably be obtained from the aggregation grounds (with hook and line). With the success of the pilot study, a funded focused research program was initiated in January 2007 to build on the long-term Bimini based research for the continued elucidation of the role of the lemon shark (*Negaprion brevirostris*) as a predator in the sub-tropical marine ecosystem. This was to be achieved by the evaluation of the significance of these large recurring winter *N. brevirostris* aggregations, to provide important life-history data for the mature life-stage. The following year, in 2008, several causes for concern arose.

Initially, and most notably, results of a National Marine Fisheries Service (NMFS) Environmental Risk Assessment (ERA) for Large Coastal Shark (LCS) species in the U.S. east coast and Gulf fisheries (Cortes et al., 2008) came to light. Results of a species ranking showed *N. brevirostris* to be by far the most 'vulnerable' of all the LCS species. 'Vulnerability' was the product of 'productivity' (not relatively low for *N. brevirostris*; Cortes et al., 2008) and 'susceptibility'. In turn, 'susceptibility' was considered a product of 'availability', 'encounterability' (shown to be of high influence over CPUE for *N. brevirostris* in Chapter 4), 'selectivity' and 'post capture-mortality'. For *N. brevirostris* all four elements of susceptibility yielded relatively high values, compared to other species (Cortes et al., 2008), thus *N. brevirostris* emerged in the ERA as 'most vulnerable'. The results of the NMFS ERA for LCS species initiated a new analysis of the data collected in the Jupiter *N. brevirostris* shark study, and an active assessment of the direct factors influencing the vulnerability of the winter aggregating *N. brevirostris* population in the Jupiter area (26°55 N, 80°06 W). This course of investigation served to increase the direct threat awareness that may have been previously overlooked.

As the result of extensive meetings with local commercial fishermen, NMFS and Florida Fish and Wildlife Commission (FWC) representatives, it became apparent that in addition to large scale pressures highlighted by the NMFS ERA, a number of local factors were a great cause for concern. Shark fishing size limits were not species specific, with a standard minimum size limit of 54". Therefore *N. brevirostris* could be harvested before ever having reached maturity (at ~ 82") and contributing to the breeding population. Changes to state and federal fishing regulations, particularly in reference to recent restrictions over *C. plumbeus*, snapper and grouper, have lead many Florida based commercial fishermen to re-rig there gears to target sharks (personal communication Capt. Mike Newman and Jupiter based commercial fishermen at FWC public shark workshop 2009). This was the result of the fact that sharks are one of the few items left on their permits that were still profitable targets. A combination of low bag limits and finning regulations (e.g. where-by since 2002 sharks have to be landed whole with fins attached leading to problems with handling and storage; NOAA/NMFS, 2006), make sharks unfavourable targets for large commercial vessels. Large commercial vessels usually target more pelagic sharks such as *Prionace glauca* (blue shark), which were found to be least vulnerable by the ERA (Cortes et al., 2008). The regulations however still left sharks as an extremely attractive option for smaller shore-based commercial vessels. The smaller vessels can make short trips out from port and reach their quotas quickly, with captured sharks stored on deck, meaning no storage problems in keeping them whole until they are landed at the dock the same day. Many of these shore based vessels operate out of the Jupiter and St Lucy inlets, on, and in close proximity to, the aggregation grounds respectively (personal communications Capt. Mike Newman and David FWC biologist McGowan 2009) .

The small shore based commercial vessels traditionally targeted the plentiful *Carcharhinus plumbeus* (sandbar sharks) on the edge of the continental shelf (Anderson, 1990, Anderson et al., 1985, NMFS, 1999, NOAA, 1995, NOAA/NMFS, 2006, Pratt et al., 1990). However, the prohibition of *C. plumbeus* and changes to the bag limits, from weight to heads, made small shark species unfavourable relative to the larger *N. brevirostris* and *C. leucas* located further inshore. Additionally escalating fuel prices over past years made inshore sets more favourable as they require less time under power, resulting in increase commercial targeting in the shallow coastal waters (20 – 30 m), where the winter *N. brevirostris* aggregations occur (personal communications Capt. Mike Newman 2009). Of most concern however was the confirmation that commercial fishermen, both in the Florida Keys out of the Stock Island fishery and locally in the Palm Beach County area, were specifically targeting *N. brevirostris* (personal communication Capt. Mike Newman and Jupiter based commercial fishermen at FWC public shark workshop 2009). *N. brevirostris* are attractive to the commercial fishermen due to their large size at maturity. Also, of the un-prohibited species (see Appendix 1) left on the fishing permits, *N. brevirostris* are considered to have one of the 'best meats' fetching a relatively high price at market, and they have a good fin:body ratio with the fins fetching high prices for the Asian shark fin soup market (personal communication Capt. Mike Newman and FWC biologist Dave McGowan 2009).

The final and most alarming revelation was that the local commercial shark fishermen were fully aware of the Jupiter winter *N. brevirostris* aggregations and were planning to directly target them in the 2010 season (personal communications Jupiter commercial fishermen 2009). The local commercial shark fishermen had been made aware of the *N. brevirostris* aggregations as the result of extensive advertising by the local dive shops for 'lemon shark aggregations dives' (Handwerk, 2005, Deep6, 2009, CDC, 2009). The potentially catastrophic effects of direct fisheries targeting of teleosts breeding aggregations are well documented (Pears et al., 2007, Graham et al., 2008, Lindeman et al., 1998). In the case of the *N. brevirostris* aggregations, effects would likely be magnified by the *N. brevirostris* life-history traits detailed in section 1.1.3.

Fortunately, following the increased awareness of the above issues, a potential avenue for preventative action became available. In April 2008, FWC announced they were in the process of reviewing their shark management protocols with the intention to move towards more stringent shark fishing state regulations (FWC, 2009c). In light of this new information the BBFS research group directly contacted FWC representatives to relay findings and concern in relation to the heightened threat to the north-western Atlantic *N. brevirostris* population, and specifically the Jupiter winter *N. brevirostris* aggregations. In response, FWC invited the BBFS research group to provide them with data based results to justify the potential of specific species based management protocols being implemented within the Florida state-wide shark management protocols. The aim of this study was to provide important *N. brevirostris* life-history data, with particular attention to aggregating behaviour, movements and migrations, in order to facilitate effective, educated and necessary recommendations for future FWC shark management decisions. This aim was achieved by genetic sampling and analysis to further reveal the structure of the north-western Atlantic *N. brevirostris* population, external tagging under the NMFS Cooperative Shark Tagging Program (CSTP), passive tracking with the Vemco® acoustic system and the attachment of short and long-term pop-off archival satellite tags, to collectively reveal large scale movements/migrations away from the aggregation grounds, and environmental sampling to reveal potential presence/ absence cues.

5.2. Methodologies

5.2.1. Fishing technique

The first and arguably most important question to be answered was 'are the Jupiter *N. brevirostris* obtainable for research purposes?' Initial attempts to catch specimens with rod, reel and baited hook yielded promising results, and suggested that rod and reel was a suitable technique for obtaining specimens. However, when sharks were required for implantation of acoustic transmitters the effectiveness of the rod and reel fishing decreased without logical explanation. A number of other techniques were discussed and tested, including attempts to directly feed the aggregating *N. brevirostris* baited hooks on scuba, but all techniques yielded less than satisfactory results. Following a referral, a new technique called 'polyball fishing' was adopted. Described and executed by Capt. Mike Newman, polyball fishing is the favoured technique employed by local commercial shark fishermen (personal communication Capt. Mike Newman 2007). Each rig consisted of an inflatable 'polyball' surface float with a twisted nylon drop-line, tipped with a single baited gangion. The gangion consisted of a 4 m section of 400 lb test monofilament connected to a 3 m section of 1/16 stainless steel aircraft cable leader and tipped with an 18/0 circle hook. At the monofilament end, the gangion is tipped with a 'Flemish Eye' to allow the gangion to be easily detached and changed by a tuna clip. Bait was freshly speared great barracuda (*Sphyraena barracuda*) steaks of ~25 cm cross width. Between two and six rigs were deployed each session in a linear formation with ~50 m separation perpendicular to the direction of current. The baits were set to drift ~3 m above the seabed, with drop-line length set based upon on-board depth finder readings. Rigs were checked for sharks every 30 minutes or when physically pulled out of formation. If a shark became successfully hooked, it was pulled up to the surface by hand and processed.

5.2.2. Shark processing

Shark processing was conducted in accordance to the methodologies described in section 3.2.3, with the following additions. Dependant on the behaviour of the animal, a wooden oar, wrapped in old t-shirts and bound together with duct tape, was inserted into the mouth. When the sharks bit down they would generally hold on, which would tend to have a pacifying effect and allowed the work-up process to be conducted more efficiently and safely. All mature *N. brevirostris*, unless showing signs of high stress at time of capture, were issued with a Vemco® V16H acoustic coded transmitter of 3 – 7 years battery life. Transmitters were programmed to produce an acoustic uniquely coded signal every 3 – 5 minutes. Initially in the tracking feasibility tests, the transmitters were attached externally using stainless steel M-type darts (Holland et al., 1999, Holland et al., 1990, Holts and Bedford, 1993). From 2006 onwards transmitters were internally implanted as it has been shown that internal implantation results in greatly increased long-term host retention (Holland et al., 1999). The transmitter was implanted by securing the shark to the side of the vessel and then inverting the shark to place it into tonic immobility (Watsky and Gruber, 1990, Holland et al., 1999). A small incision, ~3 cm in length, was made into the peritoneal cavity, slightly anterior of the outer edge of the far side pelvic fin. The transmitter was inserted and then the incision was close with a single centrally placed suture (Holland et al., 1999, Carlisle and Starr, 2009).

5.2.3. Acoustic fishing

'Acoustic fishing' was conducted to assess the potential presence of previously tagged sharks during fishing efforts. A Vemco VR2W acoustic monitor was suspended over the side of the fishing vessel. If any *N. brevirostris* previously caught and issued with an acoustic transmitter were present during fishing efforts, but not captured on the fishing gear, the transmitter ID was recorded on the monitor. On returning to the research base after the day's fishing effort was complete, the monitor data was downloaded to reveal the number of individual ID codes from previously acoustically tagged *N. brevirostris* that were present, but not captured.

5.2.4. Acoustic monitor range assessment

Acoustic monitor systems utilised in the marine environment do not have a constant detection range, with a number of factors influencing the detection range, including water depth, temperature, turbidity and background noise (Vemco, 2008). Three 'sentinel transmitters' were deployed, at fixed distances from the MGE and MGW receivers, to assess acoustic monitor detection range variation. The MG monitor sights were selected for range assessment as they have been found to receive the highest level of *N. brevirostris* activity, defined by both transmitter detections and diver observations. The MG site is also around average depth (30 m) relative to the other monitor sites within the array. The sentinel transmitters were programmed to transmit a uniquely coded signal twice every hour. The MGE and MGW monitor locations were separated by 300 m, thus it was possible to position the three sentinel tags linearly to produce four distance intervals, 150 m, 300 m, 600 m and 900m, from the two monitors (Figure 100). Range, up to the maximum displacement of the sentinel tags, based code detection could be determined from the monitor records following each download.

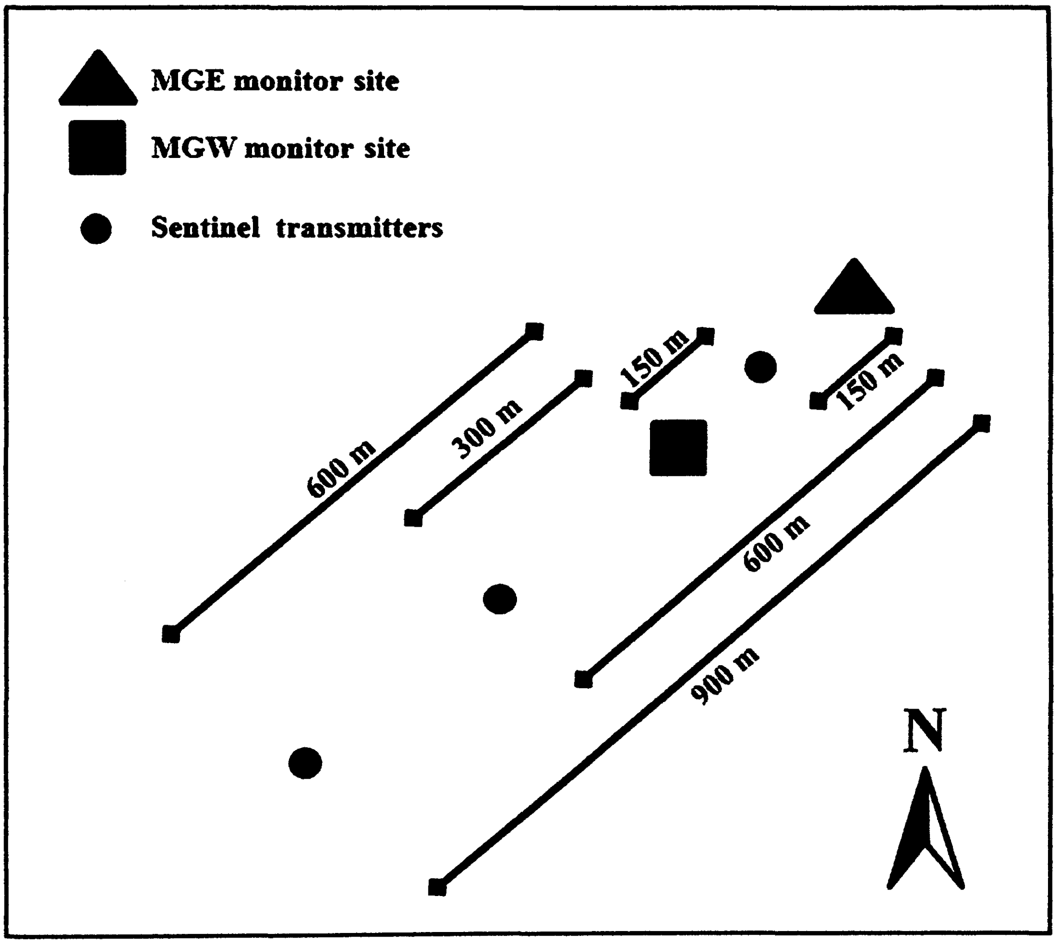


Figure 100. Positioning of sentinel transmitters relative to MG111 monitor sites, lines represent distance intervals from sentinel transmitters to acoustic monitor, above for the MGE site and below for the MGW site

5.2.5. Bimini Biological Field Station (BBFS) acoustic monitor array

Over a two year period from 2007 - 2008, an 18 station acoustic monitoring array was established between the coast of Delray Beach (26°28 N, 80°02 W) and Hobe Sound (27°03 N, 80°02 W) spanning a total of 65 km (Figure 101). The array incorporated two inlets, Palm Beach and Jupiter, with site locations based upon day-light diver sightings of *N. brevirostris* aggregations, and likely paths between them. Sites were predominantly located on the 30 m reef-line and artificial reefs of the region. A combination of Vemco VR2 Mk1/Mk2 and VR2W receivers were utilised with a steady and ongoing upgrade programme in place, moving towards complete VR2W utilisation. Moorings for the monitors varied dependant on location, depth and substratum. The most commonly utilised method was a sunken auger anchor and a stainless steel rig suspended by a hard plastic float. The monitor was centrally mounted on a bracket and ¼" nominal stainless-steel cable was used above to the float and below to the auger anchor. The bracket itself was dependent on the Vemco model at each station, but all were stainless steel with eye for d-rings at each end, and formed the link between the upper and lower sections of the mooring. When a acoustically tagged *N. brevirostris* was in acoustic range of a monitor site during an acoustic coded transmission, the acoustic monitor would store the date, time and unique ID code of the transmitter on an internal hard-drive. Monitors had a 13 month battery life and were downloaded three times a year, with batteries changed annually.

5.2.6. Florida Atlantic Coast Telemetry (FACT) array group

The FACT array group is a collaboration of smaller research groups, including BBFS, FWC, NOAA, University of Florida, Florida International University, the Loxahatchee River District, and Dynamac Corporation at Cape Canaveral, all utilising Vemco acoustic systems to track different marine species off the Florida Atlantic coast. The group met twice annually to discuss collective monitor site positioning to achieve expanded, comprehensive and efficient acoustic coverage of the southeast Florida near shore marine areas. A data sharing agreement was put in place to provide each research group with detections of their specific study

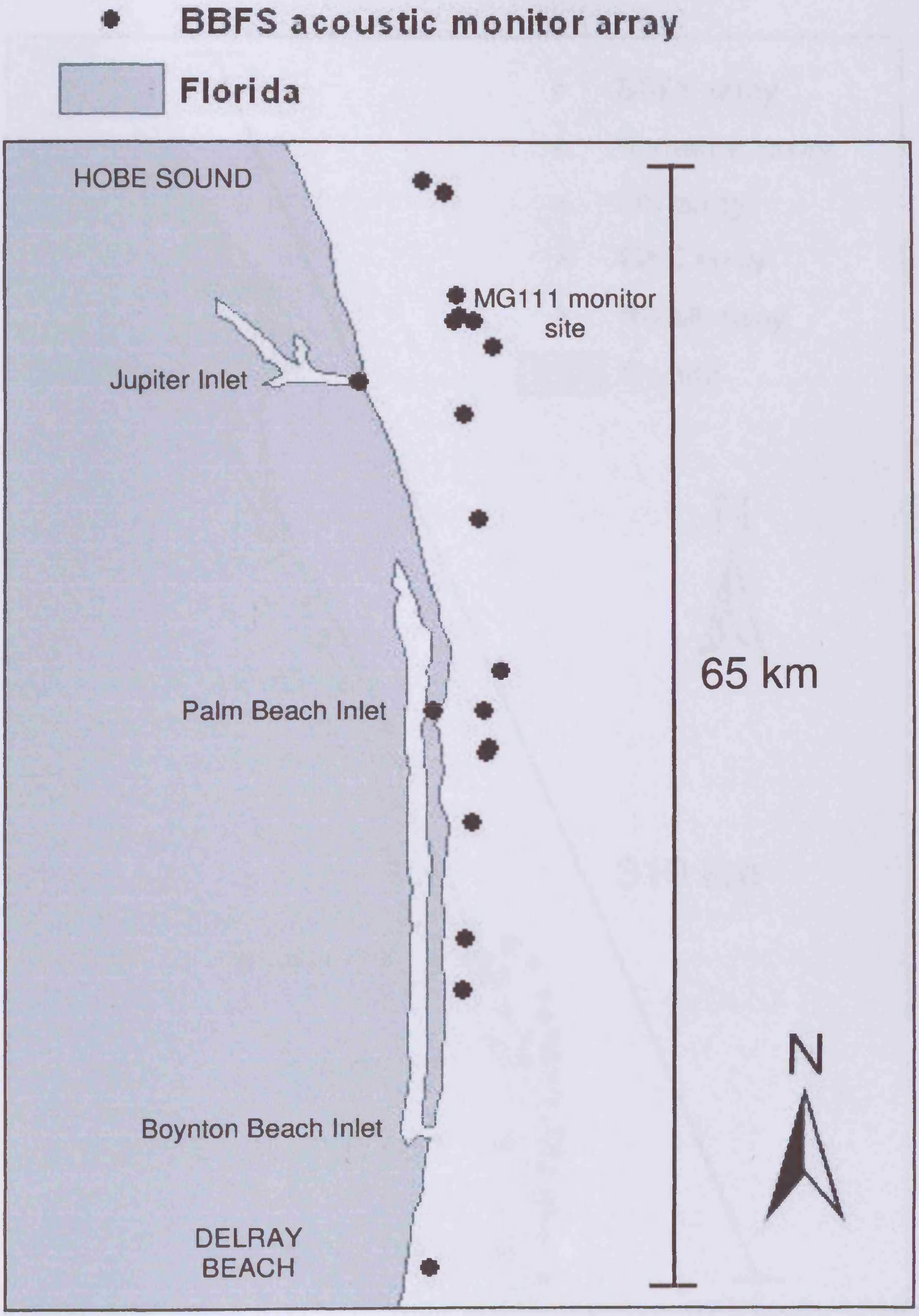


Figure 101. Extent of BBFS dedicated *N. brevirostris* acoustic monitor array

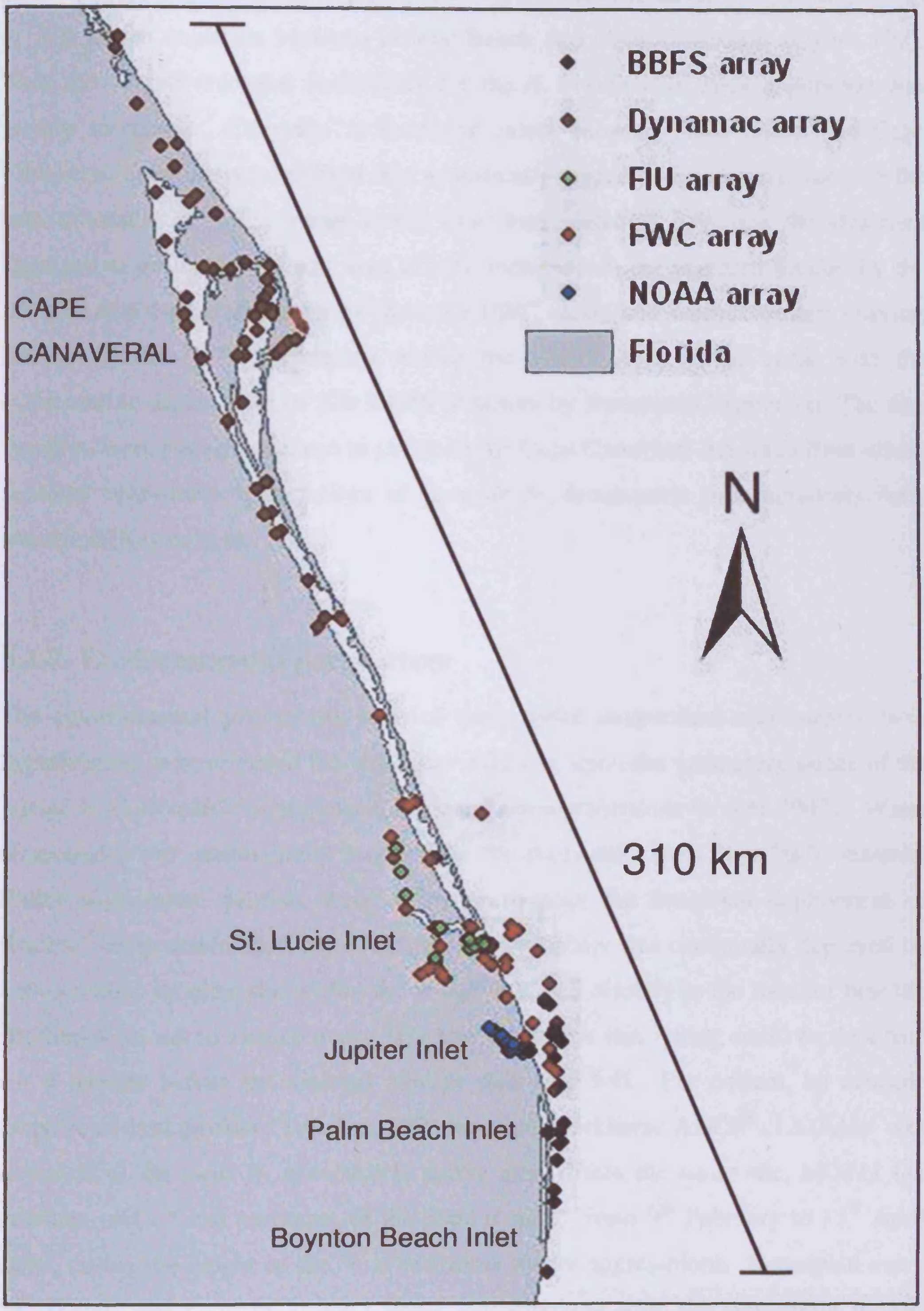


Figure 102. Full extent of expanded acoustic monitor coverage achieved by FACT array group collaboration

population across the entire extent of their movements within the expanded array area. Collectively the group deployed 165 Vemco acoustic monitors spanning a total of 310 km of coastline between Delray Beach and Cape Canaveral (Figure 102). Thus the overall detection availability for the *N. brevirostris* study population was greatly increased. Coverage included all inlets between Palm Beach and Cape Canaveral, therefore any incident of a acoustically tagged *N. brevirostris* entering the Inter-coastal Waterway system would have been detected. Around the identified aggregation grounds coverage was greatly increased in the northern section by the addition of a further 29 monitors from the FWC snook and snapper project (Taylor, 2007). Direct BBFS expansion within the FACT array group came with the collaborative deployment of five BBFS monitors by Dynamac Corporation. The five monitors were positioned close to shore on the Cape Canaveral Air-force Base where seasonal near-shore aggregations of juvenile *N. brevirostris* had previously been identified (Reyier et al., 2008).

