2. Biology and ecology of striped marlin

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Table 2.1 – Summary of the biological characteristics of striped marlin, *Tetrapturus audax*

Species	**Tetrapturus audax**
Common name	Striped marlin
Size (adult)	Adults reach over 290cm total length and over 200 kg
Growth rate	Rapid
Distribution	Pacific Ocean (mostly temperate) and Indian Ocean (tropical to temperate waters)
Stock structure	Uncertain in both oceans, but probably at least two populations in Pacific
Movements	Majority of recaptures are within 500 nm and 1 year of release.
Life span	Uncertain: ~10 years
Reproductive age	Uncertain: ~2-4 years
Fecundity	11-29 million eggs (based on dissections)

2.1 Introduction

The billfishes are generally perceived as an "enigmatic" and biologically unique group of pelagic fishes. They are targeted by both recreational and commercial fisheries all over the world. Yet despite this, there still remain large gaps in our knowledge of the biology and ecology of these species. This situation is no different for striped marlin, about which we know little regarding its age, growth, reproduction, movements and stock structure (Table 2.1). The following section reviews available knowledge pertaining to this species, including the most recent findings, some of which are yet to be published. Understanding the biological characteristics of this or indeed any fish species, is one of the keys to determining the status of a species, and therefore in determining what level of fishing pressure can be allowed without threatening the sustainable nature of a fishery targeting it. While the status of striped marlin is uncertain in both Indian and Pacific Oceans, a review of biological knowledge can provide indicators to the species susceptibility to fishing pressure, which are still of use in guiding fisheries management and decision making.

2.2 Taxonomy and identification

2.2.1 Scientific and common names

The scientific name for striped marlin is *Tetrapturus audax* (Philippi, 1887). Common names for this species vary around the world, and include A'u (Hawaii), malasugi (Philippines), barred marlin or Pacific striped marlin (USA), makajiki (Japan), takeketonga (New Zealand), marlin raye (France) and marlin rayado (Spain). Fishermen in Australia commonly refer to these fish as "stripies".

2.2.2 Origins and classification

The taxonomic status of the billfishes, of which striped marlin is only one of a group of species, is currently subject to two areas of debate. These pertain to firstly, the relationship between the billfishes and other teleost groups, and secondly, the interrelationships between the various billfish species.

In relation to the first debate, early morphological analyses suggested that the billfishes and scombroids (Scombridae; comprising tunas, mackerels and related species) are closely related, based on numerous common morphological features (e.g. internal endothermic features) (Collette et al. 1984; Johnson, 1986). However other morphological studies of osteological features suggested that billfishes are not scombroids at all, but rather are aligned more closely in origin with the percoids (Potthoff et al. 1986). These findings have gained support from more recent molecular studies (Block et al. 1993; Finnerty and Block, 1995) whose analyses of similarities in nucleotide and amino acid sequences refute the idea that billfishes and scombrids are closely related, and support the notion of billfish radiating from the percoids (Finnerty and Block, 1995). These studies suggest that endothermic traits arose independently in each group, and that similarities in morphological traits are due to convergences or reversals (Collette et al. 2001). A more comprehensive molecular analysis is currently underway which will hopefully resolve these issues further (Collette, Bruce; Smithsonian Institute, personal communication), given that the cytochrome b data do not resolve all the problems raised by the conflict in morphological data.