5.2.7. Environmental parameters

The environmental parameters profiled were water temperature and current, both hypothesised to have posed the strongest influence upon the presence/absence of the winter *N. brevirostris* aggregation (personal communications Gruber 2007). Water temperature was continuously profiled for the study area from May 2007 onwards. Water temperature profiles were achieved through the rotational deployment of iButton® temperature profilers. A temperature profiler was continually deployed on each acoustic monitor site within the array, mounted directly to the monitor bracket. iButtons were set to sample every 100 minutes and at this setting could be deployed for 4 months before the internal storage disk was full. For current, an acoustic Doppler current profiler 'Teledyne RDI Sentinel Workhorse ADCP®, 1200kHz' was deployed at the most *N. brevirostris* active area within the study site, MG111 (an artificial reef ~5 km northeast of the Jupiter inlet), from 9th February to 11th April 2008, during the height of the *N. brevirostris* winter aggregations. It sampled every 24 seconds and recorded current speed and direction from the substratum to sea-surface.

5.2.8. Large scale movements and migration

Large scale movements and migrations were recorded through a combination of methods and media described in the following subsections.

5.2.8.1. National Marine Fisheries Service (NMFS) - Cooperative Shark Tagging Program (CSTP)

The historical *N. brevirostris* NMFS CSTP mark-recapture Atlas (Kohler et al., 1998) was referenced to defined current documentation of *N. brevirostris* large scale movements and migration. NMFS M-type dart tags issued to *N. brevirostris* during the fishing efforts on the Jupiter aggregation grounds yielded displaced mark-recapture data through the CSTP. Additionally NMFS tags issued by other CSTP members provided origin information for a number of *N. brevirostris* captured during the fishing efforts on the Jupiter aggregation grounds.

5.2.8.2. Acoustic transmitter returns

Internal transmitters were painted bright orange for easy visual detection, and marked with the word 'REWARD' along with contact information, prior to *N. brevirostris* implantation. Post capture discoveries of internal transmitters by fishermen prompted the reporting of recapture locations revealing large-scale movements.

5.2.8.3. Atlantic Coast Telemetry (ACT) array group

The ACT array group operates as an excel spreadsheet list circulated between research groups utilising Vemco acoustic systems to track different marine species off the U.S. Atlantic coast. The list consists of each group member's personal and deployed transmitter details. If multiple detections of an unidentified transmitter are discovered upon download of a monitor, the transmitter ID can be cross referenced with the list to reveal the identity of the owner. The transmitter owner can then be contacted to be informed of their tag detection on another members monitor. Through a combination of contact from ACT list members, and active contact of other list members, to prompt cross reference of their dataset with the BBFS *N.*

brevirostris ID codes, a number of large scale *N. brevirostris* movements and migrations were revealed.

5.2.8.4. Pop-off archival satellite tags

A combination of two Microwave Telemetry PTT-100® and six Wildlife Computer MK10® pop-off archival satellite tags were utilised in an attempt to document larger scale movements by *N. brevirostris* away from the aggregation grounds following the winter period. From observations of penned *N. brevirostris* with previously externally attached telemetry equipment, it was noted that the individuals would often role and scrape them on the substratum (Sundstrom and Gruber, 2002), occasionally resulting in dislodgement. Also free trailing apparatus were found to cause bad skin abrasions on *N. brevirostris* within a few weeks of attachment (Sundstrom and Gruber, 2002). Therefore the decision was made to develop an attachment method that would not only protect the tag from scraping, thus reducing the chance of a premature detachment, but also prevent the tag from rubbing on the body of the shark.

Initially a wire loop method was used to attach a short-term (10-day) PTT-100 on a mature male *N. brevirostris* on the 25th February 2008. It consisted of two hard steel wire loops to hold the tag against the dorsal fin. Incisions were made through the first dorsal initially using a 4 mm gauge needle. The wire was passed through the needle for easy passage and the needle was removed. Either side of the fin crimps and plastic washers were used to hold the loops in place, with around 5 mm of freedom left either side of the fin. Following the release of the satellite tag it was envisaged that the steel wire would rust through, releasing the apparatus from the fin. Once attached the satellite tag was positioned against the fin, protecting the tag from being scraped off and eliminate abrasion caused by rubbing. Additionally, restricting movement of the tag could have reduced attention from other fish that has led to damage from biting in the past (personal observations 2007 – 2009). The first tag attached by this method to the mature male *N. brevirostris* (PCL = 187 cm) successfully detached on the intended date, suggesting this idea had promise for further development.

In an advancement of this design, a single 6 cm long PVC tube replaced the two wire loops. The sleeve was grooved at each end to allow for the two wire attachment points. These were 1/16" steel cable coated in heat shrink plastic to prolong durability. The sleeve was slotted over the MK10 tag prior to attachment to the shark. The plastic anchor dart provided was replaced by two umbrella darts, attached to the release pin by a single piece of 400 lb mono separated and secured by a single crimp near the pin. The rationale for the double dart anchor was, if one was broken then the second would prevent the tag from detaching and surfacing prematurely. One final addition was to secure a cable-tie to the tag below the light sensor and cover the whole tag and sleeve, bar all sensors, in anti-fouling paint. The cable-tie was to act as a fail-safe in case the sleeve should somehow come loose and otherwise slide up to cover the light sensor. The attachment protocol remained identical to the wire loop except for the following points. First the shorter anchor dart was applied, then the longer one slight anterior of the first. The wire attachment points were then marked with a scalpel to allow the tag to rest alongside the first dorsal fin. A cordless drill with an 11/64 bit was then utilized to create easier passage through the tough cartilage for the 4 mm gauge needle. Also where the crimps contacted the wire, the heat shrink was scraped away with a scalpel to facilitate long-term corrosion, allowing the apparatus to eventually detach from fin after the tag releases. The total procedure took around five to ten minutes over the side of the vessel in moderate sea conditions. Following attachment the MK10 was again positioned alongside the first dorsal fin (Plate 4).

The two PTT-100 tags were set to detach after a 10 day period. The MK10 tags were set to detach after 120 days, as it was estimated that after this time, following their departure from the aggregation, the tagged *N. brevirostris* would be at their maximum geographical displacement (based on the preliminary results from the acoustic tracking arrays). An example of the full MK10 setting parameters, for deployment on the Jupiter *N. brevirostris*, is located in the appendix (3).

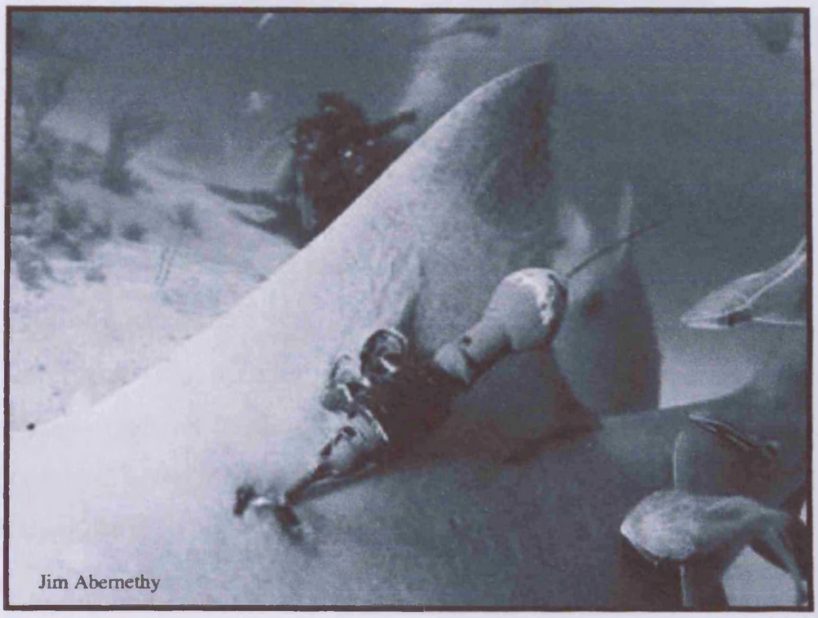


Plate 4. Position of MK10 tag on *N. brevirostris* first dorsal with PVC sleeve harness

5.2.9. Analytical methods

5.2.9.1. Deduction of acoustic monitor range

The downloaded data sets from MGW and MGE monitors were imported into VUE® software for manipulation. For each sentinel tag, and therefore each distance range, detections were isolated from the main dataset and the total was recorded. The true detection proportion (*TDP*) of total transmissions was calculated by:

$$TDP = \left(\frac{RT}{TT}\right) \times 100$$

where *RT* = received total and *TT* = total transmissions. It is however estimated that with the Vemco acoustic monitoring system, when a transmitter is in range of a monitor, around 60 % of produced transmission are successfully detected and stored (personal communications Vemco 2007). Therefore the actual proportion (AP) of the expected detection proportion (*EDP*) was calculated by:

$$AP = \left(\frac{TDP}{EDP}\right) \times 100$$

where *EDP* = 60. Thus it was possible to assess the proportion of hours spent at each distance range for the duration of the deployment.

5.2.9.2. Definition of aggregating period duration

All detection results were imported into a Statistical Analysis System (SAS®) database for further data manipulation. For each hour of each day, the number of detections was calculated for the entire three year period. The results were then used to identify periods of high *N. brevirostris* activity, and thus periods of residence and absence at the identified aggregation monitor sites.

5.2.9.3. ***N. brevirostris* group/aggregating behaviour**

Results for the site of greatest utilisation, MG111 (defined above), were isolated. Due to variations in V16H blanking intervals between transmissions, the number of detections per hour did not directly relate to the number of sharks present per hour. The detections were converted from number of detections per hour to number of unique ID codes recorded each hour. Therefore the level of group presence at the MG111 aggregation site was identified. Subsequently results were converted to number of unique ID codes recorded per day to remove the influence of diel activity variations (see below).

5.2.9.4. Diel activity variation

The number of detections for each hour of the day, for all days the monitors were deployed, was calculated and then plotted as a function of time to reveal any diel patterns in the number of detections.

5.2.9.5. Identification of environmental cues

Mean temperatures for the aggregation grounds were calculated from the results of all monitor site temperature profilers. The mean water temperatures were then correlated with the number of detections per hour by day to determine any relationships. Additionally distinct group latitudinal movements, within the monitor array, were compared temporally to temperature and current profiles to assess for any relationships. Finally, depth and temperature profiles from the short-term PTT-100 deployments were also assessed for patterns.

5.2.9.6. Study population mortality rates and *N. brevirostris* sustainability

Conformation of *N. brevirostris* study population mortalities were made through tag returns. For a given year, mortalities were calculated as a proportion for total study population to give a value for Fishing Related Mortality (f). For a given year sustainability was assumed if $f < r$, where r = r-intrinsic value; i.e. the maximum potential of a species for population growth. r-intrinsic value estimates for *N. brevirostris* were obtained from the existing literature (Gedamke et al., 2007, Cortes, 2000).

5.3. Results

5.3.1. Study population

The total *N. brevirostris* study population consisted of 67 *N. brevirostris* ranging from 134 – 225 cm PCL (mean = 192 ± 2 s.e.; Table 9). Of the 67, 36 were male and 31 were female. From the total 67 *N. brevirostris*, the Vemco acoustic tracking system population, i.e. those issued with V16H transmitters, consisted of 54 individuals ranging from 165 – 225 cm PCL (mean = 195 ± 1.7 s.e.). Of the 54, 27 were male and 27 were female.

Table 9. Jupiter *N. brevirostris* study populations summary

Research Year	Males	Females	Min PCL (cm)	Max PCL (cm)	Total N. brevirostris
2005	4	1	134	191	5
2006	2	1	159	204	3
2007	7	3	165	205	10
2008	18	9	172	217	27
2009	5	17	175	225	22
Total M-type Dart Tagged	36	31	134	225	66
Total V16H transmitterred	27	27	165	225	54
Total Study Population	**36**	**31**	**134**	**225**	**67**

5.3.2. Acoustic fishing

On all fishing expeditions that *N. brevirostris* were captured, acoustic fishing revealed the additional presence of previously acoustically tagged individuals (Figure 103). Up to 18 previously acoustically tagged *N. brevirostris* were present (mean = 8 ± 2 s.e.), yet not a single *N. brevirostris* recapture was recorded. Higher numbers were recorded towards the end of the year's fishing efforts, with the addition of individuals tagged early in the research year campaign returning to their capture location for re-detection.

5.3.3. Deduction of acoustic monitor range

Following positioning of the sentinel tags the MG111 monitors were achieved a minimum range of 150 m for 90% of the time, 300 m for 87% of the time, 600 m for 37% of the time and 900 m for only 2% of the time (Figure 104).

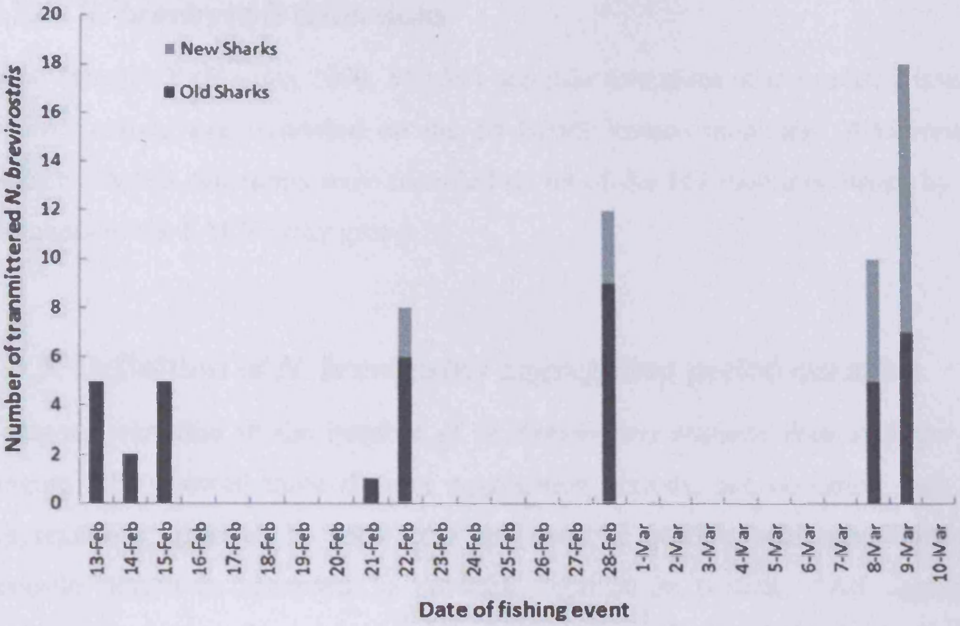


Figure 103. Acoustic fishing detections of previously acoustically tagged *N. brevirostris*

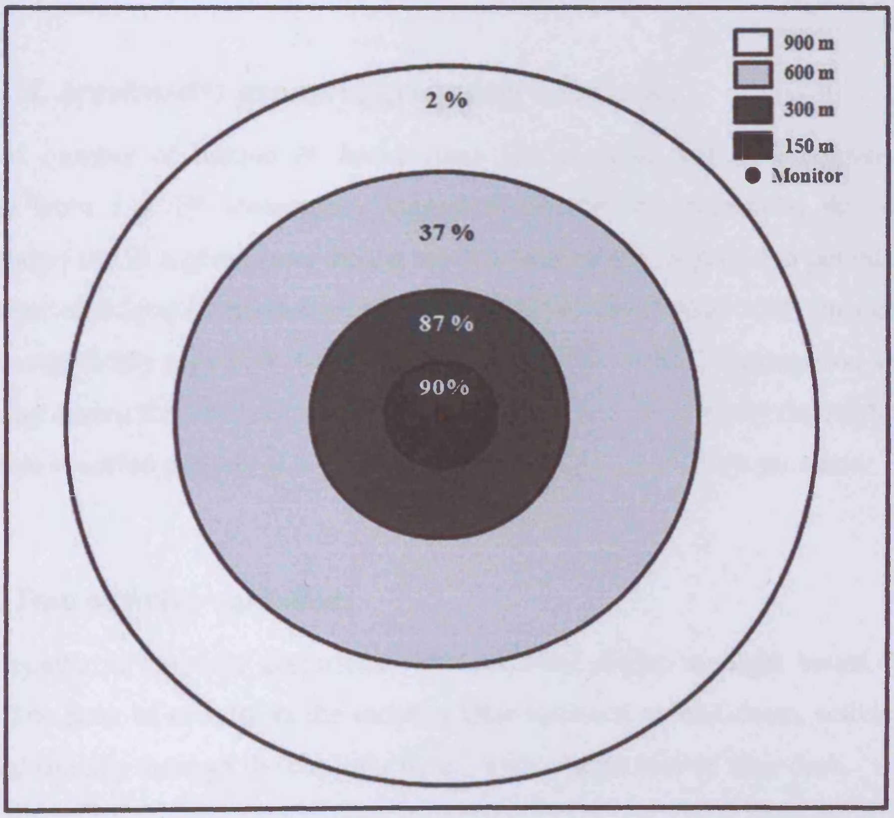


Figure 104. Proportion of deployment time the MG111 acoustic monitors were achieving each distance range

5.3.4. *N. brevirostris* detections

From January 2007 – Jan 2009, 510,561 acoustic detections of transmitters issued to *N. brevirostris* were recorded on the 18 BBFS Vemco monitors. Additionally a further 115,523 detections were recorded on 44 of the 147 monitors owned by other members of the FACT array group.

5.3.5. Definition of *N. brevirostris* aggregating period duration

Temporal variation in the number of *N. brevirostris* acoustic detections per hour (Figure 105) showed three distinct aggregation periods, one occurring each year. Aggregations appeared to both form and disperse quickly, with very few, to no acoustic detections recorded in between aggregation periods. All aggregating periods occurred in the winter months of each year, 2007 – 2009, beginning each year at the end of December and ending in late April. Activity increased, relative to the previous period in both subsequent years to 2007.

5.3.6. *N. brevirostris* group/aggregating behaviour

Plots of number of unique *N. brevirostris* IDs recorded per hour (Figure 106), showed from 1 – 19 acoustically tagged *N. brevirostris* present at the MG111 aggregation site in a given hour during the seasonal winter aggregation period. Plots of number of unique *N. brevirostris* IDs recorded per day (Figure 107), showed from 1 – 25 acoustically tagged *N. brevirostris* present at the MG111 aggregation site in a given day during the seasonal winter aggregation period. Plotting by day, rather than hour, also revealed periods of consistent daily group *N. brevirostris* presence.

5.3.7. Diel activity variation

The majority of acoustic detections were recorded during daylight hours (Figure 108). The peak of activity at the monitor sites occurred around dawn, activity then declined steadily through the daylight hours, with a rapid decline after dusk.

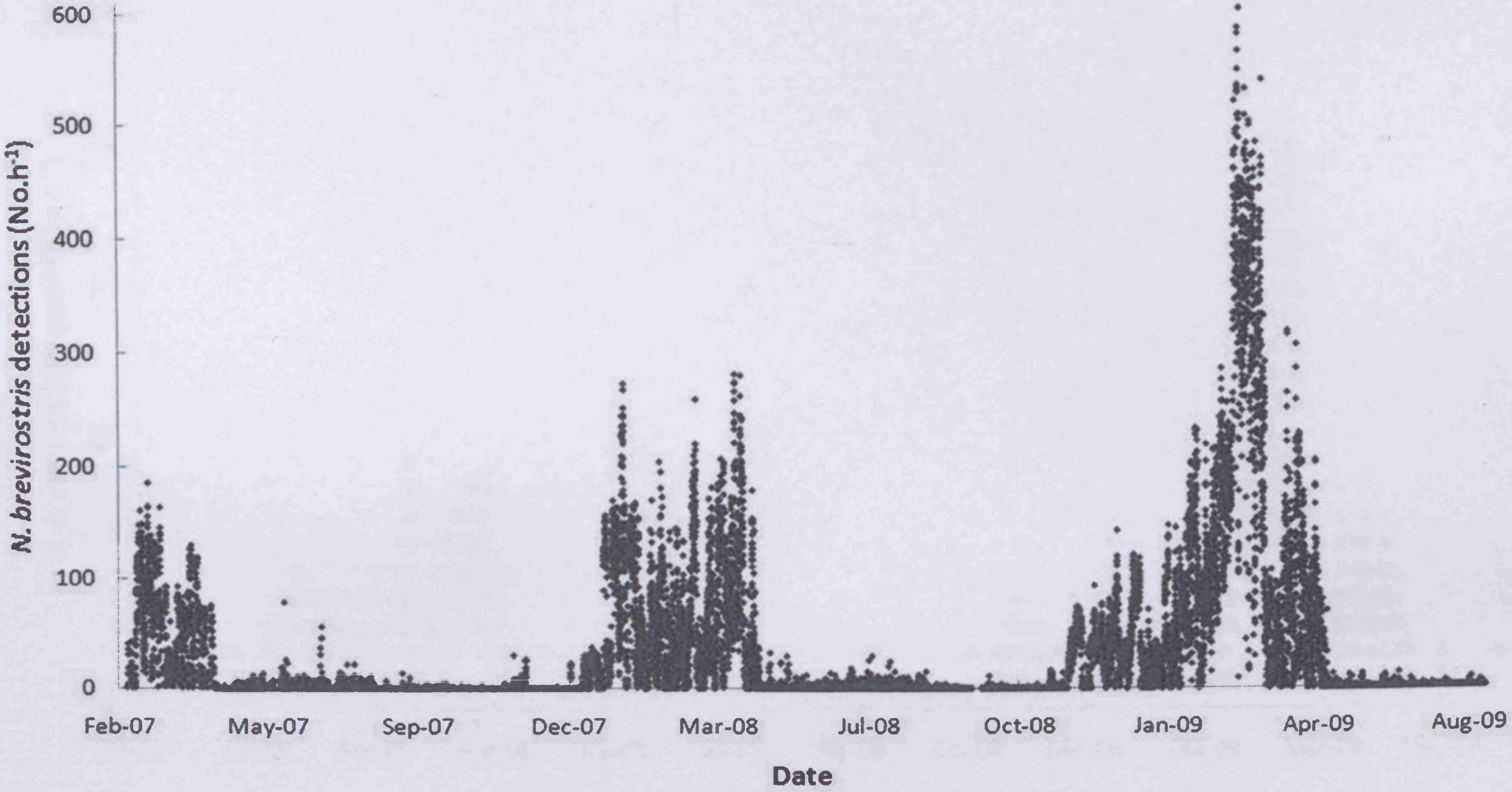


Figure 105. Number of detections from acoustically tagged *N. brevirostris* per hour for all aggregation ground monitors from January 2007 - June 2009

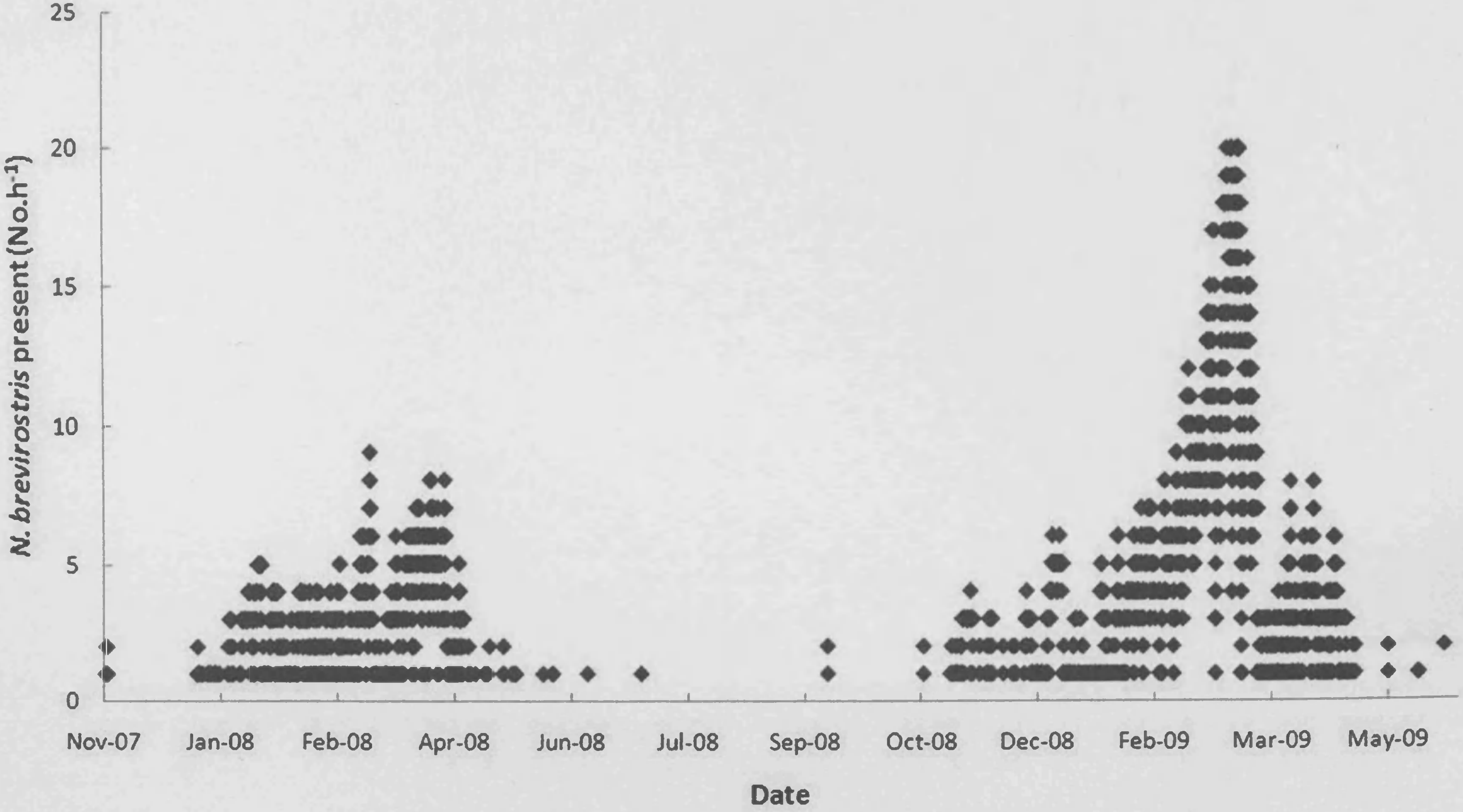


Figure 106. Number of unique detections from acoustically tagged *N. brevirostris* per hour at the MG111 monitors

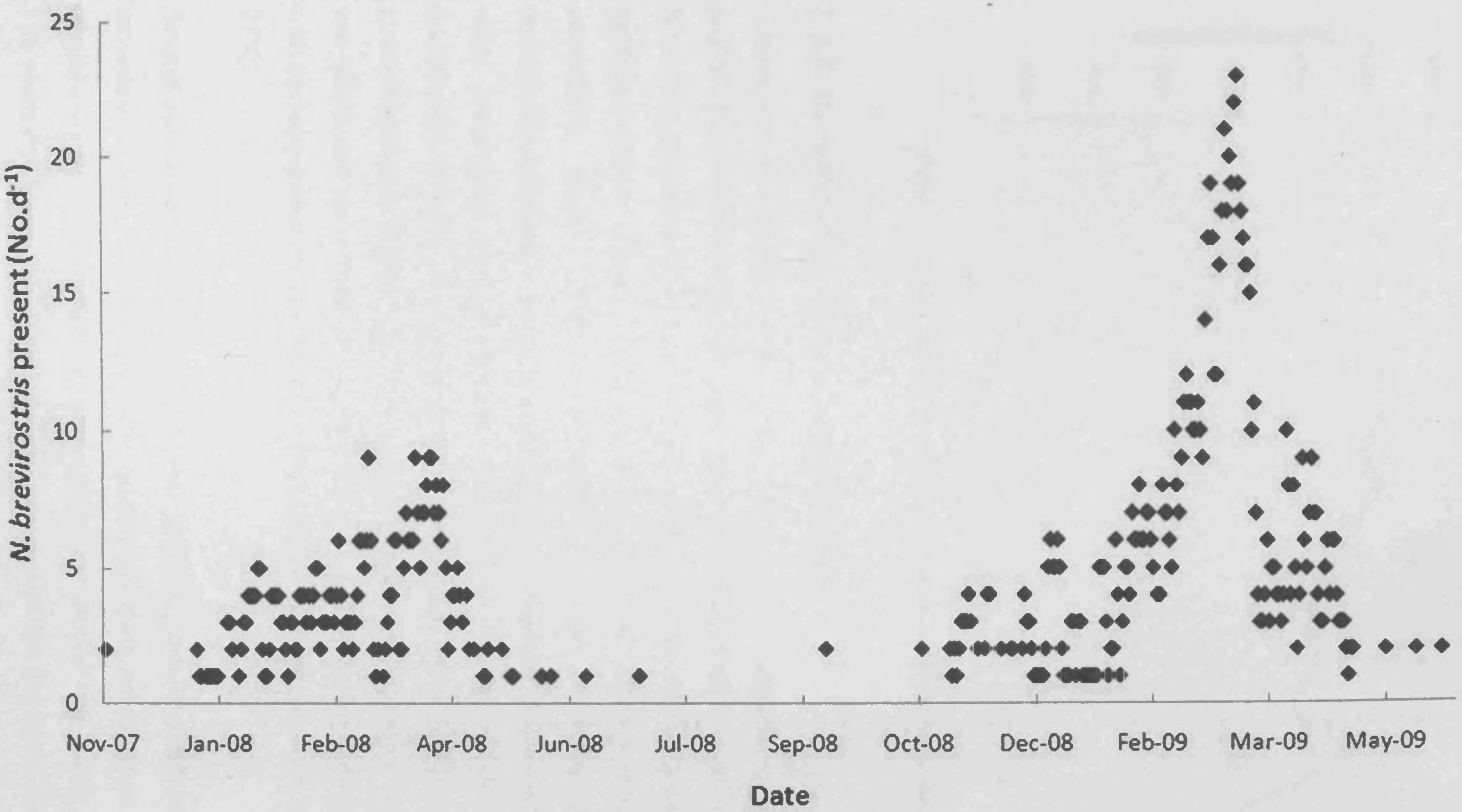


Figure 107. Number of unique detections from acoustically tagged *N. brevirostris* per day at the MG111 monitors

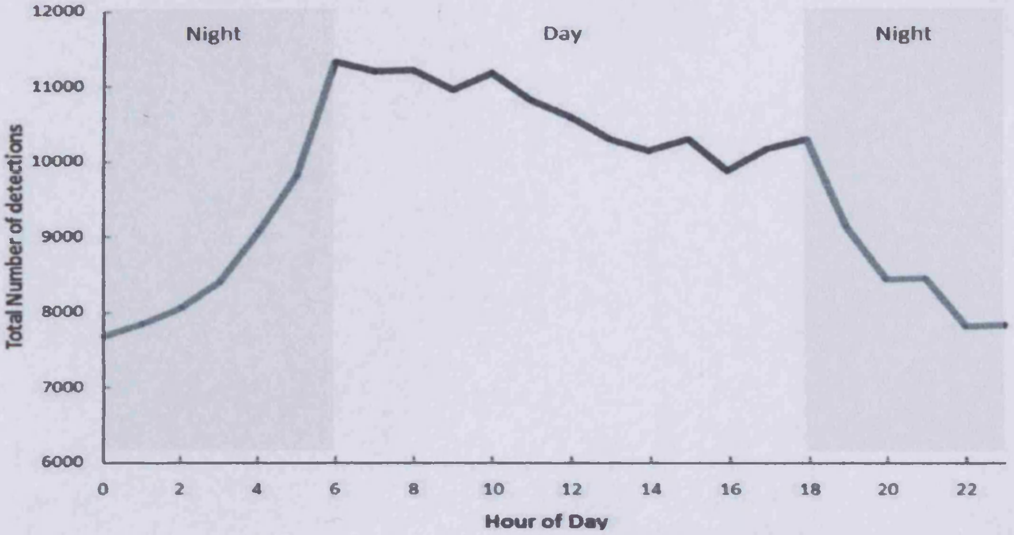


Figure 108. Number of *N. brevirostris* detections by hour of the day

5.3.8. Identification of environmental cues

Comparison of *N. brevirostris* activity with the mean temporal water temperature profile (Figure 109) revealed a clear three year pattern of a negative relationship between mean water temperature and monitor site activity. Closer focus on the 2008 aggregation season (Figure 110) revealed that once water mean temperature dropped consistently below ~24/23°C, acoustically tagged *N. brevirostris* activity dramatically increased. Activity remained at consistently high levels until mean water temperature rose consistently above ~24/23°C, at which time activity dramatically reduced. The number of *N. brevirostris* detections recorded at each given temperature (Figure 111) showed a dramatic peak at around ~24/23°C. This was offset, and lower than, the greatest number of hours spent at each temperature, with the temperature for the majority of the deployment time recorded between ~25 – 27°C.

Several acoustically tagged *N. brevirostris* showed a distinct southward latitudinal movement within the array grounds, relative to their predominant area of site attachment, early March 2008, then returned north around mid-March (Figure 112). The southerly movement coincided with both a reduction in current strength (Figure 113), and a drop in mean water temperature (Figure 114). The northerly movement coincided with both an increase in current strength and increase in water temperature.

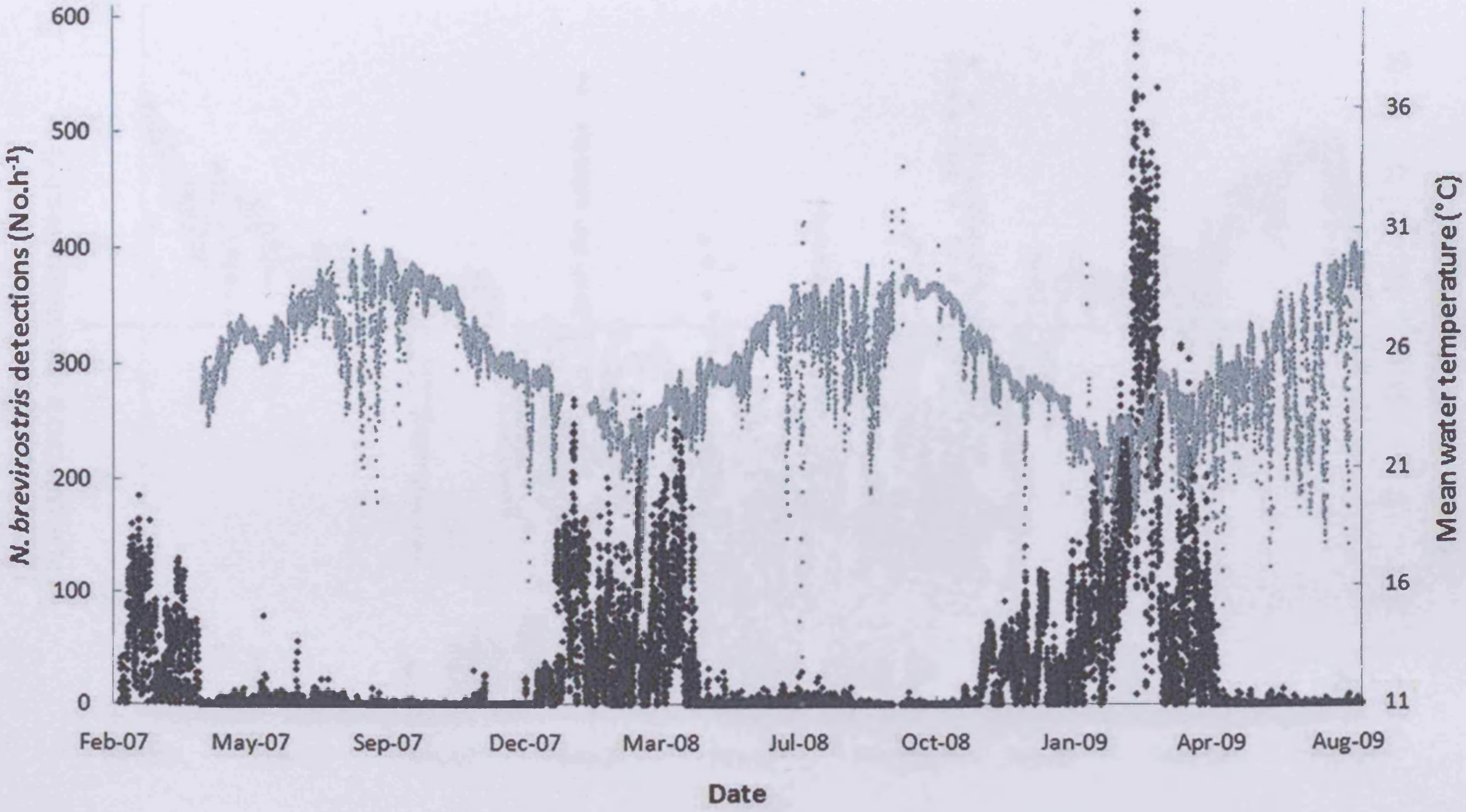


Figure 109. Number of *N. brevirostris* detections per hour and mean temperature for all aggregation ground monitors from January 2007 - June 2009

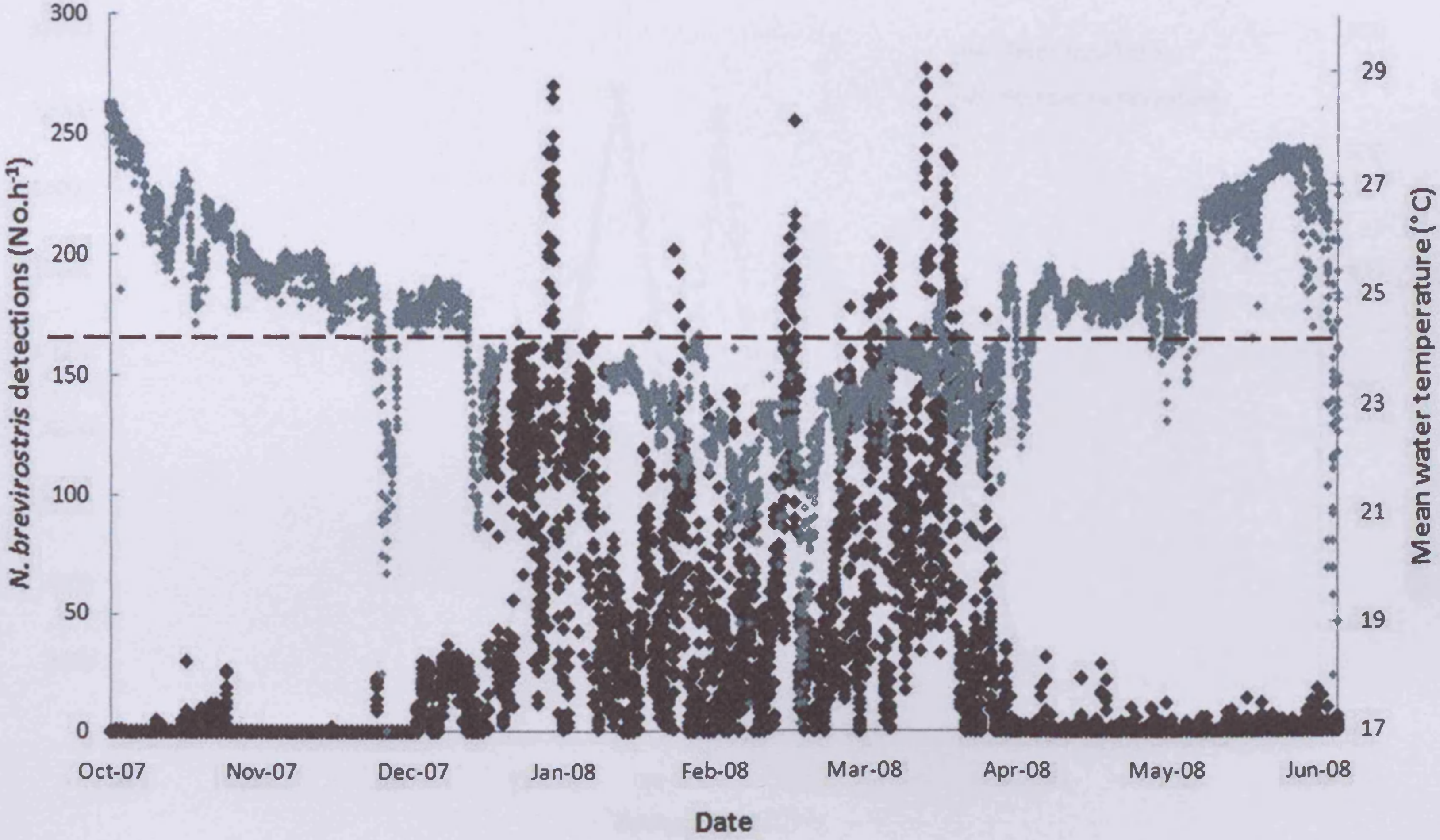


Figure 110. Number of *N. brevirostris* detections per hour and mean temperature for all aggregation ground monitors from January 2008 - June 2008 (dashed line represents 24°C level)

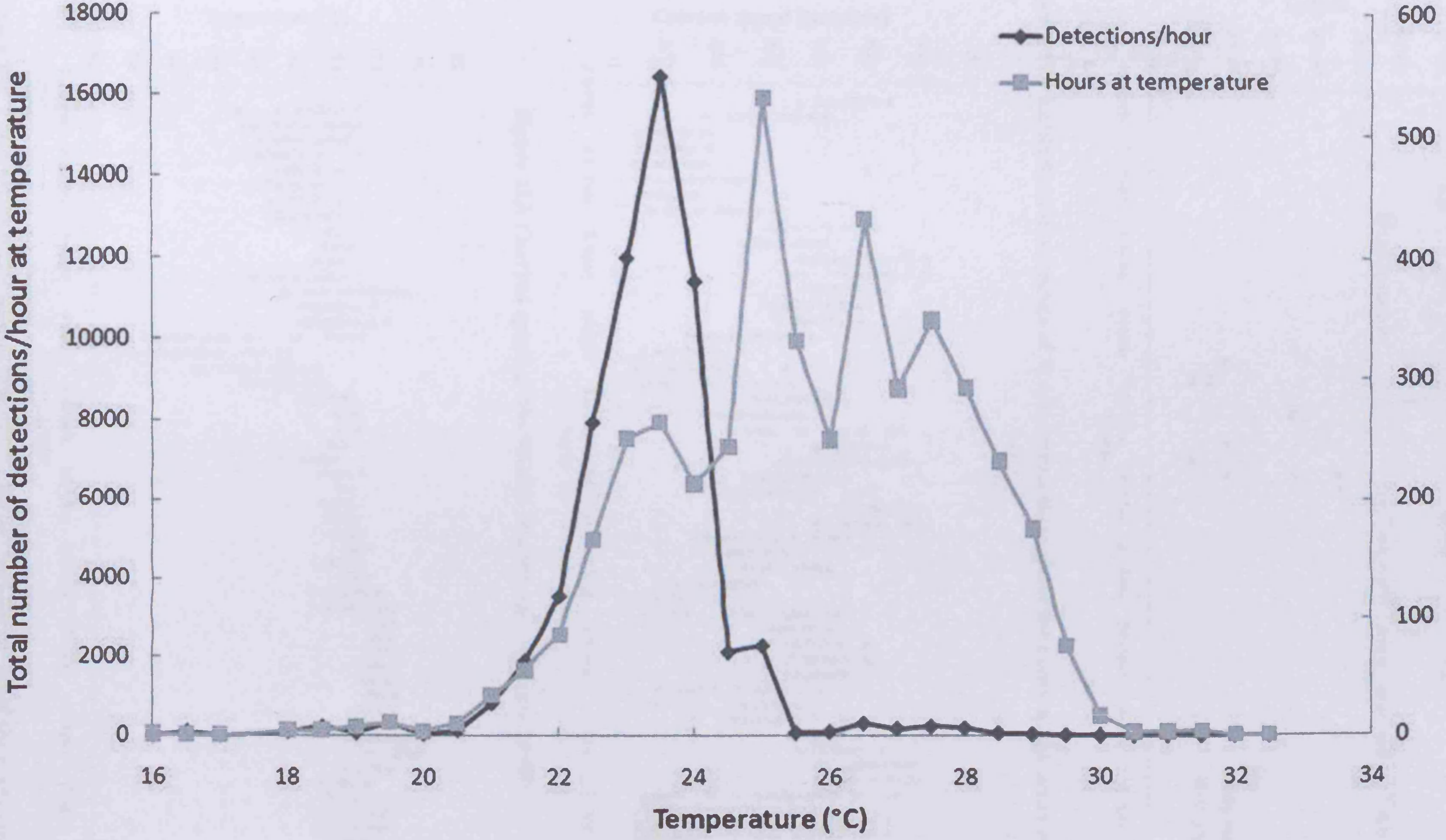


Figure 111. Number of *N. brevirostris* detections per hour and number of hour at water temperature for duration of deployment

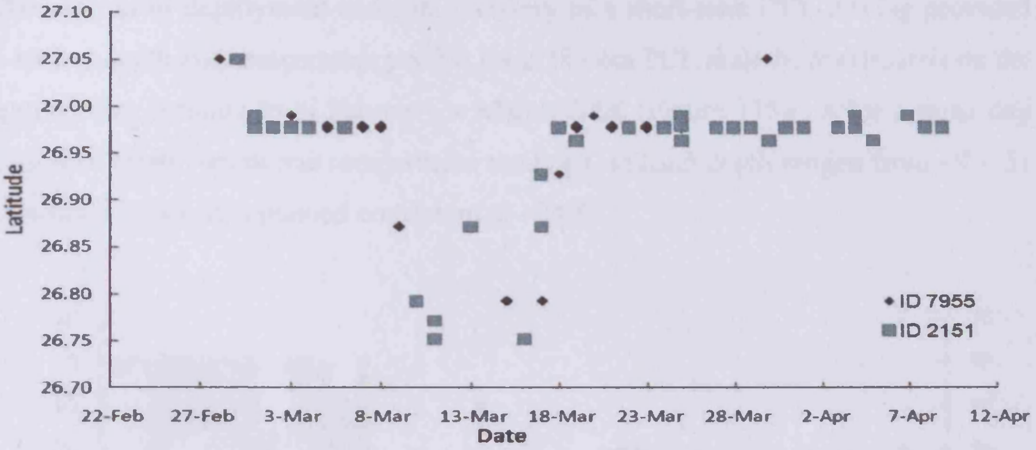


Figure 112. Latitudinal movements of *N. brevirostris* throughout the extent of the array coverage