The second debate pertains to relationships within the "billfish" group, and in particular the relationship between striped marlin and white marlin. The billfishes are taxonomically separated into two families, the Xiphiidae (swordfish) and the Istiophoridae (marlin, sailfish and spearfishes)(Figure 2.1) (Nakamura, 1985). The latter group comprises three genera, these being *Istiophorus* (sailfish), *Makaira* (black and blue marlins) and *Tetrapturus* (striped marlin, white marlin and spearfish species). Striped marlin are found in the Indian and Pacific Oceans while white marlin are found only in the Atlantic. However, the status of striped and white marlin as separate species is debated. While they share many similar morphological traits, including slender bodies, fine bills and high dorsal fins (Pepperell, 1999), earlier morphological studies also identified some differences in size and body characteristics (e.g. dorsal, pectoral fin shape and maximum size), leading to their classification as separate species. More recently, this has been challenged by a growing body of molecular evidence which suggests that they are either; sub-populations of the same species, or, that their evolutionary divergence was an extremely recent event. Graves and McDowell (2003) conclude that, based on separate analyses of allozymes, mitochondrial DNA, ascnDNA, micro satellite DNA, cytochrome b (Finnerty and Block, 1995) and control region sequence data, that there is no more genetic difference between striped and white marlin samples analysed to date, than there is between isolated populations of the same species of many different types of marine fish species. Indeed, there is greater intraspecific variation in the cytochrome b region in a single species from the *Makaira* genus (*Makaira nigricans*) than between the entire species grouping of the genus *Tetrapturus* (Finnerty and Block, 1995). Furthermore, the level of genetic divergence in mitochondrial DNA between white and striped marlin is only slightly more than that between samples of striped marlin taken from geographically distant regions in the Pacific (Graves and McDowell, 1995). It should be noted however that some small genetic variances between the two species have been recently identified, adding weight to their status as separate species (Graves and McDowell, in press). This report will continue to treat them as separate species.

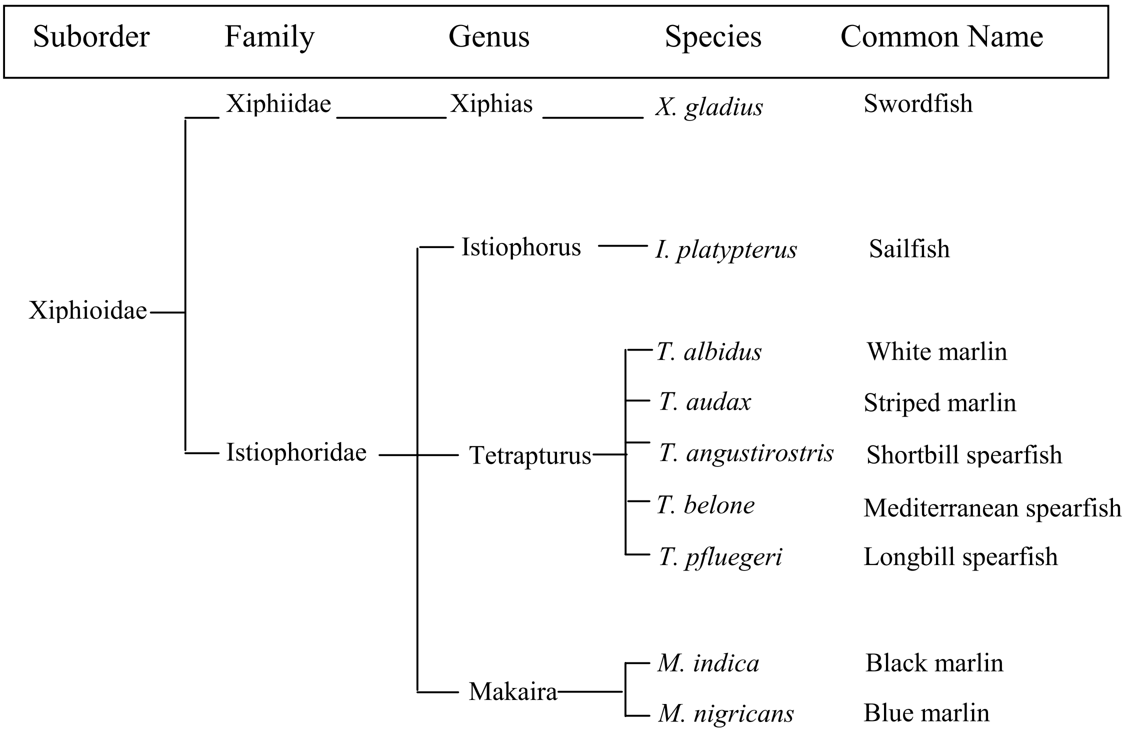


Figure 2.1 – Taxonomic relationships between the different species of billfish (Xiphioidae) as determined by molecular and morphometric studies.