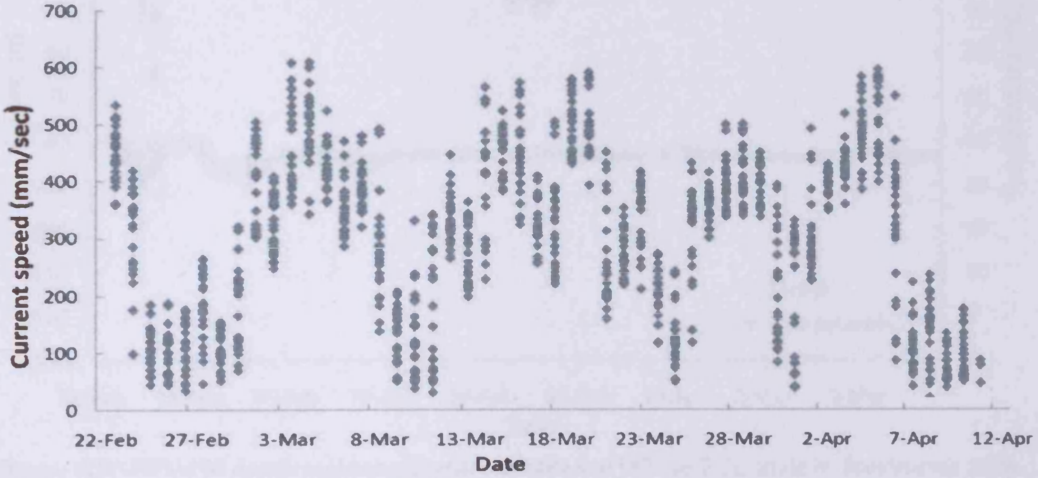


Figure 113. Current speed at the MG111 monitor sites (latitude 26°98)

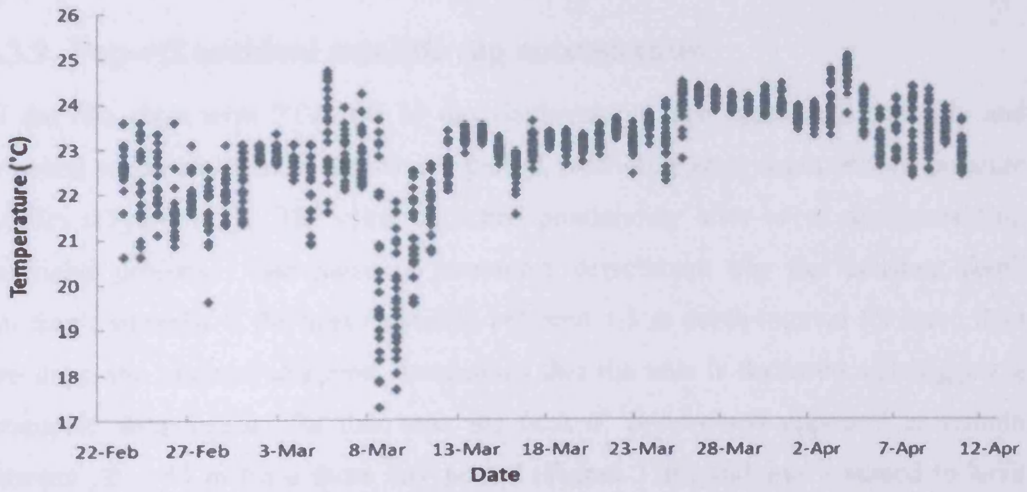


Figure 114. Mean monitor site water temperature throughout the extent of the array coverage

The successful deployment and data recovery of a short-term PTT-100 tag provided a 10 day depth and temperature profile for a 187 cm PCL male *N. brevirostris* on the aggregation grounds from February – March 2008 (Figure 115). After a three day period of erratic depth and temperature readings, utilised depth ranged from ~9 – 51 m, while temperate remained consistent at ~24°C.

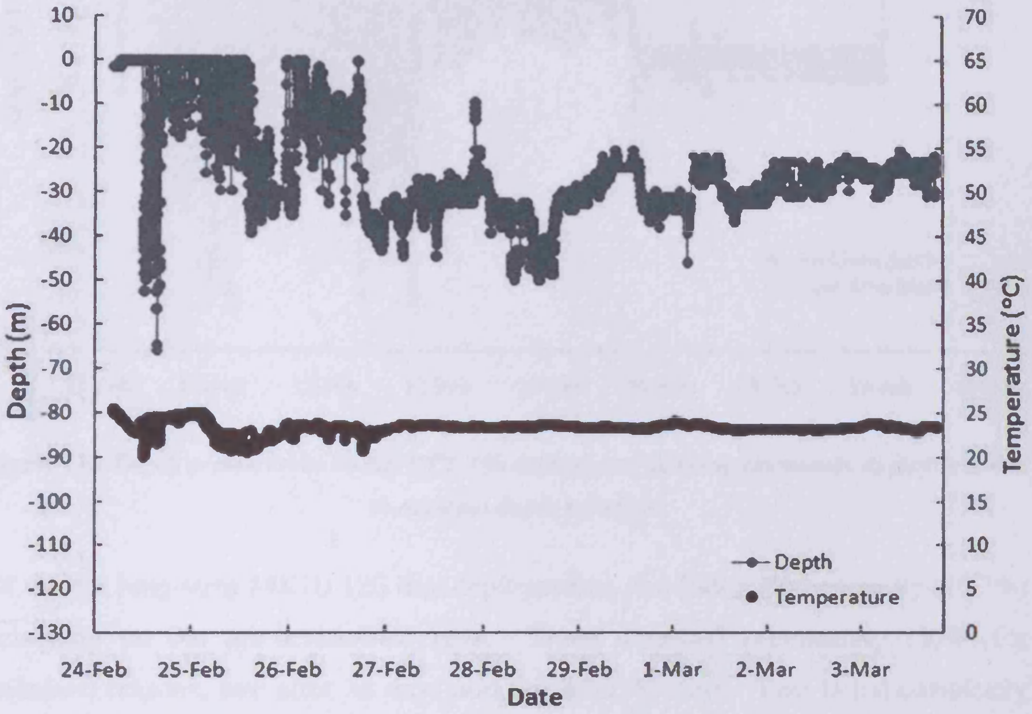


Figure 115. PTT-100 depth and temperature profile for 187 cm PCL male *N. brevirostris* 2008

5.3.9. Pop-off archival satellite tag success rates

Of the two short term PTT-100 10 day deployments, one functioned correctly and detached successfully after the 10 day period, providing good depth and temperature profiles (Figure 115). The other detached prematurely after seven days providing unreliable profiles. The cause of premature detachment was the 'constant depth function', whereby if the host remained between a 5 m depth interval for more than two days, the internal computer determines that the host is deceased and triggers a premature detachment. In this case the host *N. brevirostris* appeared to remain between 26 – 30 m for a three day period (Figure 116), and was assumed to have died.

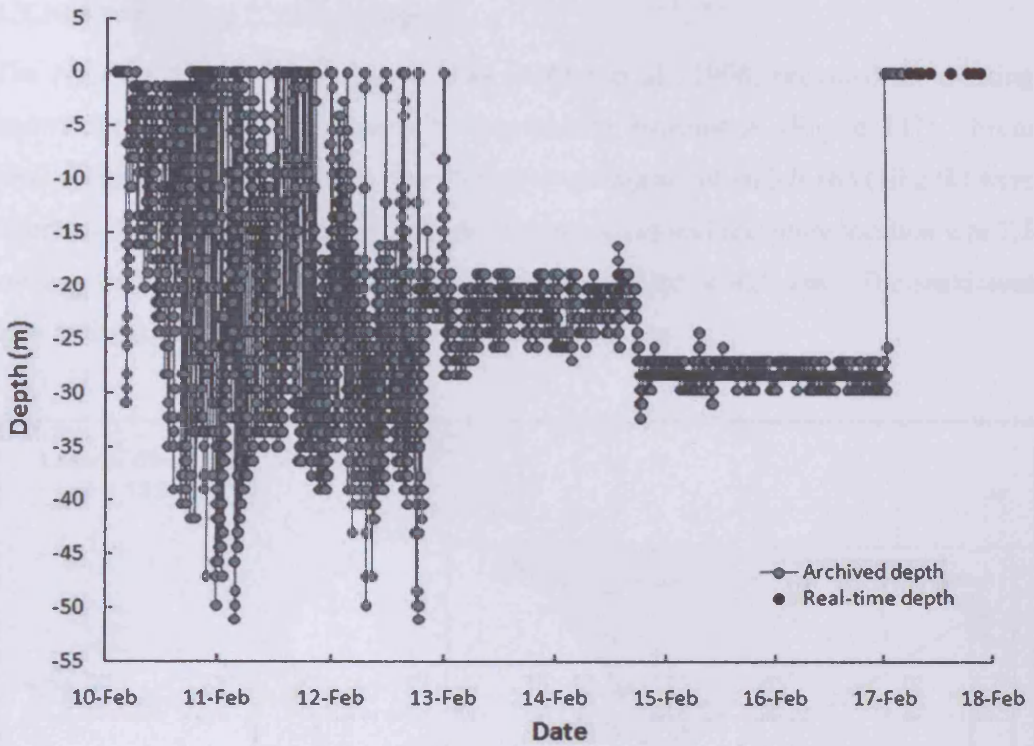


Figure 116. Depth profile from 10 day PTT-100 deployment showing premature deployment due to constant depth function

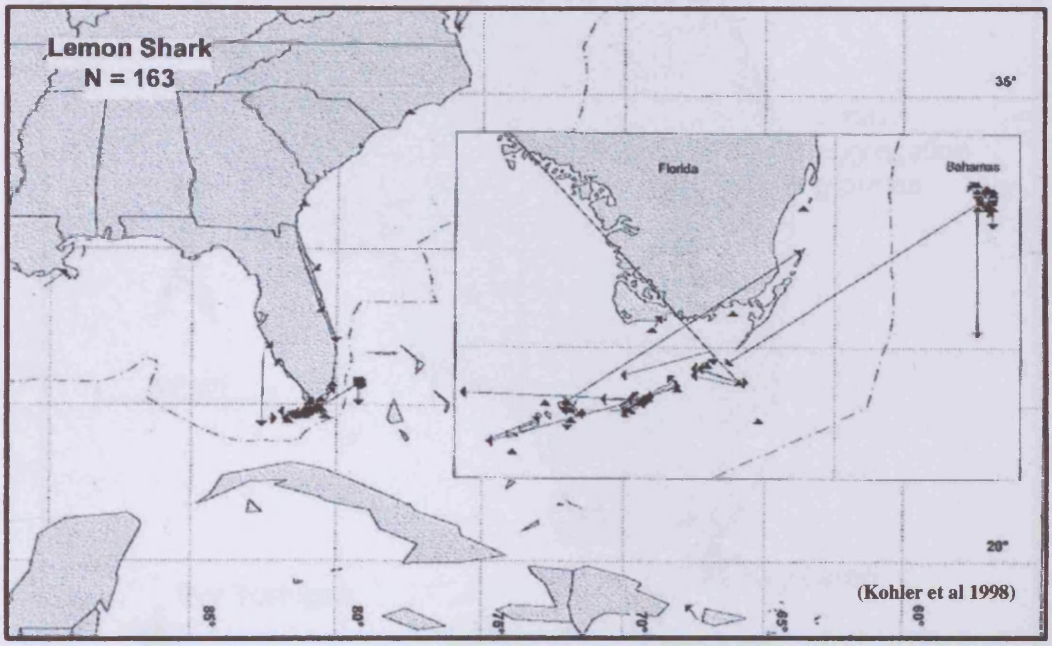
Of the six long-term MK10 120 day deployments, one functioned correctly (16.7%) detaching on the pre-determined date. Three detached prematurely (50%) for unknown reasons, two after 38 days and one after 45 days. Two failed completely (33.3%) with no transmissions ever received. Overall for both models, PTT-100 and MK10, of the eight deployed, two were completely successful (25%), four detached prematurely (50%) and two failed completely (25%).

5.3.10. *N. brevirostris* large scale movements/migrations

Large scale moments were documented through a number of different techniques. In order to define which techniques were utilised the following code system is used: NMFS Cooperative Shark Tagging Program = CSTP, Vemco acoustic tag detection through FACT array = FACT, Vemco acoustic tag detection through ACT array = ACT, internal acoustic tag return = ATR, and pop-off archival satellite tag location = ST.

5.3.10.1. Existing CSTP results

The NMFS CSTP Atlantic Shark Atlas (Kohler et al., 1998) provided the existing knowledge of large scale mature *N. brevirostris* movements (Figure 117). From 1962 – 1993, a total of 1602 *N. brevirostris* were tagged, of which 163 (10.2 %) were recaptured. The maximum average speed between tag and recapture location was 7.5 km d^{-1}, with the maximum recorded distance travelled at 425 km. The maximum time at liberty for a single *N. brevirostris* was 4.1 years.



(Kohler et al 1998)

Figure 117. NMFS CSTP *N. brevirostris* movement results, beginning of line represents original location and arrow head represents recapture location

5.3.10.2. State-wide movements

A number of state-wide movements were recorded under the Jupiter *N. brevirostris* research project, representing movements between the Jupiter aggregation sites and four other locations (Figure 118).

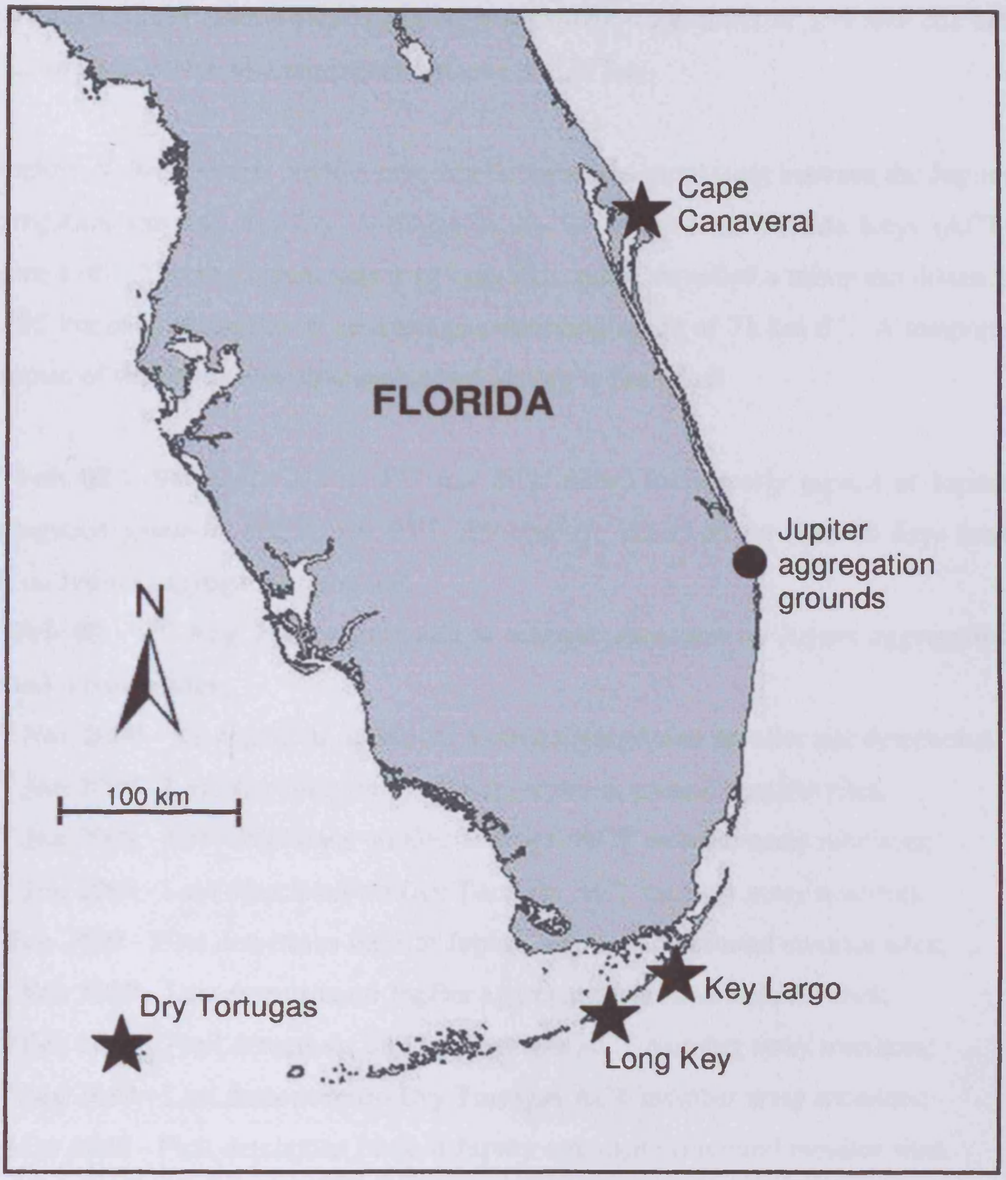


Figure 118. State wide movements of Jupiter study population *N. brevirostris* (stars represent documentation locations away from the aggregation grounds)

A mature *N. brevirostris* was recorded at the time of capture in 2007 to have travelled to the Jupiter aggregation sites from Long Key (Figure 118), by the presence of an NMFS M-type dart tag (CSTP). The *N. brevirostris* was a 193 cm PCL male and had travelled a minimum distance of 275 km since the time of its original capture by a recreational fisherman in 2003. Movements were made by two mature *N. brevirostris* from the Jupiter aggregation sites to the waters off the coast of

Key Largo (CSTP and ATR). Both *N. brevirostris* were males of 199 and 201 cm PCL, and had travelled a minimum distance of 225 km.

A mature *N. brevirostris* made a repeated documented movement between the Jupiter aggregation site and the Dry Tortugas in the far west of the Florida Keys (ACT; Figure 118). The individual was a 177 cm PCL male, travelled a minimum distance of 505 km each transition at an average swimming speed of 71 km d^{-1}. A temporal synopsis of this *N. brevirostris* monitored history is provided:

9th Feb 08 - Shark ID 2147: 177 cm PCL male, acoustically tagged at Jupiter aggregation grounds, short-term PTT-100 applied, detached on time 10 days later still on Jupiter aggregation grounds;
9th Feb 08 - 7th Aug 2008 - Intermittent acoustic detection on Jupiter aggregation ground monitor sites;
20th Nov 2008 - Re-appeared on Jupiter aggregation ground monitor site detections;
14th Jan 2009 - Last detection on Jupiter aggregation ground monitor sites;
27th Jan 2009 - First detections on Dry Tortugas ACT member array monitors;
28th Jan 2009 - Last detections on Dry Tortugas ACT member array monitors;
7th Feb 2009 - First detections back at Jupiter aggregation ground monitor sites;
10th Feb 2009 - Last detection on Jupiter aggregation ground monitor sites;
17th Feb 2009 - First detections on Dry Tortugas ACT member array monitors;
17th Jan 2009 - Last detections on Dry Tortugas ACT member array monitors;
5th Mar 2009 - First detections back at Jupiter aggregation ground monitor sites.

In 2009, movements were made, towards the end of the aggregating period from the Jupiter aggregation sites to the close shore waters of Cape Canaveral by 18 acoustically tagged *N. brevirostris* (FACT), where large seasonal aggregations of juvenile *N. brevirostris* had previously been reported (Reyier et al., 2008). Of the 18 *N. brevirostris* that exhibited this movement, five were males and 13 were females, size ranged from 172 – 225 cm PCL, minimum distance travelled was 225 km and the average speed was 21 km d^{-1} (± 6.5 s.e.). Following the movement from Jupiter to Cape Canaveral, none of the 18 *N. brevirostris* had returned to the Jupiter aggregation monitor sites by the time of the last download in September 2009. There was a 29 day delay from the departure of the last acoustically tagged juvenile *N. brevirostris* and the arrival of the first acoustically tagged mature *N. brevirostris* (Figure 119; Franks et al., 2009).

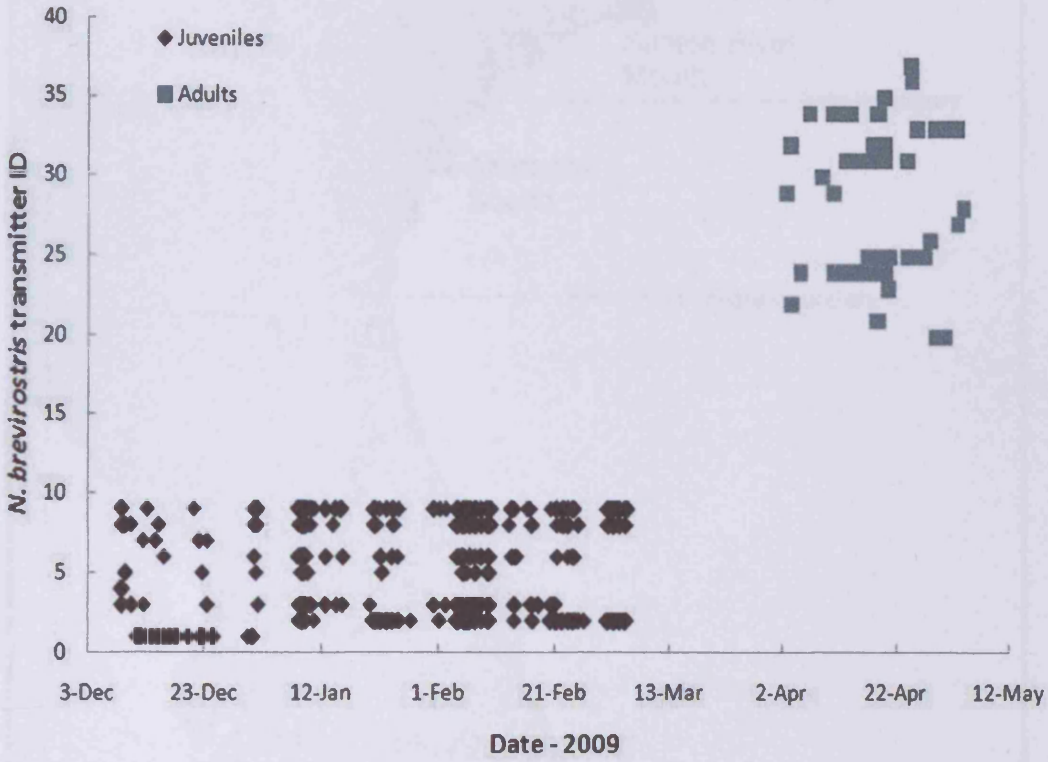


Figure 119. Residence periods for juvenile and adult *N. brevirostris* at the Cape Canaveral nursery site (Franks et al., 2009)

5.3.10.3. Movements/migrations across state boundaries

A number of movements/migration that cross state boundaries were recorded under the Jupiter *N. brevirostris* research project, representing movements between the Jupiter aggregation grounds and three other locations (Figure 120). This would therefore expose these individuals to various different state level fishing regulations throughout the course of a given year.