2.2.3 Morphology and Identification

The striped marlin is a large species that can grow up to over 200 kg and lengths over 300cm (Pepperell, 1999). The overall body form of striped marlin is elongate and moderately laterally compressed, with a large head. The mouth contains small file shaped teeth (actually modified scales) on both jaws and the palate, while the body is densely covered by irregular scales which are buried quite deeply in the skin. Two caudal keels are located either side of the tail near the peduncle, and the tail itself is deeply forked. The third, and sometimes the fourth and fifth spines of the first dorsal fin are similar in height to, or slightly less than the body depth. The sides of the body are characterised by 10 or more cobalt coloured stripes. These stripes separate a dark upper body and creamy white ventral surface (Anonymous1996) and are particularly apparent when feeding. During such activity the stripes can quickly reverse colour pattern to phosphorescent blue stripes on a black or deep purple background (Pepperell, 1999). These stripes comprise specialised skin cells with chromatophores that are controlled by the nervous system (Davie, 1990). Two other species in the Indo-Pacific region, namely the blue marlin (*Makaira mazara*) and black marlin (*Makaira indica*), have very similar external colourings, markings and shape and may be confused with striped marlin. A number of different methods have been developed over the past decade that allow the marlin species such as striped marlin to be more easily identified, both alive and dead.

Morphologically, striped marlin can be distinguished from black and blue marlin by virtue of a number of characters, including: flat leaf shaped pectoral fins that fold flat against body (Ueyanagi and Wares, 1975), a tall and "floppy" first dorsal fin whose height is close to or equal to the body depth, long pelvic or ventral fins, irregular spaced scales deep in skin, a long and slender, acutely pointed lower jaw, and often orange salmon-like flesh (Pepperell and Grewe 1998). The ratio of two lengths, these being the tip of lower jaw to the caudal fork, and the rear of eye orbit to the caudal fork, can be used to separate the striped and blue marlins. The ratio for these two species is 0.83-0.86 and 0.86-0.89 respectively (Pepperell and Grewe 1998). Striped marlin are also more slender than black and blue marlins. Adult billfish can also be identified using molecular analysis of DNA. Ward, Grewe and Inness (1998) described a polymerase chain reaction (PCR) based method which amplified adult mitochondrial DNA from each species and used gel electrophoresis to separate out the digested DNA fragments, resulting in a DNA fingerprint or pattern unique to each of the six species tested (corresponding to the 6 found in Australian waters). These same methods have recently been adapted to the identification of larval istiophorids (Luthy and McDowell, 2001), which are much more difficult to separate morphologically than adult billfish (Collette et al. 1984). This molecular approach to identifying larval istiophorids has at this stage has only been applied to Atlantic billfishes but should soon be adapted to Pacific billfish also. Previously, morphological characters used to identify larval striped marlin included melanophore patterns on the lower jaw (Nishikawa, 1991), weaker body pigmentation patterns when compared to larvae of other billfish species (Nishikawa and Rimmer, 1987), and the downward sloping angle of the preopercular spines which are present in early stages (Ueyanagi, 1974; Nishikawa and Rimmer, 1987).

2.3 Global distribution

2.3.1 Introduction

Striped marlin are one of the most abundant and widely distributed species of billfish. Their worldwide distribution is determined by a combination of physical and abiotic factors (e.g. . landmasses and water temperature), which appear to limit them to the Pacific and Indian Oceans. Analyses of tagging data (Appendix I) have demonstrated that this species is capable of long distance migrations (over 3000 nm) but also that trends in mean displacements (distance between tag-release and recapture) differ between different release regions. Many factors may contribute to these differences, including differences in angler and commercial effort and effort distribution between these regions, along with oceanographic and biological factors. Just over 60% of recaptures occur within 200 nm of the release point, and 84% occur within 500nm. These trends suggest some level of broader regional fidelity. Timewise, 77% of recaptures occur within 6 months, 91.4% within a year of tag and release. Analyses of migrations trends, catch distributions, spawning grounds, morphological and molecular heterogeneity have led to considerable debate over the stock structure of this species in both the Pacific and Indian Oceans. Current evidence suggests that the Pacific is a single stock with some level of substructuring. However, genetic and tag-recapture evidence suggest that the possibility of a separate or partially separated stock in the southwest Pacific cannot be discounted at this stage. There is still far too little known about the Indian Ocean population, and again, population structuring cannot be ruled out. The following section explains current thinking on these issues in some detail.

2.3.2 Distribution: the environmental constraints on distribution

Worldwide distribution constraints: Striped marlin occur in both the Pacific and Indian Oceans. Their distribution pattern is distinct from other Istiophorid species in that striped marlins tend to prefer more temperate or cooler waters, particularly in the Pacific Ocean (Nakamura, 1985). Most pelagic species distribution can be closely tied to water temperature, and several studies have related striped marlin catch rates, as indicators of distribution and abundance, to sea surface temperature (SST) (Squire, 1985). Squire (1987) demonstrated that the distribution of striped marlin in the northeast Pacific Ocean changed according to seasonal shifts in warmer waters in this region. Howard and Ueyanagi (1965) proposed that the 20°C-25°C isotherms bound the distribution of striped marlin in the Pacific Ocean. Their conclusions are supported by recent data collected from 66 striped marlin tagged off southern California with pop-up archival satellite tags (Domeier et al. 2003). These data amounted to 918 days of depth and temperature data and showed that striped marlin in this region spent 95% of their time between 20°C-25°C. However, this may have been the range of temperatures available to the marlin in this region and time. There is likely to be variation in temperature preference for this species between regions and over time, as a study by Squires (1974) in the same region concluded that striped marlin were caught predominantly in waters between 16.1 and 22.8 °C. Ortega-Garcia et al (2003) found that recreational gamefishing catch rates were highest in waters between 22ºC-24ºC off Mexico. Analyses of domestic longline standardised catch rates off the east coast of Australia (Chapter 8) demonstrate that abundance of striped marlin is highest in waters at around 24°-25°C. The lowest sea-surface temperature at which a striped marlin has been captured by commercial vessels off the east coast is 15.2°C while the highest is 30.5 °C. However, 97% of longline captured striped marlin were caught in waters between 18 °C and 27 °C. Analyses of standardised catch rates show striped marlin abundance off the east coast to be highest in waters between 22ºC-26ºC. This analysis generates similar conclusions to that of Uda (1957) whose analysis of longline data demonstrated that the optimum SST for striped marlin is in the range of 18.5 °C to 24 °C, with a maximum range of 16 °C to 29 °C. Hanamoto (1974) found that the pattern in the expansion and contraction of the shallow thermocline off Baja California coincided to a large degree with the pattern of expansion and contraction of good fishing grounds for striped marlin (i.e., to changes in their abundance/local distribution). Both Talbot and Ware (1975), Squire (1985) and the analyses presented in Chapter 8, found that SST only explained a certain proportion of variance in catch rates as indices of abundance (e.g. 15-25%), and there are clearly other oceanographic factors which play an important role as well.

Striped marlin are holoepipelagic, meaning that they inhabit the isothermic surface layer of the ocean at all stages of their life cycle (Ueyanagi and Wares, 1975). Consequently they are limited mostly to the tropics and sub-tropics where a permanent thermocline exists, but can penetrate higher latitudes in warm seasons, depending on ocean current patterns (Ueyanagi and Wares, 1975). The latitudinal range limits of occurrence have been estimated from longline data as extending from about 45ºN to 40ºS in the Pacific and from continental Asia to 45ºS in the Indian Ocean (Nakamura, 1985). Off the east coast of Australia, changes in distribution most likely occur as a result of behavioural responses to feeding and reproductive needs of striped marlin (Ueyanagi and Wares, 1975). These will also depend on seasonal warming of surface waters, thermocline and current formations, and seasonal food abundances (Ueyanagi and Wares, 1975). It should be noted that larger marlin may have a higher tolerance (due to greater thermal inertia) to colder water temperatures, hence water temperature may play a role in the size frequency of marlin in different regions, and particularly at higher latitudes where larger fish are found. Tag-release data presented in Chapter 6 demonstrate that marlin caught in colder waters off Tasmania have a higher mean weight than those caught off the central eastern coast of mainland Australia.