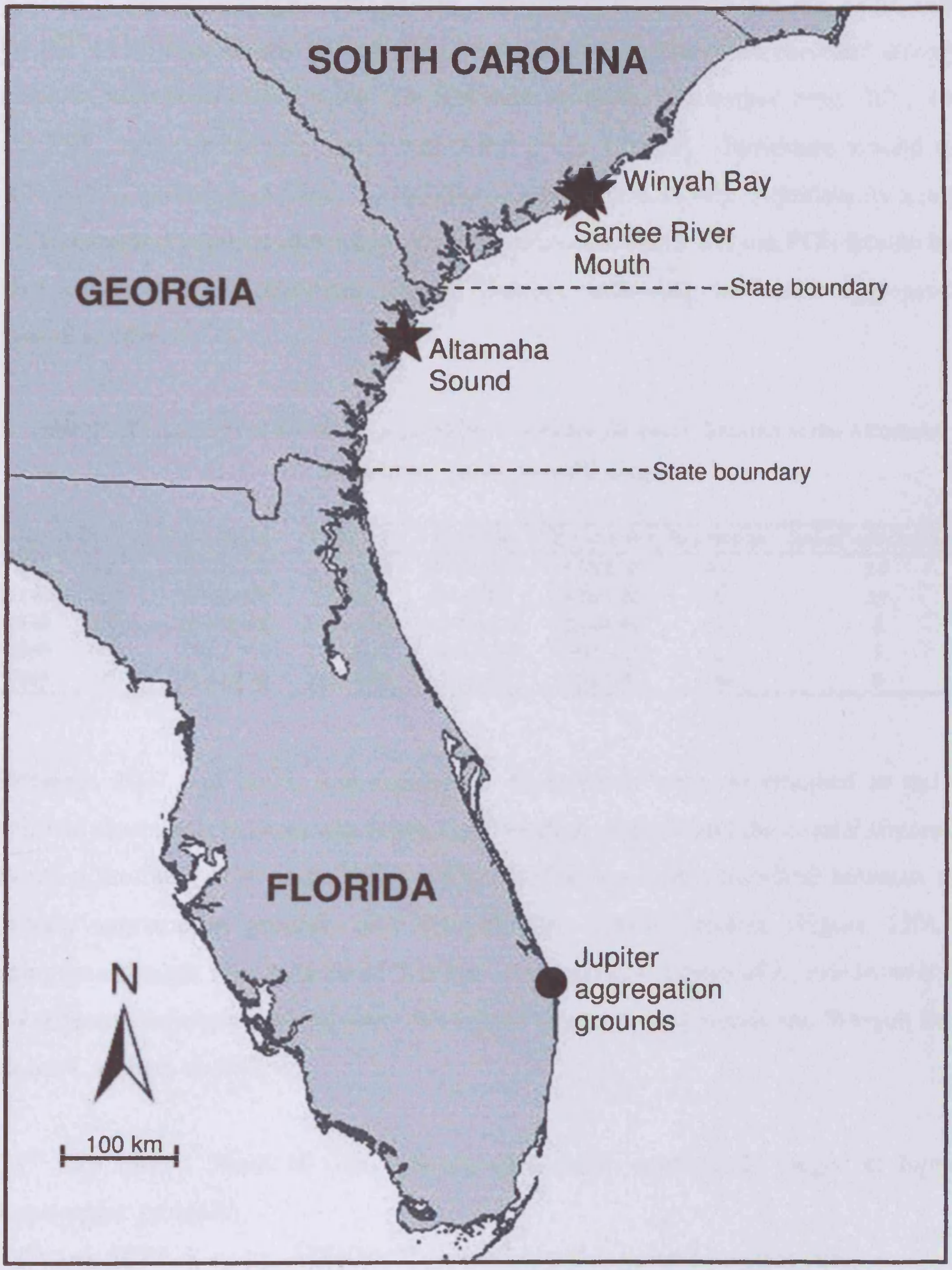


Figure 120. Movements of Jupiter study population *N. brevirostris* across state boundaries (stars represent documentation locations away from the aggregation grounds)

Between 2008 and 2009, six mature *N. brevirostris* were documented to have made seasonal repeated journeys between the Jupiter aggregation grounds and the

Altamaha Sound, Georgia. The journey represents a minimum distance of 512 km. Of the six *N. brevirostris* that exhibited this movement, five were recorded through acoustic detections (ACT; Table 10) and were all male; size ranged from 180 – 197 cm PCL, mean swimming speed was 9 km d^{-1} (± 1.6 s.e.). Residence around the Altamaha sound ranged from 1 – 130 days (mean = 40 ± 25 s.e). Additionally a pop-off transmitted location of a MK10 tag (ST) revealed that a 199 cm PCL female had also travelled to the Altamaha Sound, Georgia, following the winter aggregation season in Jupiter.

Table 10. Transitions of the study population *N. brevirostris* males detected at the Altamaha Sound, GA, under the ACT array

ID	PCL (cm)	Last Jupiter	First GA	Last GA	First Jupiter	Residence	Speed Nth (km/day)
36	197	18-Apr-08	10-Jun-08	15-Aug-08	13-Dec-08	66	10
2140	188	25-Apr-08	5-Jun-08	5-Jun-08	24-Nov-08	1	12
2148	180	15-Feb-08	14-Aug-08	14-Aug-08	25-Jan-09	1	3
7949	192	16-Apr-08	11-Jun-08	11-Jun-08	6-Nov-08	1	9
7959	187	14-Apr-08	10-Jun-08	18-Oct-08	1-Dec-08	130	9

Between 2007 and 2009, four mature *N. brevirostris* were documented to move/ migrate seasonally between the Jupiter aggregation grounds and the coastal waters of South Carolina (ACT and CSTP). Two males repeatedly travelled between the Jupiter aggregation grounds and Winyah Bay, South Carolina (Figure 120), a minimum straight line distance of 720 km. A temporal synopsis of *N. brevirostris* ID 34 movements/migrations between the Jupiter aggregation grounds and Winyah Bay, South Carolina, as follows:-

23th Feb 2007 - Shark ID 34: 199 cm PCL male, acoustically tagged at Jupiter aggregation grounds;

11th Apr 2007 - Last detection on Jupiter aggregation ground monitor sites;

2nd Jul 2007 - First detections on Winyah Bay, SC, ACT member array monitors, minimum average speed = 8.7 km d^{-1};

29th Oct 2008 - Last detections on Winyah Bay, SC, ACT member array monitors, residence = 119 days;

5th Jan 2008 - First detections back at Jupiter aggregation ground monitor sites, minimum average speed = 10.6 km d^{-1};

17th Apr 2008 - Last detection on Jupiter aggregation ground monitor sites, residence = 103 days;
18th Jun 2008 - First detections on Winyah Bay, SC, ACT member array monitors, minimum average speed = 11.6 km d^{-1};
1st Sep 2008 (date monitor removed) - Last detections on Winyah Bay, SC, ACT member array monitors, true residence unknown as still present when monitor removed, however minimum = 75 days;
22nd Nov 2008 - First detections back at Jupiter aggregation ground monitor sites, true average speed unknown due to uncertain SC departure day, however minimum average speed = 8.8 km d^{-1}.

A temporal synopsis of *N. brevirostris* ID 2141 movements/migrations between the Jupiter aggregation grounds and Winyah Bay, South Carolina, as follows:-

8th Aug 2007 - Shark ID 308820: 198 cm PCL male, issued NMFS M-type dart tag at Winyah Bay, SC;
5th Feb 2008 - Shark ID 308820, acoustically tagged at Jupiter aggregation grounds with acoustic ID 2141;
18th Apr 2008 - Last detection on Jupiter aggregation ground monitor sites;
29th Jun 2008 - First detections on Winyah Bay, SC, ACT member array monitors, minimum average speed = 10 km d^{-1}.

Following the removal of the Vemco monitors from Winyah Bay by the ACT array member project leader, they were relocated 10 km southeast to the mouth of the North Santee River, South Carolina (Figure 120). Following departure from the Jupiter aggregation grounds in 2009, two female *N. brevirostris* were detected on the North Santee River Mouth monitors (Table 11), a minimum straight line distance of 715 km.

Table 11. Transitions of the study population *N. brevirostris* detected at the Santee River Mouth, SC, under the ACT array

ID	Sex	PCL (cm)	Last Jupiter	First GA	Residence	Speed Nth (km/day)
7950	**Female**	208	8-Mar-09	30-Jul-09	144	5
55115	**Female**	210	13-Mar-09	21-Jun-09	100	7

5.3.10.4. Movements across fishery management zone boundaries

Collectively, all the documented mature *N. brevirostris* large-scale movements/ migrations (CSTP, ATR, FACT, ACT and ST) represented transitions between three of the designated management zones of the U.S. pelagic longline fisheries (Figure 121).

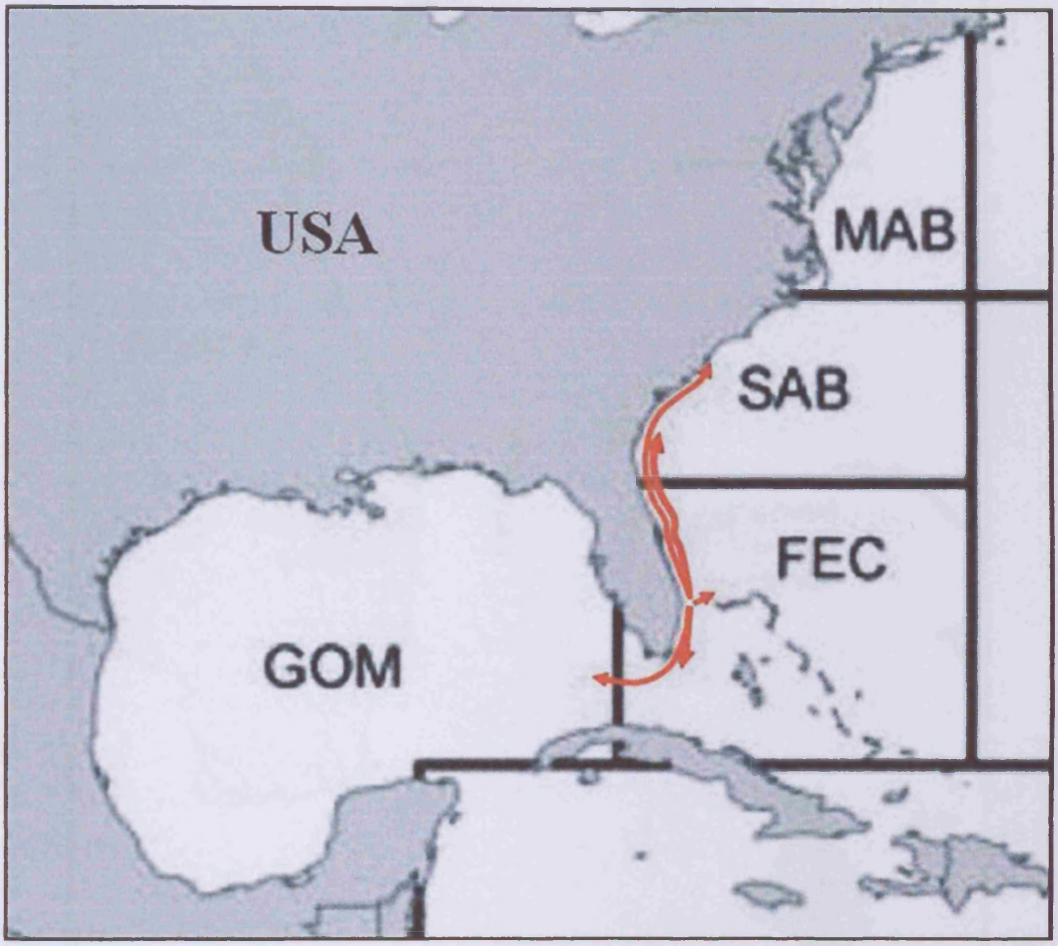


Figure 121. Movements of Jupiter study population *N. brevirostris* across designated management zones of the U.S. pelagic longline fisheries; Mid Atlantic Bight (MAB), South Atlantic Bight (SAB), Florida East Coast (FEC) and Gulf of Mexico (GOM). Base map with management zones from Mandelman et al. 2008

5.3.10.5. International movements

Though it suffered a premature detachment after 45 days, an MK10 tag attached to a 197 cm PCL male *N. brevirostris* provided a pop-up location that documented an international movement (ST). At the time of detachment and first transmissions the

MK10 tag was located on the Little Bahama Bank, Bahamas, near a popular *N. brevirostris* and *G. cuvier* feeding site known as 'Tiger Beach' (Figure 122).

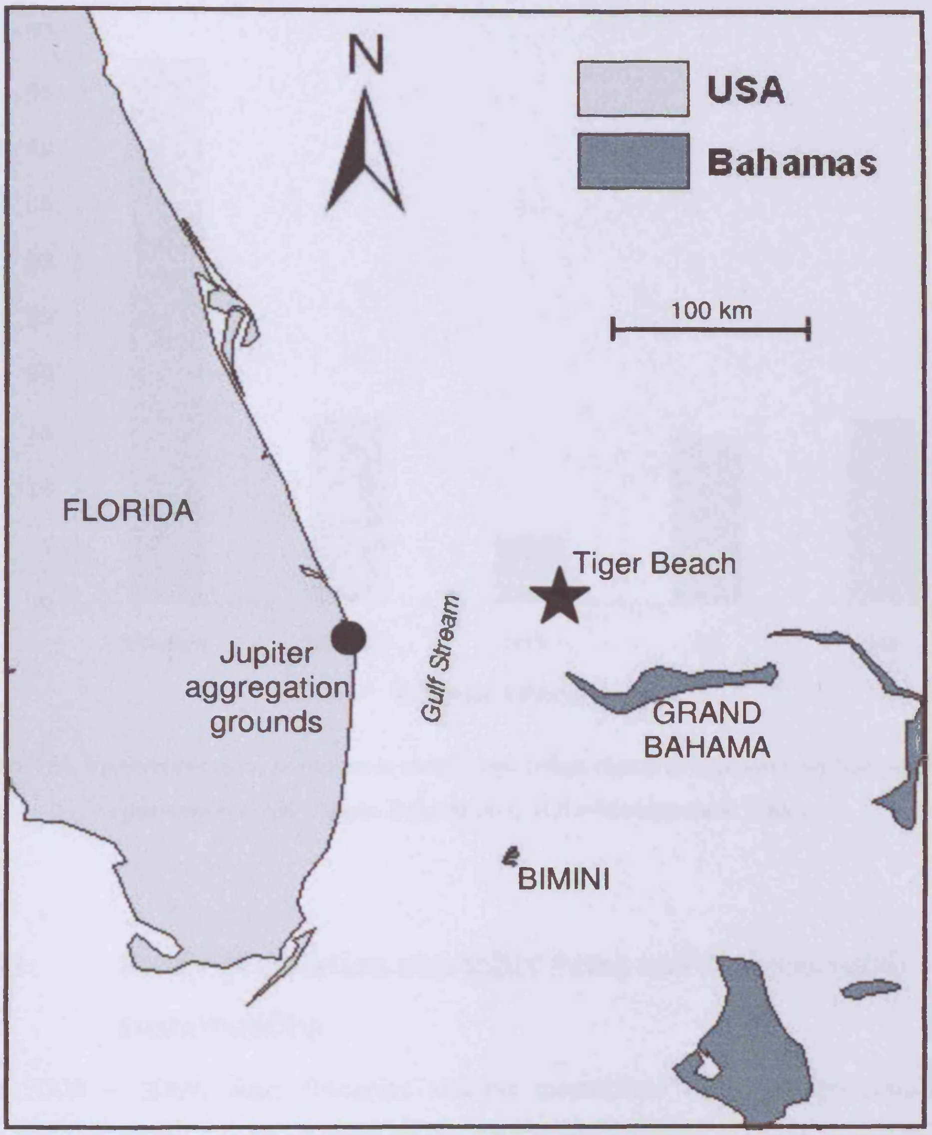


Figure 122. International movements of Jupiter study population *N. brevirostris* (circle represents deployment location, star represents transmission location)

5.3.10.6. *N. brevirostris* large scale movements/migrations summary

With all large-scale movements considered, mature *N. brevirostris* captured during the study at the Jupiter aggregation grounds were recorded in other locations over a coast line spanning a minimum length of 1,225 km. The maximum recorded distance travelled in a displacement was 720 km. The average speed of *N. brevirostris* making these journeys was 20.2 km d^{-1} (± 8.6 s.e.). A summary of the proportion of

N. brevirostris from the Jupiter study population that were recorded to cross relevant distance parameters is provided in figure 123.

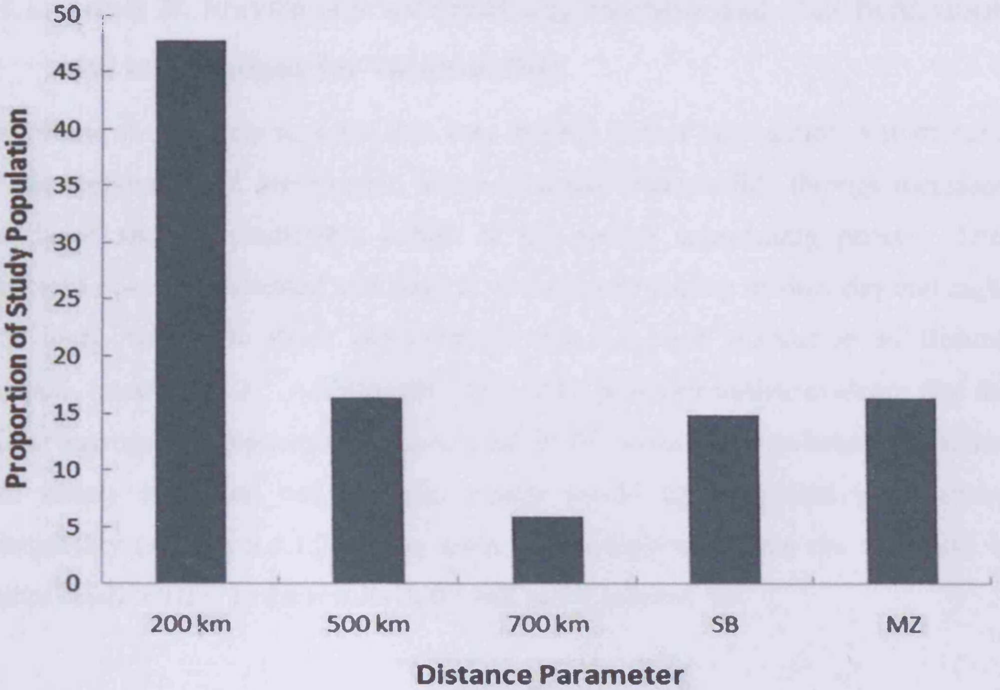


Figure 123. Proportion of *N. brevirostris* study population that travelled over various distance parameters; SB = State Boundaries, MZ = Management Zones

5.3.11. Study population mortality rates and *N. brevirostris* sustainability

From 2008 – 2009, four fisheries related mortalities of study population *N. brevirostris* were documented through the CSTP and acoustic tag returns in response to the 'reward' labels. This represented 6% of the 67 *N. brevirostris* in the total study population, therefore $f = 0.06$. Existing r-intrinsic value estimates for *N. brevirostris* are 0.02 (Cortes, 2000) and 0.03 – 0.06 (Gedamke et al., 2007). Therefore for the annual period from 2008 – 2009 for the *N. brevirostris* study population $f \geq r - intrinsic$. Following the absence of detections during the summer months, 45% of acoustically tagged *N. brevirostris* did not return to the aggregation ground monitors sites from 2007 – 2008, and 34% did not return from 2008 – 2009.

5.4. Discussion

5.4.1. Adult *N. brevirostris* seasonal aggregation and diel behaviour and implications for vulnerability

The results of this study revealed that very distinct annual aggregation periods exist for the Jupiter adult *N. brevirostris*, which increased vulnerability through increased abundance and the predictable nature of the annual aggregating period. Diel variations observed indicated that adult *N. brevirostris* display distinct day and night behaviours, similar to those observed for the sub-adult population in Bimini, Bahamas (section 3.3.3). Additionally, the results provided further evidence that the Jupiter aggregations represent period of adult *N. brevirostris* group behaviour, rather than simply incidental congregation, which would have resulted in increased vulnerability (section 5.4.1.2). The main aforementioned points are discussed in further detail relative to the results in the following subsections.

5.4.1.1. Determination of *N. brevirostris* aggregating period duration

Both terrestrial and marine species that periodically and predictably congregate can be extremely vulnerable to overexploitation (De Mitcheson et al., 2008). The results of the detections per hour plots (Figure 105) showed that acoustically tagged *N. brevirostris* activity at the monitor sites occurred on an annual and distinct seasonal basis, therefore both periodically and predictably, during the winter months of December - April. The annual increase in recorded activity was subjective as progressively more sharks were added to the study population. The local shift in commercial shark targeting, from large pelagic to small coastal operated vessels (personal communications Capt. Mike Newman and FWC biologist Dave McGowan 2009), has resulted in a considerable temporal extension in annual fishing efforts. The smaller vessels, in addition to the reduced bag limits, have less capacity for LCS landings, therefore it now takes considerably longer for the permit holders to reach their annual quotas. With the annual aggregation duration of 4 months, even if the locally operating commercial shark fishermen were not specifically targeting the *N. brevirostris* aggregations, their fishing efforts would still probably overlap. Thus the annual concentration of *N. brevirostris* at Jupiter, Florida, is likely to be subjected to both direct (personal communication Capt. Mike Newman, Jupiter based commercial fishermen at FWC public shark workshop 2009) and incidental capture. Grantham et al. (2008) found seasonal spatial closers most effective for reducing shark bycatch in the South African pelagic longline fishery, and the predictable nature and spatial concentration of the Jupiter *N. brevirostris* aggregations would make this population more suitable for a management strategy of this nature. Seasonal closures to protect aggregating groups are only effective however if they span the entire duration of the species' aggregating period (Pears et al., 2007). Fortunately the identified consistent temporal duration of the Jupiter *N. brevirostris* aggregations has been revealed by the results of this study, which would provided the appropriate duration for a time closure.

5.4.1.2. *N. brevirostris* group/aggregating behaviour

The results of the identified number of unique transmitter IDs per hour at the MG111 aggregation site (Figure 106), indicates consistent *N. brevirostris* group presence. Periods of high acoustically tagged *N. brevirostris* presence in the same hour suggests that more *N. brevirostris* were also present during the same periods. Further group presence was supported by identified acoustically tagged *N. brevirostris* only representing a sub-study-population of a larger seasonally aggregating population. Grouping unique transmitter IDs by day rather than hour removed the influence of diel activity variations (section 5.3.7) and revealed periods of consistent daily group presence during the seasonal winter aggregation periods. Prolonged day-to-day periods of group presence indicates that group behaviour is a common occurrence in the mature life-history of the seasonally local *N. brevirostris* population. Group behaviour has been documented to greatly increase vulnerability to fisheries pressures for both teleosts (Pears et al., 2007, De Mitcheson et al., 2008, Graham et al., 2008) and shark (Vaske et al., 2009) species. Thus during the aggregating periods, the mature *N. brevirostris* are subject to elevated levels of vulnerability, due to group behaviour in addition to the significant influence of multiple shark presence on bait attempts, as documented by the video trials (section 4.4.1.2). Additionally regular multiple *N. brevirostris* catches witnessed in the night-time BBFS Jupiter fishing efforts (personal observations 2007 – 2009) would suggest that *N. brevirostris* are also exhibiting group behaviour at night, and subsequently high catchability. With local commercial shark fishing efforts occurring at all hours, *N. brevirostris* are at continual high risk of capture whilst seasonally locally present.

5.4.1.3. Diel activity variation

The Jupiter *N. brevirostris* population showed distinct diel activity patterns during their seasonal residency. It is logical that the acoustically tagged *N. brevirostris* would produce more acoustic detections at the monitor sites during daylight hours (Figure 108), as the monitor site locations were based on daylight hour diver observations of aggregating behaviour. A possible explanation for the observed patterns of a dawn activity peak and subsequent decline is as follows. The rapid decline following the dusk period is probably a group movement in search of prey (Gruber et al., 1988, Morrissey and Gruber, 1993a, Sundström et al., 2001). *N. brevirostris* have never been witnessed to actively hunt at the aggregation sites (personal observation and personal communications with local sport divers 2007 – 2009), with few successful captures achieved in these locations at night (personal observations 2007 – 2009), therefore it is likely that they move to other areas to seek prey at night when their metabolism is higher (Nixon and Gruber, 1988). The decline in activity continues until midnight, at which point activity at the know aggregation sites begins to increase again. The majority of longline catches in Bimini occurred between dusk and midnight (section 3.3.3), therefore it is likely that this is the time period at which *N. brevirostris* most actively seek prey.

Following the hunting activity, the Jupiter *N. brevirostris* probably returned to the aggregation sites to rest and digest their meals (Sims et al., 2006a). The peak of activity at the aggregation sites follows dawn, suggesting that this is the time of greatest *N. brevirostris* resting behaviour. This would explain the low number of *N. brevirostris* longline catches in Bimini during this time period (section 3.3.3). For individuals that were successful in feeding the night before, the digestion period would be in part dependant of the size of the meal consumed (Newman, 2003, Cortes and Gruber, 1990, Wetherbee et al., 1990, Cortes and Gruber, 1994). Therefore hunger driven feeding motivation would vary in intensity, during the course of the daylight hours, between individuals (Wetherbee et al., 1990). As hunger increases in some individuals they may have been motivated to leave the aggregation sites to seek prey (Wetherbee et al., 1990, Cortes and Gruber, 1994, Cortes and Gruber, 1990), thus different individuals would depart at different times, explaining the steady decline throughout the daylight hours, until dawn when the group feeding behaviour started again. *N. brevirostris* will sporadically feed at the aggregation sites, with scavenging observed should individuals be presented with an opportunity, as successful fishing attempts were made during daylight hours at the aggregation sites (personal observations 2007 – 2009). Therefore *N. brevirostris* are susceptible to fishing pressure at all hours of the day.

5.4.1.4. Study population

The Jupiter *N. brevirostris* study population (Table 9) and Vemco acoustic population were of a suitable size to provide a representative sub-sample of the larger aggregating *N. brevirostris* population (Zar, 1984). The study population was also a good representation of both male and female individuals with near equal numbers in the total population and equal numbers in the Vemco acoustic population. This indicates, assuming equal catchability between sexes, that the Jupiter *N. brevirostris* population is comprised of near equal proportions of males and females. Only one recapture from 2005 – 2009 meant that it was not possible to provide population abundance estimates, however given that the most individuals observed in a single aggregating population is ~100, this probably represents a substantial proportion of the total seasonally aggregating population.

5.4.2. Adult *N. brevirostris* movements/migrations and implications for vulnerability

This study documented a number of large scale movements and repeated migrations made by adult *N. brevirostris* that represented advancement in the understanding of adult *N. brevirostris* life-history. Annual movements across U.S. state and international boundaries highlighted the spatial difficulties associated with managing Highly Migratory Species (HMS; Bradshaw et al., 2008, Levesque, 2008, Grant and Quinn, 2007, Shillinger et al., 2008), and demonstrated the broader geographical vulnerability of adult *N. brevirostris*. Documented transition from the U.S. east coast and Bahamas showed clear evidence of adult *N. brevirostris* mixing between the respective population distributions. Collectively, the post aggregation period dispersal distribution of adult *N. brevirostris*, away from the Jupiter area, showed that the seasonal aggregation represented a concentration of individuals from a wide catchment area (a latitudinal minimum of 1,225 km of). Therefore, during the aggregation periods *N. brevirostris* were subject to increased vulnerability to targeted commercial fishing efforts (De Mitcheson et al., 2008, Pears et al., 2007, Vaske et al., 2009). The main aforementioned points are discussed in further detail relative to the results in the following subsections.

5.4.2.1. Existing Cooperative Shark Tagging Program (CSTP) results

The most significant CSTP result was the movement of one individual from the waters of Bimini, Bahamas, to the state waters of Florida inside the U.S. EEZ (Kohler et al., 1998). This strongly indicates that there are direct physical links between the *N. brevirostris* populations of Florida and the Bahamas, as suggested genetically by Feldheim et al. (2001a). Based on the CSTP mark-recapture results (Figure 117), current knowledge of *N. brevirostris* large-scale movements/migrations was somewhat limited. The CSTP mark-recapture design ordinarily involves that removal of the external tag at the time of recapture (Kohler and Turner, 2001). As a result only a single movement could be recorded from each individual and therefore no repeated migrations. A temporal increase in the number of research groups involved in the CSTP has recently resulted in many mark-recaptures being released with the external tag still in place, so there is future potential for the CSTP to provide evidence of repeated migrations (personal communication Kohler 2005 – 2009). Most notably from the existing results none of the mark-recapture locations represent movements of mature *N. brevirostris* across U.S. state boundaries relative to original tag location (Kohler et al., 1998).

5.4.2.2. State-wide movements

State wide movements were recorded, both south to the Florida Keys and north to seasonal juvenile *N. brevirostris* aggregation grounds (Reyier et al., 2008) of Cape Canaveral, away from the Jupiter aggregation grounds. The identified movements between the Florida Keys and Jupiter aggregation grounds (Figure 118) showed that *N. brevirostris* present on the Jupiter aggregation grounds are annually subject to fisheries pressures from both fisheries local to the Jupiter area and the substantial commercial shark fishery operating out of Stock Island (personal communications FWC biologist Dave McGowan), and the intense levels of recreational shark fishing that takes place in the Florida Keys (Valentine et al., 2008). It would appear that this dual pressure can be imposed both outside of, and during, the identified aggregating period, with repeated and rapid large scale movements between Jupiter and the Florida Keys documented within the aggregating period. Documentation of individuals from the Jupiter area as far south west as 505 km shows the currently known southerly scope of the winter Jupiter *N. brevirostris* aggregations catchment area are comprised of individuals from a large southern distribution.

The rapid and extensive repeated movements documented for the mature *N. brevirostris* between the Jupiter aggregation grounds and the Dry Tortugas were very interesting. The individual would have had to travel at a consistently high swimming speed to make the repeated journey. The swimming speeds, (71 km^{-1}), are on the estimated upper limit for *N. brevirostris* sustained swimming speeds (Sundström et al., 2001), suggesting that the individual was travelling directly to and from the Dry Tortugas. The motivation is currently unclear, seasonal grouper and snapper spawning aggregations (Lindeman et al., 1998) have been witnessed to attract large numbers of *N. brevirostris* in the Dry Tortugas (personal communications Feeley FWC 2009), however the timing of these aggregations does not coincide with the documented movements (Lindeman et al., 1998). Further monitoring and investigation is required in order to reveal the motivation driving these movements.

The occurrence of 18 adult *N. brevirostris*, originally acoustically tagged on the Jupiter aggregation grounds, in the records of the Cape Canaveral near shore acoustic monitors represents the largest ever number of *N. brevirostris* documented to simultaneously travel over large distance (200 km). The high average swimming speed (21 km d^{-1} ± 6.5 s.e.) relative to the previously highest value, documented under the CSTP, of 7.5 km d^{-1} (Kohler et al., 1998) indicating that these *N. brevirostris* were travelling to Cape Canaveral with steady movement and little residency at any locations en route. Awareness of the presence of large seasonal aggregations of juvenile *N. brevirostris* at that location (Reyier et al., 2008) could have indicated that this behaviour represents and annual feeding behaviour. However, the presence of the juveniles relative to the arrival of the older cohorts was separated temporally by 29 days (Figure 119), therefore it is unlikely that the mature *N. brevirostris* travel to Cape Canaveral to feed on the juveniles. The presence of the juveniles suggests that that the Cape Canaveral area is an *N. brevirostris* nursery (Franks et al., 2009, Reyier et al., 2008), and the fact that the majority of the adult *N. brevirostris* that made the journey are female indicates that they may have been travelling to the area for parturition. However, extensive sampling of the Cape Canaveral juvenile *N. brevirostris* has revealed that neonates comprise a very small proportion of the total population (Franks et al., 2009, Reyier et al., 2008). If the Jupiter *N. brevirostris* were utilising the area on mass for parturition, neonates would be expected to be in considerably higher proportions (Barker et al., 1997, de Freitas et al., 2009, Feldheim et al., 2002a), indicating that the Cape Canaveral juvenile population receives recruitment from another location (Franks et al., 2009, Reyier et al., 2008).

It is therefore possible that the mature *N. brevirostris* are simply present at Cape Canaveral after seasonally leaving the Jupiter aggregations on their way to cooler waters in the north. This theory is supported in that these *N. brevirostris* did not return to the Jupiter monitor sites that year following their presence at the Cape Canaveral monitor sites, and 5 of the 18 were recorded at locations further north (see section 5.3.10). The specific presence of these mature *N. brevirostris* at the exact location of the seasonal Juvenile aggregations may simply be the result of environmental conditions or prey availability that make the Cape Canaveral area favourable for both juvenile and mature *N. brevirostris* (Vogler et al., 2008). Continual research is required to further understand the relationship between the Cape Canaveral area and the Florida *N. brevirostris*.

5.4.2.3. Movements/migrations across state boundaries

The repeated annual nature of many of the *N. brevirostris* displaying large-scale movements across state boundaries (Figure 120) indicates that these movements represent annual migration patterns for U.S. east coast *N. brevirostris*. Many of the residence times at the documented locations of greatest displacement were considerable. Thus combined with the lengthy seasonal residence at the Jupiter aggregation grounds, and the likely journey times between the two locations, the identified north and south locations likely represent the majority of their annual site attachment. Swimming speeds are generally above the maximum identified from the CSTP (Kohler et al., 1998), and consistently high over the long travel periods indicating direct transitions between the north and south locations, with little residency at locations in between. Therefore the two locations may represent the latitudinal distribution limits, both north and south, for these specific individuals.

Since temperature appears to be the dominant environmental factor driving the annual *N. brevirostris* aggregations in Jupiter, with lower temperatures for the area seemingly favoured (section 5.4.3), it is logical that the *N. brevirostris* would seek the cooler waters of the more northern latitudes during the summer months. North south seasonal migrations have been documented for a number of other shark species (Hussey et al., 2009a, Skomal et al., 2009, Weng et al., 2008, Dicken et al., 2007, Grubbs et al., 2007), therefore it is logical that *N. brevirostris* would adopt a similar behaviour to maintain a preferred temperature range. In order for the desired seasonal temperature to be encountered in shallow coastal waters, *N. brevirostris* present on the Jupiter aggregation grounds during the winter must travel great distances north. Resultantly they must cross state boundaries exposing them at different times of the year to variations in state water (0 – 3 miles from shore) shark fishing regulations (FWC, 2009a, GADNR, 2009, SCDNR, 2009), with four *N. brevirostris* documented to have annually crossed not one but two state boundaries. This highlights both the difficulties associated with and shortcomings of attempting to manage Highly Migratory Species (HMS) on a state government level (Grant and Quinn, 2007, Shillinger et al., 2008).

The *N. brevirostris* documented to have exhibited large-scale migrations to Georgia and South Carolina represents a relatively large proportion of the total Jupiter *N. brevirostris* project study population (Figure 120). Geographically they have been documented in areas with the benefit of acoustic coverage under the ACT array group, but in two geographical locations that are separated by ~290 km of coastline. The separation between the two locations indicates that in the more northern latitudes, during the summer months, water temperatures, or even general environmental conditions, that are preferable to mature *N. brevirostris* are distributed over a wide area. Therefore it is logical that during the summer months the *N. brevirostris* are distributed geographically over a considerably wider area than when present at the Jupiter aggregation grounds. Thus the behaviour of the adult *N. brevirostris* observed at the Jupiter aggregation grounds in the winter months represents a considerable concentration of a population that in the summer months is distributed over a much larger geographical area.

The seasonal concentration of *N. brevirostris* in Jupiter is similar to the documented concentrations of teleosts during spawning aggregations, indicating that the Jupiter aggregation grounds constitute Essential Fish Habitat (EFH) for *N. brevirostris* (De Mitcheson et al., 2008, Graham et al., 2008, Lindeman et al., 1998, Pears et al., 2007, Rieser, 2000). Based on EFH, the Jupiter aggregation grounds could possibly be designated a Marine Protected Area (MPA) under the Magnuson-Stevens Fishery Conservation and Management Act (Rieser, 2000). Fixed MPAs could prove successful in protecting site-attached immature *N. brevirostris* such as the Bimini juvenile and sub-adult populations (Chapman et al., 2009). However, for species displaying large-scale seasonal movements, such as the adult *N. brevirostris*, designated MPAs do not offer full protection with individuals still subjected to fishing pressures when they move outside of the MPA boundaries (Hunter et al., 2006, Apostolaki et al., 2002, Kerwath et al., 2009).

5.4.2.4. Movements across fishery management zone boundaries

As the result of large-scale movements away from the aggregation grounds *N. brevirostris* are annually subject to the fishing pressures of three designated management zones of the U.S. pelagic longline fisheries (Figure 121; Mandelman et al., 2008). Subsequently the Jupiter *N. brevirostris* aggregation population are annually at risk of harvest under three federal sets of commercial shark fishing quotas (Mandelman et al., 2008). Once again this highlights the shortcomings of regional management for HMS (Grant and Quinn, 2007, Ballesteros and Gonzalez, 2007, Hunter et al., 2006, Musick et al., 2000, Shillinger et al., 2008). The north-western Atlantic *N. brevirostris* population distribution represents a single stock (Feldheim et al., 2001a), therefore a single quota for *N. brevirostris* should be in effect for all vessels operating within the limits of the north-western Atlantic *N. brevirostris* population distribution.

5.4.2.5. International movements outside of U.S. EEZ

The documentation of an international movement by a mature *N. brevirostris* outside of the U.S. EEZ, represents the second documented transition of a mature *N. brevirostris* between the U.S. and the Bahamas (Figure 122). This, in addition to the transition recorded from Bimini to the U.S. east coast (Kohler et al., 1998), strengthens the theory of a direct link between the *N. brevirostris* population of the Bahamas and the *N. brevirostris* population of the U.S. east coast. This would in part explain the documented genetic flow across the entire western Atlantic *N. brevirostris* distribution (Feldheim et al., 2001a). Though only 95 km in distance, thus not a considerably large movement, it does represent the only movement that definitely occurred over an area of considerably deep open water, the Gulf Stream, and certainly of considerable distance from the U.S. coastline. It is possible that this movement was simply a response to the years of shark feeding by the recreational dive charters at this location that has resulted in regular false *N. brevirostris* aggregations. However, in the winter months at the Tiger Beach feeding site, many of the mature female *N. brevirostris* present have considerable and fresh mating scars (personal observations 2007 - 2009). Therefore it is possible that this recorded international movement was a product of mating behaviour, which would further explain the cross-distribution genetic flow.

Regardless of the motivation for the movement this again highlights one of the many problems associated with managing stocks of sharks and other HMS. Many other shark species have been document to make movements/migrations across EEZs (Kohler et al., 1998, Skomal et al., 2009, Gore et al., 2008), therefore in order to effectively protect a shark species such as *N. brevirostris* for the duration of its complete life-history (Shillinger et al., 2008, Levesque, 2008). In addition to protection throughout the annual distribution of its movements, it is necessary to have cooperation and uniformity in regulations across state boundaries, fisheries management regions and intentional distribution limits (Levesque, 2008, Shillinger et al., 2008). For example, despite receiving full protection in Australian waters, Bradshaw et al. (2008) found *R. typus* abundance to decline by 40% over a decade, as the result of fishing pressures in other geographical areas visited in their seasonal migrations. Politically, international cooperation in shark management can be extremely difficult to achieve (Levesque, 2008). In this particular documented case for *N. brevirostris*, the relationship between the U.S. and Bahamian government is reasonably favourable. However it is quite possible the *N. brevirostris* may travel between the waters of the U.S. and Cuba, a transition that many other species have be documented to make (Skomal et al., 2009, Howey et al., 2009), in which circumstance the political volatility between the two countries would make any form of regulatory cooperation extremely unlikely.

5.4.2.6. *N. brevirostris* large scale movements/migrations summary

The total coastal span of documented *N. brevirostris* movements from the Jupiter project (1,225 km) represents a large proportion of the U.S. east coast geographical extent. The relative distance parameter study population proportions (Figure 123) are relatively high, given a low expected success rate of documentation away from the heavily monitored aggregation grounds. The addition of a relative *N. brevirostris* absence, in both the acoustic records and visual reports from local divers/fishermen, suggests that many of the other *N. brevirostris* not documented in locations away from the aggregation grounds would have probably undertaken similar movements/migrations. Therefore it would appear that the Jupiter winter aggregations represent a spatially intense concentration on *N. brevirostris* from a very large catchment area within the total *N. brevirostris* U.S. east coast distribution. The maximum recorded distance travelled for a mature *N. brevirostris* in the Jupiter project (720 km) is considerably greater than the previously documented maximum (425 km; Kohler et al., 1998). The average speed travelled between the Jupiter aggregation grounds and the documented displaced locations (20.2 kmd^{-1} ± 8.6 s.e.) is also considerably higher than the previously documented maximum (7.5 kmd-1; Kohler et al., 1998), indicating more direct movements to the *N. brevirostris* large-scale displacement locations, particularly for males, than previously believed

(Feldheim et al., 2001b, Feldheim et al., 2004). The advancements in our knowledge of large-scale movements and seasonal migrations, revealed by the Jupiter aggregation project, represent a considerable advance in the understanding of mature *N. brevirostris* life-history.

5.4.3. Influence of water temperature over adult *N. brevirostris* behaviour, movements and migrations

Monitoring of environmental parameters revealed a strong influence of water temperature over the aggregating period, movements and migrations for adult *N. brevirostris*. The adult *N. brevirostris* that for the Jupiter aggregations appear to have a water temperature preference of ~23/24°C, which dictated the annual aggregation period, and was the driving variable for both latitudinal and vertical depth movements.

N. brevirostris activity (Figure 109) showed a consistent negative relationship with temperature. Closer inspection of the 2008 aggregation season (Figure 110) indicated that the temperature cue appeared to be around ~24/23°C, with the seasonal period where mean daily water temperature remained consistently below 24°C defining the seasonal residence of the local *N. brevirostris* population. This may have been the result of a metabolic temperature preference (Sims et al., 2006a) or the result of following a prey species that's movements were defined by temperature (Hussey et al., 2009a). *N. brevirostris* present on the array grounds selected a temperature distinctly below the annual average (Figure 111). Regardless of specific cause, it does strongly appear that water temperature is the consistent cue for the *N. brevirostris* presence at this locality. This is slightly higher than the temperature range (18 - 22°C) that appears to define the immature *N. brevirostris* aggregation period at Cape Canaveral (Reyier et al., 2008), though the immature *N. brevirostris* may be departing the area ahead of environmental cues to avoid the conspecific predation risk associated by the arrival of the adults on their migration north (see section 5.4.2; Webster, 2004). Water temperature has been documented as the environmental cue driving movements and migrations for other ectothermic species, such as *Carcharhinus plumbeus* (Grubbs et al., 2007), *Carcharhinus limbatus*

(Heupel, 2007) and *Rhizoprionodon terraenovae*, which were found to have a similar temperature preference to the immature *N. brevirostris* of 20 - 22°C (Parsons and Hoffmayer, 2005).

Documented southerly migrations of several *N. brevirostris*, from the latitudinal area that they spent the majority of their seasonal residence, within the confines of the array coverage, do appear to be in response to a temporary drop in current strength (Figures 112 and 113). However, several subsequent similar drops in current strength do not correspond to similar *N. brevirostris* southerly movements. The documented *N. brevirostris* southerly migrations also appear to be in response to a temporary drop in water temperature (Figure 114). Subsequently water temperature remains stable for the remainder of the period and *N. brevirostris* latitudinal residence remain relatively constant. Therefore it would appear that water temperature is more of a driving force for local *N. brevirostris* movements than current strength. Temperature appears to have driven both the *N. brevirostris* aggregation residence period and local moments within the aggregation ground, similar to temperature influencing immature *N. brevirostris* movements in the Bimini lagoon (Sundström et al., 2001, Morrissey and Gruber, 1993a).

The depth and temperature profiles obtained from the successful PTT-100 deployment (Figure 115) also showed evidence of individual *N. brevirostris* temperature preference. Following the three day period of erratic depth and temperature, profiles appeared to become more stable. It is likely that the three day period of erratic reading represents a period of recovery for the *N. brevirostris* after the capture and prolonged attachment process. Following the period of recovery the profiles probably represent more natural behaviour around the aggregation grounds. During the period of natural behaviour, the host *N. brevirostris* appeared to regularly adjust its depth in order to maintain a very consistent water temperature of ~24°C, with no apparent vertical migrations at the expense of maintaining the temperature as documented for other shark species (Chapman et al., 2007, Shepard et al., 2006, Kubodera et al., 2007).

Collectively the numerous indications that temperature is driving both the aggregating periods and local latitudinal and vertical movements, strongly suggests that temperature is a strong driving factor in both the annual and day to day distribution of mature *N. brevirostris* attending the seasonal aggregations. It is interesting that temperature preference appears to be so specific for these mature *N. brevirostris*, as, although water temperature does appear to effect habitat selection, at the juvenile and sub-adult life-stage in Bimini small home-ranges and site attachment results in immature *N. brevirostris* enduring large annual water temperature variations (Franks and Gruber, 2007, Sundström et al., 2001, Morrissey and Gruber, 1993a). It is possible that water temperature becomes more important for *N. brevirostris* once they reach maturity and enter into reproductive behaviour, as water temperature has been documented to be of importance in the reproductive functions of other elasmobranch species (Mull et al., 2008, Hight and Lowe, 2007, Wallman and Bennett, 2006).

5.4.4. Study population mortality rates and adult *N. brevirostris* sustainability

Fishing related mortality rates recorded for the Jupiter adult *N. brevirostris* study population indicate that *N. brevirostris* were being commercially harvested at unsustainable levels. For the annual period of 2008 – 2009, the Jupiter *N. brevirostris* study population fisheries related mortality ($f = 0.06$) was greater than or equal to the maximum potential for population growth rate (r-intrinsic = 0.02 – 0.06; Gedamke et al., 2007, Cortes, 2000). Parameters for a sustainable fishery require $f <$ r-intrinsic (Gedamke et al., 2007), therefore *N. brevirostris* fisheries, targeting the Jupiter study population, even when the highest r-intrinsic estimate (0.06) is accepted, are unsustainable. Assuming that the Jupiter study population is a representative sub-proportion of the larger Jupiter aggregating population, this would suggest that fisheries targeting *N. brevirostris* from the arrogating population are also unsustainable.

The high proportion of *N. brevirostris* that did not return to the aggregation grounds from one season to the next means that the status, living or dead, of many study individuals was unknown, and those that did not return may have been harvested. Tag returns from commercial fishermen are uncommon (Kohler and Turner, 2001), and it is likely that for this project they were largely driven by unfamiliarity to the acoustic tags and curiosity in relation to the promised rewards. Therefore the documented fisheries related mortality is probably an underestimate and *N. brevirostris* fisheries are more unsustainable than suggested by this dataset. *N. brevirostris* are clearly overexploited by the U.S. east and Gulf coast fisheries.

5.4.5. Research methodology implications

The results of the a number of research methodologies employed have a number of further implications, for both the results of this study and potential future methodology employment, that are discussed in the following subsections.

5.4.5.1. Deduction of acoustic monitor range

The deduction of acoustic monitor range allowed for a clearer understanding of the acoustic monitor records representing *N. brevirostris* movements and behaviour. At 900 m, only 2% of the expected transmitted signals were recorded (Figure 104), indicating this to be the upper limit of VR2W detection range at the MG111 site under optimal acoustic conditions. At 600 m, 37% of expected transmissions were recorded, therefore the VR2W monitors were only achieving this range for less than half of the deployment time. At 150 m, 94%, and at 300 m 87%, of the expected transmissions were recorded, therefore the monitors were achieving a minimum 300 m range for the vast majority of their deployment time. Thus for the majority of received acoustic detections it can be confidently stated that a recorded transmission represented the presence of an *N. brevirostris* issued with a transmitter within 0 – 300 m of the monitor site. Therefore the majority of documented group behaviour (section 5.3.6) was representative of multiple acoustically tagged *N. brevirostris* simultaneously occupying the same circular area of 300 m radius.