The term “distribution” is generally defined by those areas where a given species of fish is consistently found in significant numbers, and generally will not include areas where they are infrequently caught (perhaps purely as a result of anomalies in SST and currents). Consequently, the Atlantic is not included in the distribution of striped marlin, despite authenticated records of a few individuals being caught west of the Cape of Good Hope (South Africa) (Penrith and Cram, 1974). The reasons why striped marlin don’t consistently occur in the Atlantic are as yet unknown. While entry from the Pacific is unlikely due to the predominance of cold currents around the tip of South America, a study of oceanographic conditions around the Cape of Good Hope could not identify any permanent oceanographic barrier to striped marlin crossing from the Indian to Atlantic Oceans (Penrith and Cram, 1974). There is also relatively little known about the mixing of stocks between the Indian and Pacific Oceans, however it is generally believed that such an event is quite likely on a periodic basis, given the right oceanic conditions.

Environmental influences on distribution and abundance in waters adjacent to Australia:
This report deals predominantly with striped marlin fisheries off Australia, and for that reason, the following section details the oceanographic conditions off the east and west coasts

of this continent and how these might relate to the distribution and abundance of pelagic fish (including striped marlin). This section should be kept in mind when considering later sections which discuss striped marlin abundance trends in this region.

The oceanographic environment has a strong influence on the spatial and temporal pattern of abundance and productivity in pelagic fishes. While this relationship is generally accepted, there is still broad variability in oceanographic conditions and species responses to these, and this can often disguise meaningful relationships. While pelagic species' distributions can span entire ocean basins, and overlap each other, within this are small scale variations in distribution which results from physiological and behavioural adaptations of each species to temperatures, depths and other factors (Campbell and Miller, 1998). Fishers who understand these differences can more effectively target particular species. The distributions of pelagic fish species off the east coast of Australia are strongly influenced by the intersection of two major current systems, the warm and nutrient-poor western Pacific circulation and the colder nutrient rich water of the West Wind Drift. The former originates from the north and feeds the south flowing East Australian Current, while the latter originates from sub-Antarctic waters. The east coast circulation is characterised by a complex frontal ocean system (Tasman Front) and may contain large warm eddies hundreds of kilometres wide that can persist for years in some cases (Campbell and Miller, 1998). Off Western Australia, the distribution of pelagic fishes close to the coast is influenced by seasonal adjustments in the Leeuwin Current that flows from the north. Both the EAC and the Leeuwin Current push south in the summer and autumn, bringing warmer water pelagic species, such as striped marlin, with them.

The boundaries of these eddies and fronts, as well as the presence of raised sea-bed (bottom topographic) features which may generate their own local circulation structures, are important sites of production and aggregation of pelagic species, and hence are targeted by fisheries (Campbell and Miller, 1998). The degree to which the two eastern current systems influence the east coast circulation system is dependent on global weather patterns and cycles (e.g. El Nino-Southern Oscillation) and as such is highly variable at both seasonal and interannual timescales. In El Nino years, cooler waters extend relatively far north, and in La Nina years the tropical currents dominate and extend further south. While the exact dynamics of these relationships are not fully understood, all these factors are believed to play a significant role in the variability of abundance of pelagic species in the eastern and western coastal waters of Australia (Campbell and Miller, 1998).