5.4.5.2. Acoustic fishing

A number of acoustically tagged *N. brevirostris* were documented to be present during fishing efforts through the acoustic fishing method (Figure 103). The documented simultaneous presence of multiple *N. brevirostris* during fishing efforts further indicates that the Jupiter *N. brevirostris* are exhibiting group behaviour. The number of acoustically tagged individuals recorded generally increased throughout the duration of the seasons' fishing efforts logically, with progressively more acoustically tagged *N. brevirostris* added to the Vemco acoustic study population. Interestingly, *N. brevirostris* caught and acoustically tagged in earlier fishing efforts returned to the fishing grounds within a few days of capture, indicating that initial capture and processing only caused minor and/or short-term disturbance to their natural behaviour. Up to 18 previously caught *N. brevirostris* were detected in a single fishing period, without a single recapture recorded. This suggests that the *N. brevirostris* of the Jupiter aggregations may have learned to associate the negative experience of capture/processing with the fishing technique employed, and were subsequently actively avoiding fishing gear.

5.4.5.3. *N. brevirostris* detections and benefits of FACT array group

The number of *N. brevirostris* acoustic detections recorded by the BBFS array (510,561) forms an exceptionally large database. The BBFS array comprises only 11% of the overall FACT array, yet has recorded around five times the number of detections than have been recorded on monitors belonging to other FACT member groups. However, it is logical that the BBFS monitors received considerably more acoustic signals, as their locations were based on known areas of *N. brevirostris* activity, thus detections on other FACT members receivers, positioned to capture transmissions from other study species, would result from more incidental detections. The additional FACT array detections were of great value as they describe movements and residence in locations that would otherwise not have been revealed by direct available resources. The 103 FACT monitors that did not receive any transmission also provide valuable information of the areas that the acoustically tagged *N. brevirostris* do not utilise. This information is not usually available as positioning receivers in these location is not justified due to unit cost (~US$1,500) of the deployment of a BBFS receiver.

Most notably, it was hypothesised that the gravid female *N. brevirostris* present on the aggregation grounds would enter the inter-coastal waterway for parturition (Kessel et al., 2008). However, with half the Vemco *N. brevirostris* study population female and many pregnant at the time on transmitter implantation, to date no detections have been recorded on any of the inlet monitors. This strongly indicates that they are not entering the inter-coastal waterway and are therefore unlikely to be using it as a nursery ground. Again this information would not have been available without the collaboration of the FACT array group.

5.4.5.4. Pop-off archival satellite tag success rates

Overall a 25% success rate was relatively low for this technology relative to its employment in the study of other species (Skomal et al., 2009, Sims et al., 2005, Howey et al., 2009, Conrath and Musick, 2008). This would suggest that the new attachment methods did not improve operational success as intended, and may have even hindered successful operation. It is likely that the new attachment methodology over-complicated what was already a very complex technology. Therefore adopting the dorsal fin bracket system is not recommended. Of the three long-term tags that detached prematurely relative to their intended deployment duration, two still provided *N. brevirostris* displacement locations that were beneficial in advancing the understanding of *N. brevirostris* mature life-history, and the population structure of the western Atlantic *N. brevirostris* distribution (see section 5.3.10).

From interpretation of these results alone the *N. brevirostris* host of the PTT-100 that detached prematurely due to the constant depth function would have died. However, all *N. brevirostris* issued with a pop-off archival satellite tag during this project were also issued with a V16H internal acoustic transmitter. Cross reference of the PTT-100 results with the Vemco acoustic detection for this shark revealed that it was not deceased and was still very active around the monitor sites following the PTT-100 premature deployment. Thus the premature detachment was most likely the result of a PTT-100 malfunction or the shark simply remaining within a small depth range for the three day period. It should be noted that without the benefit of the dual tracking techniques employed, pop-off archival satellite in conjunction with the Vemco acoustic monitoring system, the individual would have been incorrectly assumed to be dead.

5.5. Conclusion

The Jupiter *N. brevirostris* aggregations are an annually occurring seasonal event, focused around the winter months of December – April. Water temperature appears to be the environmental cue that defines the arrival, departure and residency period of the aggregating *N. brevirostris*, with an apparent water temperature preference of around 24°C. Water temperature also appears to drive local movements within the seasonal site-attached array grounds, similar to temperature driven habitat utilisation described previously for the sub-adult life-stage (Gruber et al., 1988, Morrissey and Gruber, 1993a, Sundström et al., 2001). The seasonal winter aggregations in the Jupiter area represent a concentration of *N. brevirostris* from a wide catchment area of their U.S. east coast distribution, from a coastal span of 1,225 km. Male *N. brevirostris* appear to exhibit considerably more purpose in their seasonal movements/migrations than was previously believed. The documented *N. brevirostris* transition between the U.S. and Bahamas provides strong evidence in support of previously documented *N. brevirostris* gene flow between the two geographic locations.

In addition to National Marine Fisheries Service (NMFS) Environmental Risk Assessment (ERA) result ranking *N. brevirostris* as 'most vulnerable' of the Large Coastal Shark (LCS) species to over-fishing (Cortes et al., 2008), seasonal residence off the coast of Jupiter further increases *N. brevirostris vulnerability* through an increase in *susceptibility*, where susceptibility is a product of *availability*, *encounterability*, *selectivity* and *post-capture mortality*. The Jupiter *N. brevirostris* aggregations represent a seasonal spatial concentration to a specific area, in which further concentrated aggregating groups occur. Therefore a combination of the seasonal concentrations and inshore migration of fishing activities, driven by escalating fuel prices, result in a local increase in susceptibility through increased *availability* and *encounterability* to the local commercial shark fishermen. The local aggregating behaviour significantly increases the likelihood of bait attempts by *N. brevirostris* and thus increased catchability on encounter in addition to increased encounterability. The specific targeting of the *N. brevirostris* aggregations by local commercial shark fishermen further increases local susceptibility through both increased *selectivity* and *post-capture mortality*, with increased likelihood of harvest on capture.

The increases in perceived *N. brevirostris* vulnerability has emerged when the *N. brevirostris* fisheries, prior to declared future targeting, appears to already be operating an unsustainable level. Thus there is an urgent need to actively address *N. brevirostris* vulnerability in the U.S. east and Gulf Coast fisheries, thus the BBFS research group has made the following recommendations to FWC.

5.6. Recommendations to FWC

In response to the combination of NMFS ERA results and the further seasonal local increase in vulnerability highlighted by the results of the Jupiter *N. brevirostris* study, it is highly recommended that Florida Fish and Wildlife (FWC) make the following alterations to their shark management regulations:

Addition of N. brevirostris to prohibited species list – this would be the most effective and immediate measure that should be taken, also keeping shark regulations desirably simple, with enforcement measures regarding the prohibited list already in place. Addition to the prohibited species list (Appendix 1) would be justified by the highlighted vulnerability relative to other LCS species in state waters. The ease of *N. brevirostris* identification relative to other LCS would allow for immediate post-capture release should individuals become incidentally captured.

Should the addition of *N. brevirostris* to the prohibited species list been deemed unfeasible, the following alternative alterations to shark management regulations are highly recommended:

Annual seasonal closure of Florida east coast N. brevirostris fishery from December - April – justified by the increased *N. brevirostris* vulnerability during this period. This would offer a required increase in protection at a time of identified behaviour driven increased vulnerability.

Increase minimum take size for N. brevirostris from 54" to 88", or conversely make 54" maximum take size – both actions provide protection for the breeding population, as is appropriate for *K*-selected species (Kinney and Simpfendorfer, 2009, Gruber and Hoenig, 1990).

Reduce recreational bag limit from 2 -1 LCS per vessel per day – not only reducing potential recreational fishing pressure, but also reducing the potential for considerable LCS commercial harvest under the protection of the recreational regulations.

All above recommendations can be enforced through the existing marine patrols and fish houses, with no additional management resources required. In addition to either of the above set of recommendations, a final important recommendation is made:-

Political push for incorporation and compliance of newly adopted FWC shark management regulations within the Atlantic States Marine Fisheries Commission (ASMFC) shark management regulations – providing protection for *N. brevirostris* across the entire scope of their annual seasonal movement/migration patterns. Only when protection is provided at an appropriate scale for the *N. brevirostris* full life-history will their near and long-term future in the U.S. marine environment be secured (Kerwath et al., 2009, Shillinger et al., 2008, Levesque, 2008).

6. General Discussion and Conclusion

6.1. General discussion

The key findings of this study are:

- In the northwest Atlantic, *N. brevirostris* populations are experiencing considerable anthropogenic pressure at all life-stages;
- In Bimini, Bahamas, the effects of large-scale resort development have resulted in a significant decline in *N. brevirostris* abundance in the secondary lagoon population, to level a well below the temporal average;
- On the U.S. east and Gulf coasts, seasonal aggregating behaviour is further increasing *N. brevirostris* vulnerability to overfishing, beyond the highly vulnerable status already attributed to this species, while *N. brevirostris* fisheries appear to be operating at unsustainable levels;
- At all life-stages *N. brevirostris* appear to be highly sensitive to anthropogenic activities, relative to other Large Coastal Shark (LCS) species, and therefore require special management consideration;
- Shark longline catchability is significantly influenced by multiple shark presence, resulting in greater susceptibility for species, such as *N. brevirostris*, that naturally exhibit group behaviour;
- Incidental encounterability and predation risk significantly influence *N. brevirostris* longline CPUE in Bimini;
- Adult *N. brevirostris* exhibit large-scale seasonal migrations on the U.S. east coast, which, in addition to documented international transitions, supports existing evidence for genetic mixing across the northwest Atlantic *N. brevirostris* distribution;
- Water temperature is an important environmental variable driving *N. brevirostris* behaviour at all life-stages, with an apparent adult *N. brevirostris* temperature preference of ~24°C.

The broader implications of the aforementioned key findings will now be discussed in the following subsections.

6.1.1. Implications of research techniques utilised, and variables assessed, to the field of shark research and stock assessment

Longlines have been utilised in shark research for many years and their successful utilisation in this study has highlighted their potential for long-term shark population assessments. When set up correctly, operated in the absence of sacrificial research based study, and with an appropriate level of monitoring, longlines can be employed as a shark assessment tool producing minimal capture related mortality and thus imposing little impact on the marine life populations that inhabit the study area. Analysing by Catch Per Unit Effort (CPUE) is an accepted method for dealing with disproportionate UE over time. However, in this study, contrasting patterns between periods of disproportionate UE and periods of well structured research design indicated that CPUE analysis is no substitute for solid research design. This is especially true for long-term studies, such as this, where species specific seasonal variations play a role in defining the results.

It has long been accepted that many factors affect the catch, and therefore the results, of the longline research technique (Ward, 2008, Stoner, 2004). The results of this study have highlighted the relative significance of some of these previously identified factors, often with considerable variations found. For any given longline based population assessment, confidence in the results should be increased by the specific assessment of the influence of these factors relative to the specific study area and species under review. The identification of species specific variations in this study highlights the importance of consideration of all existing species life-history information in the interpretation of catch results. Although time and effort consuming, accounting for influencing variables as much as possible is essential to increase the accuracy of the results, which are, in turn, used as the basis for management regulations. Of course, it is unfeasible in such studies to account for all potential variables and a level of assumption will always be necessary. However, the successful employment of several research techniques and the monitoring of potential driving variables at the time of longline deployment in this study, has demonstrated the potential to quantitatively account for some of the more influential factors affecting longline catches.

The simple use of temperature loggers on longline sets revealed significant positive correlations between temperature and CPUE for a number of species. The employment of underwater video surveillance of baited hooks yielded very interesting results, most notably the significant increases and variation in bait attempts and hooking success relative to multi-shark presence. These results indicated that species that have been found to naturally exhibit group behaviour would be more susceptible to capture than sharks that have been found to exhibit more solitary behaviour. This is an example of a variable that could be accounted for by using existing species life-history data to produce species specific quantitative weightings to be applied in the analysis of catch data. Long-term focused studies using the video surveillance technique could further reveal shark species specific differences in catchability relative to gear setup. This could help to answer many of the disputed issues surrounding the status of global shark stocks (Baum et al., 2005, Burgess et al., 2005a, Burgess et al., 2005b).

The identified influence of *N. brevirostris* longline encounterability over CPUE, through comparison of set locations with the historical *N. brevirostris* telemetry dataset, has further implications for existing shark stock assessments. For example, the identified influence of encounterability over CPUE further validities the arguments of Burgess et al. (2005a), against the recent disputed stock assessments (Baum and Myers, 2004, Baum et al., 2003). Questions raised by Burgess et al. (2005a) related to discontinuity in longline set depths, between datasets, relative to species' vertical habitat utilisation patterns. In this study, encounterability related to set location relative to species' horizontal habitat utilisation. However, regardless of the plane, vertical or horizontal, the results of this study still actively demonstrated the direct influence of incidental encounterability through habitat utilisation patterns over CPUE. Therefore an estimate of species specific encounterability, based on all available data relating to habitat utilisation for that species, should be factored into longline based shark stock assessments. Furthermore, encounterability estimates should be considered essential for stock assessment comparisons based on two spatially dissimilar, both vertical and horizontal, datasets.

The employment of the aerial survey technique proved very successful in the necessary ground truthing of the historical *N. brevirostris* tracking data, which in turn provided the basis to reveal the influence of encounterability over CPUE. The aerial survey technique also proved highly successful, for *N. brevirostris* in Bimini, in providing repeated population abundance estimates. This represented the first employment of the aerial survey technique for the population assessment of a Carcharhinidae species. The success of the aerial survey approach highlighted the potential for further employment of this research technique for shark population assessments in similar habitats. The aerial survey technique would prove very useful for any shark population with a high level of site-attachment to clear shallow waters; e.g. the *Carcharhinus melanopterus* juvenile nursery population of Palmyra Atoll National Wildlife Refuge, in the Pacific Ocean (Papastamatiou et al., 2009).

The extrapolation of historical *N. brevirostris* abundance estimates from the CPUE records, based on the relative estimates from the aerial survey data, showed good potential for further development and utilisation. Validation by the mark-recapture estimates, although only based on a single year's data comparison, did appear to result in logical values. Confidence in these results could be greatly increased by the extension of field operations to allow for multiple years of comparison. Therefore, for shark populations with a high level of site attachment to clear shallow waters, with an existing CPUE historical database, the initiation of a long-term (e.g. a minimum of three years) aerial survey based comparative study could provide confident population abundance estimates as far back as the extent of the CPUE database. The adapted Lincoln-Petersen model also appeared to provide logical population abundance averages over larger research periods. This suggested that the adapted Lincoln-Petersen model has potential for employment in mark-recapture based studies operating on a relatively small scale and therefore yielding a low number of recaptures that are not suitable for analysis with the standard model.

Away from the Bimini Islands, field techniques employed in the Jupiter *N. brevirostris* aggregation study also proved successful in their application, with several implications for studies of a similar nature. Firstly, the double tagging, with an acoustic transmitter, of the PTT-100 host *N. brevirostris* revealed that the premature tag detachment was the result of an internal computer malfunction and not the mortality of the host, as would otherwise have been assumed. Therefore it is suggested that any host of a pop-off archival satellite tag should be, where feasible, double tagged with an acoustic transmitter or external ID tag, or even triple tagged with all three. Triple tagging the individual would not only increase the chances of revealing the host's fate, but also increase the chances of obtaining movement information subsequent to the transmitted release location of the satellite tag. Additional movement information to the tag pop-off location could reveal repeated migratory behaviour, particularly if the original tagging location is on an acoustic array, as this would increase the chances of a second detection if the individual returned to utilise the same area in the future.

Acoustic range assessment with fixed sentinel transmitters at the MG111 site proved successful and allowed a greater understanding of the level of specific spatial utilisation relative to the monitor locations. Therefore it is highly recommended that this technique be employed whenever possible in passive acoustic telemetry studies, particularly those based in shallow water areas where range can be highly variable. For example, the study that claimed *C. limbatus* had departed the nursery grounds of Terra Ceia Bay, Florida, during a hurricane (Heupel et al., 2003) could have yielded results with a greater level of confidence if sufficient range to detect the individuals during the storm activity was demonstrated by the use of sentinel transmitters. The 'acoustic fishing' technique proved successful in identifying the presence of acoustically tagged *N. brevirostris* during the 2009 fishing efforts, which were otherwise not recorded in the catch data. Despite the relatively high numbers present during fishing efforts (up to 18 individuals) no previously captured sharks were recaptured, strongly suggesting that the negative experience associated with the first capture had led to subsequent avoidance of the polyball gear utilised. Such learned avoidance would have considerable implications for mark-recapture based population assessments targeting shark species and may well account for the relatively low number of *N. brevirostris* mark-recaptures recorded aver the 27 years of longline activity in Bimini.

The large-scale *N. brevirostris* movements documented in this study greatly highlights the substantial benefits of collaboration/cooperation between scientific research groups. Many of the large-scale *N. brevirostris* movements would not have been revealed if it were not for the establishment of the FACT and ACT array groups, and more so, the willingness of the group members to share the data when the *N. brevirostris* detections were discovered. It symbolises a great step forward in scientific cooperation in recent years that, in this case, will go on to further progress our understanding of shark population studies. The considerably expanded coverage provided by the array groups also provided extremely important information in relation to where the acoustically tagged *N. brevirostris* did not go as well as where they did. The Vemco® acoustic system was arguably the most important and successful tool employed in revealing new information relative to the adult *N. brevirostris* population dynamics. One of the most important potential documentation it offers is that of repeated movements/migrations by individuals over multiple years. During the course of the study, from 2007 – 2009, advances in technology allowed the transmitter battery life to increase in active duration from 3 to 10 years. The increase in battery life will, from the present onwards, allow the movements of individual *N. brevirostris* to be tracked over a considerable period, necessary to truly reveal the life-history traits of a species with such longevity. Finally, the extensive global coverage provided by the Vemco® system is currently unrivalled, and with the near future implementation of the Ocean Tracking Network (OTN, 2009), coverage will be considerably increased. Therefore for scientific investigations focused on Highly Migratory Species (HMS), such as *N. brevirostris*, the Vemco acoustic system can provide an irreplaceable research tool.

6.1.2. Temporal *N. brevirostris* population variations

Through the combination of the analysis of a wide range of parameters it was possible to justify the likely causes behind the identified *N. brevirostris* CPUE temporal patterns. *N. brevirostris* CPUE was erratic from 1982 – 1989 and showed an absence of a distinct pattern, but generally appeared to decline across the period. The erratic distribution was probably the result of high capture related mortality, largely the result of sacrificial based research studies, which intermittently removed a notable proportion of what is estimated to be a relatively small lagoon *N. brevirostris* population (~158 individuals). A highly significant linear increase in *N. brevirostris* CPUE was recorded from 1992 – 2000, probably driven by natural population growth in the absence of any research related sacrifices, and a resultant low capture related mortality, coupled with an apparent absence of disruptive anthropogenic influences throughout most of the period. By 2000 *N. brevirostris* CPUE was at the highest recorded levels for the entire 27 year research campaign, which indicated that *N. brevirostris* abundance had reached the carrying capacity for the lagoon ecosystem. The highest records were followed by a highly significant linear decline in *N. brevirostris* CPUE from 2000 – 2008. It would appear that the greatest driving influence behind the CPUE decline was the substantial activities of the Bimini Bay Development, which caused large scale disruption of, and destruction to, the North Bimini terrestrial and marine ecosystems. The observed CPUE increase and subsequent decline from 1992 – 2008 may have been representative of a natural cycle in *N. brevirostris* population abundance. However, even if the observed cycle did represent a natural pattern, it is likely the identified anthropogenic influences would have greatly magnified the extent of the pattern by disrupting the size class proportions within the *N. brevirostris* lagoon population, where conspecific predation affects population abundance. Thus it would appear that anthropogenic influences have been the main driving influence behind the identified patterns in *N. brevirostris* CPUE throughout the entire research period from 1982 – 2008.

Temporal shifts in shark community structure were observed between the three research periods. *N. brevirostris*, *G. cirratum* and *G. cuvier* remained three of the four species representing the highest proportions throughout all three research periods, whereas *C. limbatus* replaced *R. porosus* in the second period and remained one of the dominant four species for the third. *N. brevirostris* CPUE proportions were high between 1982 – 1989 and increased to make *N. brevirostris* the species of highest abundance within the Bimini shark community structure from 1992 – 2003. *N. brevirostris* showed a subsequent and dramatic proportional decrease for the period from 2003 – 2008, and showed the lowest proportional CPUE of the four species. The observed increase and subsequent decrease in catch proportions is logical, given the likely identified influences driving the temporal patterns observed in the CPUE records. *G. cirratum* and *C. limbatus* both showed a steady increase between all three research periods, both subsequently comprising a large proportion of the lagoon total shark population, relative to *N. brevirostris*, by the end of the study in 2008. *G. cuvier* remained high in proportion and relatively stable throughout all three research periods, thus also comprising a large proportion of the lagoon total shark population, relative to *N. brevirostris*, by the end of the study in 2008. The low *N. brevirostris* proportion within the community structure at the end of the study, relative to the other three species, suggested that *N. brevirostris* were more affected by the identified local anthropogenic driving influences. Greater influence of localised anthropogenic activities was probably the result of a high-level of *N. brevirostris* site-attachment, and therefore high dependence on the Bimini mangrove nurseries and lagoon ecosystem for prey resources and refuge, at the juvenile and sub-adults life-stages (Sundström et al., 2001, Franks and Gruber, 2007, Morrissey and Gruber, 1993a, Morrissey and Gruber, 1993b).

6.1.3. Advances in knowledge of *N. brevirostris* life-history

The results of this study have provided vital *N. brevirostris* life-history information that will enable better regulation design and conservation management to protect *N. brevirostris*, both on a local scale in Bimini, and on a broader scale in the north-western Atlantic distribution. Population abundance estimates from both the mark-recapture data and aerial survey data extrapolations support and confirm previous estimates, based on personal observations and personal communications (Gruber 2008), for the Bimini lagoon population, with an average annual *N. brevirostris* abundance of ~158 individuals. At the time of highest CPUE records in 2000, the extrapolated *N. brevirostris* population abundance estimate was ~222 individuals, which suggested that this is the *N. brevirostris* carrying capacity of Bimini lagoon population under stable environmental conditions. The spatial distribution of the Bimini lagoon *N. brevirostris* population appears to be largely driven at the sub-adult life-stage by predation risk, which directly influenced longline encounter rates and in turn *N. brevirostris* catchability. The influence of predation risk was supported by an apparent negative relationship with *G. cuvier*, the most likely species to pose predation risk on *N. brevirostris* (Lowe et al., 1996). Conversely a positive relationship was identified with *G. cirratum*, a species unlikely to pose a predation risk on *N. brevirostris*, and no relationship was found between *C. limbatus* and *N. brevirostris*.

Although activity had previously been found to be highest for *N. brevirostris* at dawn and dusk (Morrissey and Gruber, 1993a, Sundström et al., 2001), it would appear that *N. brevirostris* main period of feeding activity is between an hour after dusk until midnight. Water temperature appeared to be the greatest driving environmental influence of *N. brevirostris* behaviour. The influence of water temperature was recorded at both the *N. brevirostris* sub-adult life stage, in defining both CPUE and relative population abundance, and the adult life-stage in defining local movements and large-scale migration cues. The results of this study have provided a much clearer understanding of mature *N. brevirostris* utilisation of the U.S. east coast. The Jupiter winter *N. brevirostris* aggregations were found to contain individuals from a wide catchment area (a minimum coastal span of 1,225 km) of the U.S. east coast distribution. The largest ever recorded adult *N. brevirostris* displacements were made during this study, and found to be repeated migrations, providing further insight into this species mature behaviour as a Highly Migratory Species (HMS). Average swimming speeds on all large-scale movements were in excess of the previously recorded maximum average swimming speed for a adult *N. brevirostris* (Kohler et al., 1998). The relatively high average swimming speeds suggest that large-scale movements made by adult *N. brevirostris* are direct between intended destinations, an advance in understanding that is most significant for male *N. brevirostris*, which, based on the genetically reconstructed parental profiles (Feldheim et al., 2004), were believed to be nomadic and to display largely random movements at the adult life-stage. Additionally, through the collaboration of the FACT array group, it was revealed that the pregnant female *N. brevirostris* of the Jupiter aggregations did not use the inter-coastal waterway for parturition, as previously believed.

Evidence was obtained to support the theory of a single *N. brevirostris* stock for the north-western Atlantic distribution, which would facilitate the documented genetic flow throughout their distribution (Feldheim et al., 2001a). A significant temporal negative relationship was identified between the National Marine Fisheries Service (NMFS) Large Coastal Shark (LCS) landings and the Bimini *N. brevirostris* longline CPUE records, and indicated that the adult population abundance off the U.S. east and Gulf coasts are directly related to the Bimini lagoon population abundance. Additionally, the documentation of the largest recorded *N. brevirostris* annual displacements showed that a level of mixing throughout the U.S. east and Gulf coast and Bahamas distribution would be feasible and logical. Thus the winter aggregations in Jupiter, Florida, represent a considerable concentration of *N. brevirostris* individuals from within the single north-western Atlantic stock unit.

The advances made in the understanding of *N. brevirostris* life-history from the results of this study, were only made possible by the extensive previously existing *N. brevirostris* life-history data provided by many years of focused research on this shark species. The advances in life-history information are relevant not just for *N. brevirostris*, but also for many other Carcharhiniforme species, as the *N. brevirostris* will continue to be used to substitute the lacunae in the life-history data of other species, wherever necessary and acceptable.

6.1.4. *N. brevirostris* current population status/need for protection

Based on the results of this study and additional existing information, the current status of *N. brevirostris* abundance in Bimini and the U.S. east and Gulf coasts is of great concern. For *N. brevirostris* of the Bimini lagoon population, abundance appeared to be very low (52) in 2008, relative to the temporal average estimates (158). Given *N. brevirostris* life-history traits, identified in section 1.1.3, and the identified reduction in Bimini *N. brevirostris* nursery survival rates (Jennings et al., 2007), a population recovery to more stable levels would be extremely difficult. There is very strong evidence from this study to suggest that the Bimini Bay Development activities have impacted not only on the nursery-bound juveniles, but also the secondary lagoon based *N. brevirostris* sub-adult population. Recovery potential could further be hindered, and even continued *N. brevirostris* population reduction sustained, if the Bimini Bay Development activities are continued and the full extent of the proposed mega-resort (Appendix 2) completed.

At the mature life-stage *N. brevirostris* have been found by the recent NMFS Environmental Risk Assessment (ERA) for LCS species to be highly vulnerable to overfishing in the U.S. east and Gulf coast fisheries (Cortes et al., 2008). The results of the Jupiter *N. brevirostris* study indicated that aggregating behaviour, off the southeast coast of Florida, additionally and considerably increases *N. brevirostris* vulnerability from December – April each year. The seasonal increase in *N. brevirostris* vulnerability, as the result of winter aggregating behaviour, was not considered in the original NMFS ERA (personal communication Cortes 2009). Therefore, in the winter months, the Jupiter concentration of *N. brevirostris* results in a vulnerability increase in a localised area. Then in the summer months, the same *N. brevirostris* are distributed over a considerable area of the U.S. east and Gulf coasts, where they are still highly vulnerable (Cortes et al., 2008) and subject to an increase number of commercial fisheries quotas. Thus *N. brevirostris* are probably more vulnerable than the high vulnerability status indicated by the NMFS ERA, further justifying the need for special management consideration for this species.

Collectively, the *N. brevirostris* populations that form the focus of this combined study are under considerable pressure from anthropogenic activities at all life-stages. In Bimini, *N. brevirostris* nursery survival rates have been reduced at the juvenile life-stage, with subsequent negative effects to the sub-adult life-stage secondary lagoon based population, through reduced recruitment potential caused by the Bimini Bay Development activities. This highlights the importance of protecting *N. brevirostris*, like all *K*-selected species, nursery grounds throughout the extent of the species distribution (Webster, 2004, Heihaus, 2007). Finally, at the mature life-stage, in the U.S. east and Gulf coast fisheries, a combination of life-history traits and commercial targeting has resulted in high *N. brevirostris* vulnerability to overfishing. It would appear that as a species, *N. brevirostris* are highly sensitive to current anthropogenic pressures.

6.1.5. Progress with *N. brevirostris* protection

Continued lobbying from 2000 onwards, based on scientific research results provided by the BBFS research group, including the author, has now resulted in the implementation of conservation measures. Following a change in government in May 2007, from the Progressive Liberal Party (PLP) to the Free National Movement (FNM) Party, the Bimini Marine Protected Area (MPA) proposal (Figure 2) was resurrected. Subsequently, the establishment of the North Bimini MPA, in conjunction with four additional MPAs throughout the Bahamas, was announced by the Bahamas Environment Science and Technology (BEST) Commission and Bahamas National Trust (BNT) on the 13th January 2009 (BBFS, 2009b). The specific implications on the Bimini Bay Development plans are currently unclear, but it was stated that any further development would be restricted to 'dry land'; i.e. above the high tide mark. Restriction in development of the marine area below the high tide mark would mean that the majority of the remaining fringing mangroves would be protected by the implemented MPA boundaries (Figure 2). However, the longevity of political support for the MPA is uncertain, as highlighted by the previous shift in support away from the MPA and towards the Bimini Bay Development, with the change in political parties to the PLP in the previous election. At least in the near-term, providing that the restrictions associated with the establishment of the MPA are enforced, pressure upon the Bimini *N. brevirostris* nursery area will be reduced or at least minimised. A reduction in anthropogenic pressure in Bimini may reduce the associated negative impacts to the *N. brevirostris* population.

At this time (October 2009) the Florida Fish and Wildlife Commission (FWC) are still in the process of reviewing state shark management regulations. In response to correspondence with the Bimini Biological Field Station (BBFS) research group, including the author, and the results of this study, FWC have taken the recommendation of 'the addition of *N. brevirostris* to the prohibited species list' into consideration. FWC are currently in the process of organising two public meetings to assess public opinion on 'a proposal to prohibit all recreational and commercial harvest of lemon sharks from Florida waters' (FWC, 2009b). Following review of the public meeting proceedings, a further meeting regarding the proposal will be held on the 10th December at the FWC headquarters in Tallahassee, Florida, where BBFS scientists, including the author, will present final evidence in support of the proposal. Subsequently, based on the BBFS evidence, and the reviewed of the public meeting proceedings, a final decision will be made on the addition of *N. brevirostris* to the prohibited species list by January 2010.

6.2. General conclusion

This study represents advancement in knowledge of *N. brevirostris* life-history, particularly for the adult life-stage. The level of analysis conducted was only possible due to the wide range, and multidisciplinary nature, of previous studies focused on *N. brevirostris* over the past 46 years, and more intensely since the establishment of the BBFS in 1990. This study, and those that preceded it, highlight the importance of long-term investigation for species with life-histories similar to *N. brevirostris*. Thus *N. brevirostris* is not only a model shark species, but the success of the long-term study of *N. brevirostris* provides a model for investigation into LCS species in general. In addition, this study has highlighted a number of new research techniques, and new applications of existing research techniques that can be employed to investigate the life-histories of other shark species.

The continuation of the large-scale *N. brevirostris* study being conducted by the BBFS research group, including the author, involving focused research efforts in the Bahamas (Bimini and Tiger Beach), Florida (Jupiter, the Marquesas Keys, the Dry Tortugas, Cape Canaveral), Georgia (the Altamaha Sound) and South Carolina (the Santee River Mouth and Winyah Bay), should further reveal the complex population dynamics of the north-western Atlantic *N. brevirostris* distribution.

The most resounding revelation from this study was that both *N. brevirostris* populations that formed the research focus appear to be sensitive to existing anthropogenic impacts. In Bimini, it is essential that the Bimini Bay Development be scaled back to ensure the long-term recovery and survival of both the nursery-bound juvenile and lagoon based sub-adult *N. brevirostris* populations and to avoid major disruption to the highly specific natal homing behaviour of the mature *N. brevirostris* that comprise the Bimini breeding population (Feldheim et al., 2009). In Florida, it is highly recommended that the results of this study be used by FWC to justify the addition of *N. brevirostris* to the prohibited species list. Subsequently extension of the prohibited status of *N. brevirostris* to the federal level would protect a large proportion of the *N. brevirostris* north-western Atlantic distribution and represent a considerable advancement towards ensuring the long-term future of this species. The ultimate achievement would be to secure some level of *N. brevirostris* harvest regulation an international level, with the Convention on International Trade of Endangered Species (CITES) providing a possible platform. Regulation and protection on an international scale such as CITES, relative to the extent of distribution, is the only effective way to protect and manage Highly Migratory Species (HMS) stocks. However, in the case of the north-western Atlantic *N. brevirostris* population, addition to the prohibited species list would increase fishing pressure of other Large Coastal Shark (LCS) species, such as *C. leucas*, in the region. Although *C. leucas* were found to be generally less vulnerable than *N. brevirostris* to overfishing by the National Marine Fisheries Service (NMFS) Environmental Risk Assessment (ERA; Cortes et al., 2008), the similar life-history patterns of many LCS make them highly unsuitable candidates for providing a sustainable fishing resource.

Similar to most environmental issues, the continued over-exploitation of LCS stems from the source; i.e. the high demand for shark fins for the Asian market. Demand, as always, drives supply and thus the profitable motivation for harvest. Therefore, LCS will continue to receive heavy fishing pressure, considerably so in less well regulated nations than the U.S., across the globe as long as the shark fins continue to fetch a high price at market. The only way to truly reduce the targeting of LCS across the globe is to reduce the demand at its deep rooted source in Asian culture. Only by addressing this problem at the base of Asian culture, the children that will form the future source of demand, with education and awareness-building through accurate and well researched information, will the long-term future of global shark populations be secured.

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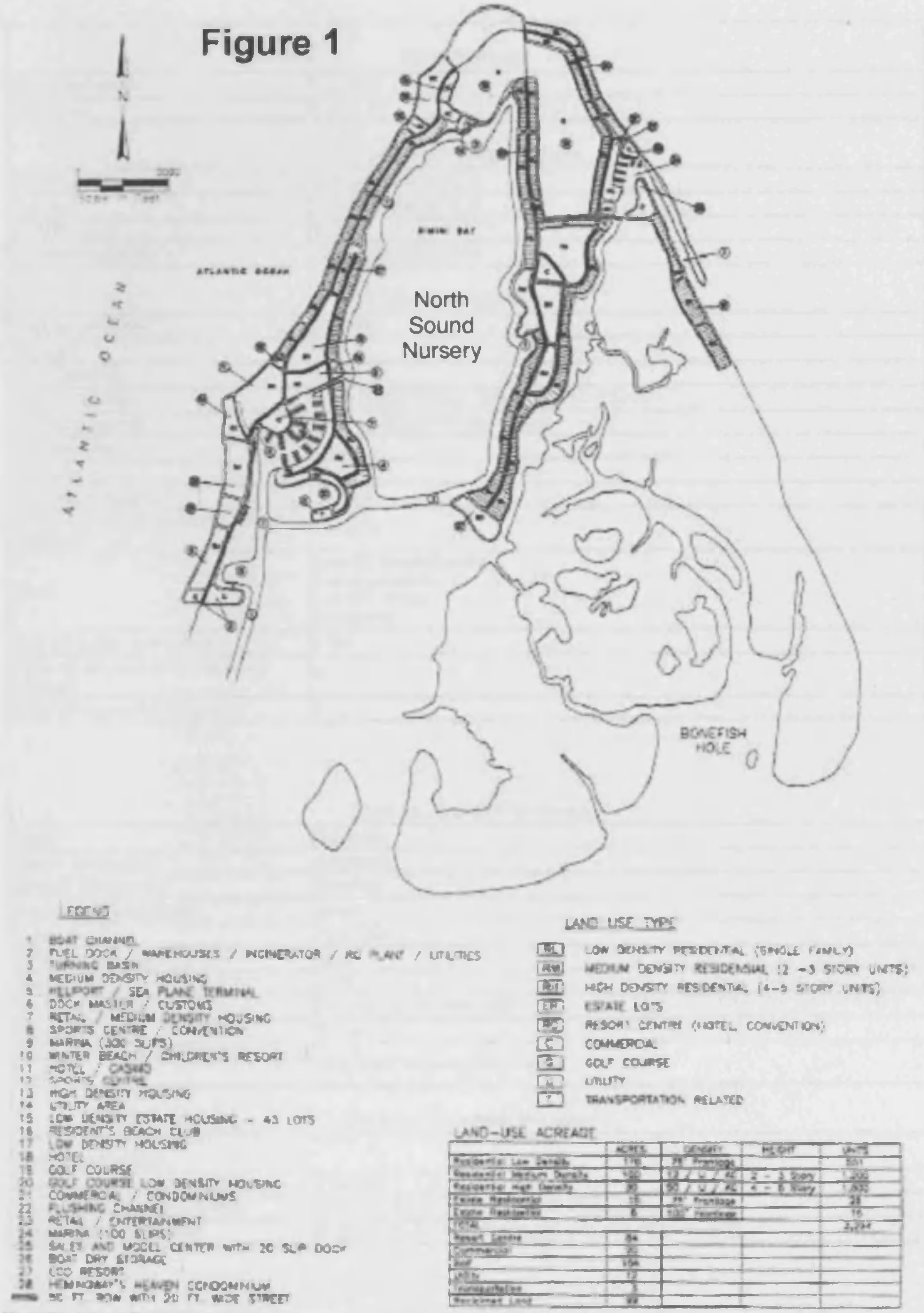
8. Appendix

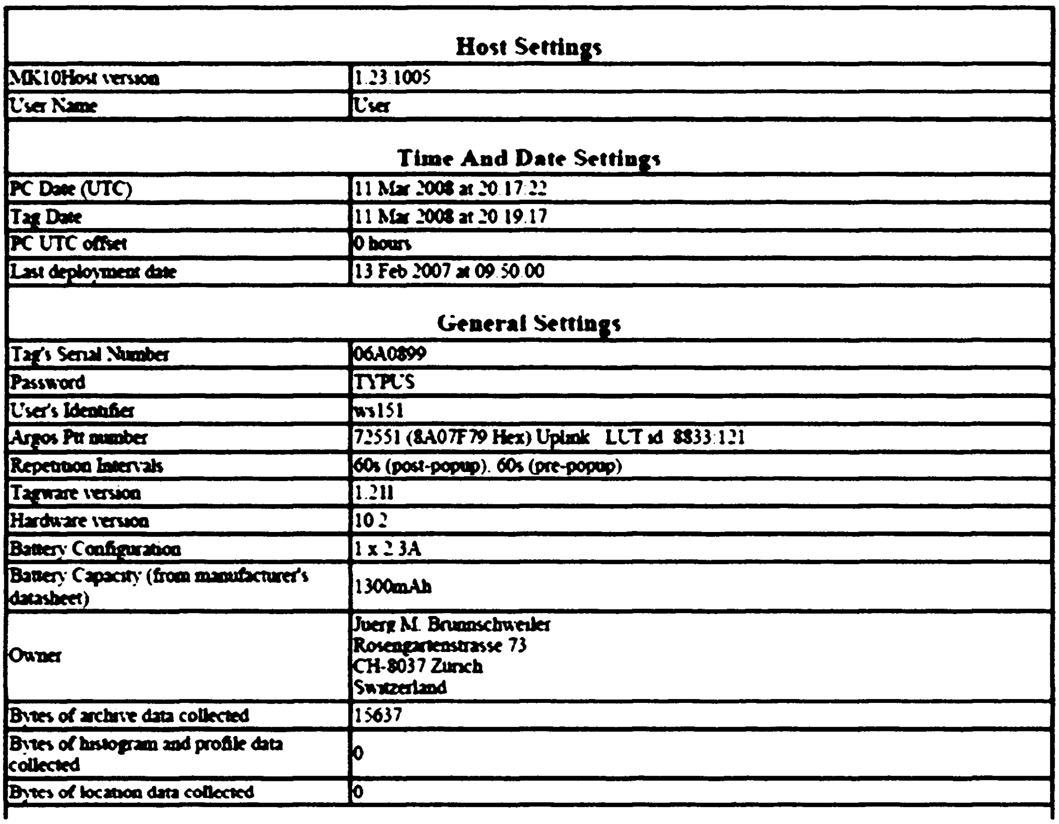
Appendix 1. List of U.S. designated Large Coastal Sharks (LCS) including Prohibited Species List (NOAA/NMFS 2006)

Common name	Species name
Sandbar	*Carcharhinus plumbeus*
Silky	*Carcharhinus falciformis*
Tiger	*Galeocerdo cuvier*
Blacktip	*Carcharhinus limbatus*
Spinner	*Carcharhinus brevipinna*
Bull	*Carcharhinus leucas*
Lemon	*Negaprion brevirostris*
Nurse	*Ginglymostoma cirratum*
Scalloped hammerhead	*Sphyrna lewini*
Great hammerhead	*Sphyrna mokarran*
Smooth hammerhead	*Sphyrna zygaena*
Prohibited Species	
Sand tiger	*Odontaspis taurus*
Bigeye sand tiger	*Odontaspis noronhai*
Whale	*Rhincodon typus*
Basking	*Cetorhinus maximus*
White	*Carcharodon carcharias*
Dusky	*Carcharhinus obscurus*
Bignose	*Carcharhinus altimus*
Galapagos	*Carcharhinus galapagensis*
Night	*Carcharhinus signatus*
Caribbean reef	*Carcharhinus perezi*
Narrowtooth	*Carcharhinus brachyurus*

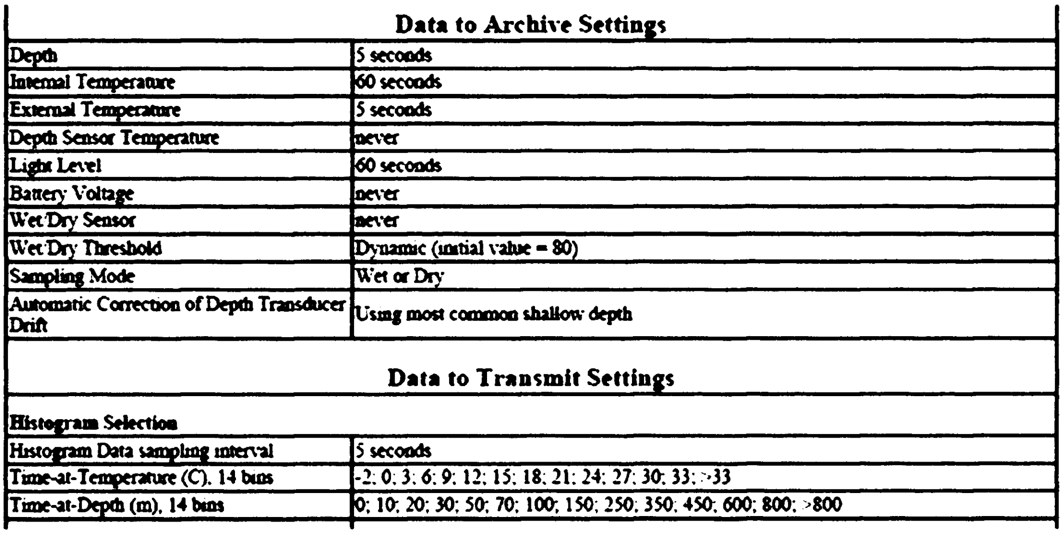
Appendix 2. Bimini Bay Development Plans (Puentes 2004)



Appendix 3. Wildlife Computer MK10 deployment parameters



Host Settings	
MK10Host version	1.23.1005
User Name	User
Time And Date Settings	
PC Date (UTC)	11 Mar 2008 at 20:17:22
Tag Date	11 Mar 2008 at 20:19:17
PC UTC offset	0 hours
Last deployment date	13 Feb 2007 at 09:50:00
General Settings	
Tag's Serial Number	06A0899
Password	TYPUS
User's Identifier	ws151
Argos Ptt number	72551 (8A07F79 Hex) Uplink LUT id 8833:121
Repetition Intervals	60s (post-popup), 60s (pre-popup)
Tagware version	1.211
Hardware version	10.2
Battery Configuration	1 x 2.3A
Battery Capacity (from manufacturer's datasheet)	1300mAh
Owner	Juerg M. Brunnschweiler Rosengartenstrasse 73 CH-8037 Zurich Switzerland
Bytes of archive data collected	15637
Bytes of histogram and profile data collected	0
Bytes of location data collected	0



Data to Archive Settings	
Depth	5 seconds
Internal Temperature	60 seconds
External Temperature	5 seconds
Depth Sensor Temperature	never
Light Level	60 seconds
Battery Voltage	never
Wet/Dry Sensor	never
Wet/Dry Threshold	Dynamic (initial value = 80)
Sampling Mode	Wet or Dry
Automatic Correction of Depth Transducer Drift	Using most common shallow depth
Data to Transmit Settings	
Histogram Selection	
Histogram Data sampling interval	5 seconds
Time-at-Temperature (C), 14 bins	-2; 0; 3; 6; 9; 12; 15; 18; 21; 24; 27; 30; 33; >33
Time-at-Depth (m), 14 bins	0; 10; 20; 30; 50; 70; 100; 150; 250; 350; 450; 600; 800; >800

20-min time-line	disabled
Hourly % time-line	disabled
PAT-style depth-temperature profiles	enabled
Light-level locations	enabled
Histogram Collection	
Hours of data summarized in each histogram	6
Histograms start at GMT	00:00
Do not create new Histogram-style messages if a tag is continuously dry throughout a Histogram collection period	is disabled
Relative transmit Priorities	
Histogram, Profiles, Time-lines, Stomach Temperature	4 transmission(s)
Fast-GPS and Light-level Locations	1 transmission(s)
Behavior and Time-Series	0 transmission(s)
Status	Every 20 transmissions

Release Settings	
Normal Realease	
Release day	95 days after deployment at 00 00
Premature release	
Minimum depth to start premature release detection	20m
Time at constant depth to initiate release	72 hours
"Constant" depth can vary by	±1 meters
Allow a few outliers	is disabled
Must be at surface to release	is enabled
Generate a premature release if all depths are deeper than some value	is disabled
Pre-release days to transmit with doubled priority	0
Channel Settings	
Depth	Channel: 0; Range: -40m to 1000m; Resolution: 0.5m; ADaddress: 02
Internal Temperature	Channel: 1; Range: -40C to 60C; Resolution: 0.05C; ADaddress: 04
External Temperature	Channel: 2; Range: -40C to 60C; Resolution: 0.05C; ADaddress: 03
Depth Sensor Temperature	Channel: 3; Range: -40C to 60C; Resolution: 0.05C; ADaddress: 05
Light Level	Channel: 4; Range: 0 to 0; Resolution: 0.25; ADaddress: 12
Battery Voltage	Channel: 14; Range: 0volts to 5volts; Resolution: 0.0048volts; ADaddress: 13
Wet/Dry Sensor	Channel: 15; Range: 0 to 255; Resolution: 1; ADaddress: 21