2.4 Pacific Ocean – Distribution, migration and stock structure

2.4.1 Distribution

Adult distribution: Historic Japanese longline records indicate that adult striped marlin have a somewhat horseshoe shaped distribution in the Pacific Ocean (Nakamura, 1983) which is unique among Pacific billfish and tunas. The base of this distribution is centred on the south central American coast, and has extensions which run either side of the equator right across to the Western Pacific Ocean (Nakamura, 1983) (Figure 2.2). The central equatorial region in the western and central Pacific is characterised by very low and intermittent hook rate for striped marlin, and thus is not considered part of their normal distribution (Ueyanagi and Wares, 1975). According to early longlining data, the areas of highest abundance were in the central north and the eastern Pacific, while the waters of the south and western pacific were areas of lesser abundance (Ueyanagi and Wares, 1975). In the south and southwest pacific, adults are most abundant during the 4th and 1st quarters (spring and summer) and least abundant in the late 2nd and 3rd quarters (winter). This region includes the eastern Australian AFZ, where striped marlin are present from the Coral Sea to Tasmania (depending on currents and seasons). In the northwest Pacific, catch rates are high in the Kurushio and South China Sea during the monsoon with high catch rates shifting to off Japan in the spring. Catch rates are highest in the central Pacific from fall to spring, while in the eastern Pacific they are relatively high all year round (Ueyanagi and Wares, 1975). Each of these regions experiences localised or small scale shifts in abundance that coincide with changing seasons. These local changes result from migrations and movements associated with feeding and reproductive requirements of the species, and are discussed in the section “Migrations and movements”.

Juvenile distribution: Age and size at first maturity is still uncertain for striped marlin, however, Hanamoto (1977) estimated size at first maturity as being approximately 29kg for striped marlin caught in the Coral Sea. Few striped marlin in this size range are caught in the south-western Pacific Ocean but individuals in the 5-30kg range are commonly caught in the north central Pacific Ocean region by longline, and by Hawaiian recreational fishermen, where they are believed to occur in greater concentrations (Squire and Suzuki, 1990; also, Appendix I). Relatively few striped marlin over 60kg are caught in these fisheries (Yoshida, 1974). SPC observer data also indicate a juvenile population in the central Pacific with a significant proportion of striped marlin being less than 135cm length between 30°S and 30°N (Figure 2.3). This contrasts with the Western Pacific where relatively few marlin in this size range are caught. Given that known spawning areas occur in the western Pacific, the possibility that juvenile marlin migrate out of this region until becoming mature needs to be investigated. One of the problems in assessing juvenile distribution is that juvenile striped marlin are easily confused with juveniles of other marlin species.

Larval distribution: The larvae of striped marlin have been found in four widely separated regions in the Pacific Ocean and do not show a continuous distribution as such (Figure 2.2). Their occurrence is highly seasonal, with adult spawning and larval hatching occurring predominantly during late spring and early summer months, in both the northern and southern hemispheres (Nakamura, 1983). Hence the appearance of larval populations occurs six months apart between the two hemispheres. Spawning grounds are generally located towards the warmer, more tropical limits of the normal adult distribution. Larval populations have been identified in the following regions:

1) *Northwest Pacific Ocean*: larvae have been reported as occurring in the region south east of Japan, between latitudes 10ºN-30ºN, longitudes 130ºE-170ºE, with larval abundance peaking in May and June. Larvae have also been found in a more restricted zone (20-30ºN, 135-155ºE) between July and September (Nishikawa et al. 1978), as well as in the South China Sea to the southwest in April/May (Nakamura 1949).

2) *Southwestern Pacific*; In the region of the South Coral Sea, Hanamoto (1977) identified mature females located within the region 20-30ºS and 150-165ºE, with mature fish constituting 60-70% of catch at this time (4th quarter). Actual spawning distribution, based on occurrence of larvae, spans latitudes 10-30°S, longitudes 145ºE-180º, with abundance peaking in November and December (Nakamura, 1983).

3) *Northeast Pacific*: Recent surveys have found striped marlin larvae inside and near the mouth of the Gulf of California (104-116ºW, 18-28ºN) from June through to November (Armas et al. 1999; Armas et al. 2001). Larvae were only caught at sampling stations with SST of between 27.8 – 31.5ºC, despite the temperature range in the gulf being between 19.4-32.0ºC over the sampling period. This contradicts early studies of gonad index in striped marlin females that suggested that they use this region to feed during maturation but then move away from the region to spawn. Potentially, these larvae might be carried westwards by the north equatorial current, which might partly explain recruitment of large numbers of juveniles in the central north region around Hawaii.

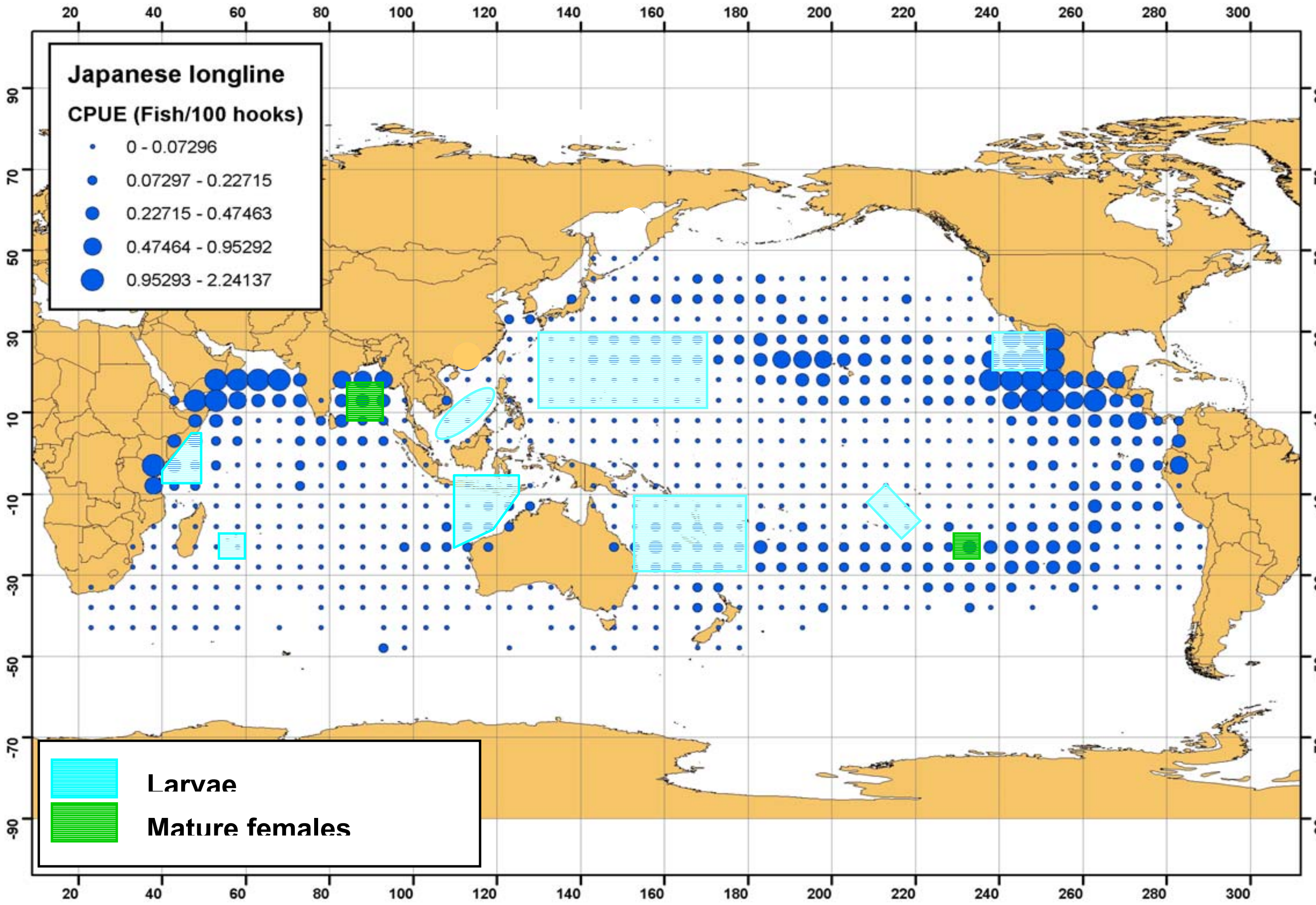
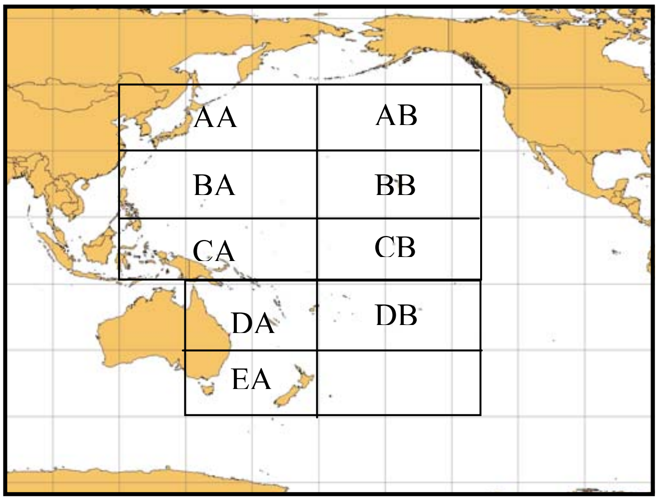


Figure 2.2 – Distribution (as indicated by mean annual Japanese longine CPUE for the period 1970-2000), spawning grounds (light blue – where larvae identified), and suspected spawning regions (green – where mature female marlin identified) of striped marlin in the Indian and Pacific Oceans. Distributions determined from catch rate data from historical Japanese longline records, while spawning grounds have been identified from various scientific surveys.

A.



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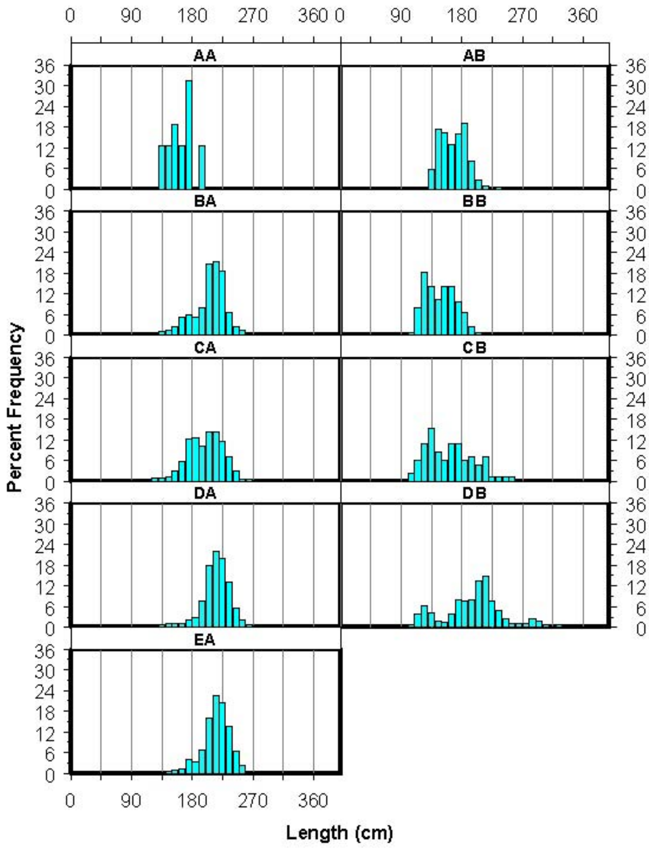

Figure 2.3 – Length (Lower jaw fork length) frequencies of striped marlin in different regions of the Pacific Ocean, as calculated from data collected by on board observers for the SPC (Source: SPC 2003).

4) *Southeast Pacific Ocean:* mature females were identified in the region spanning 125ºW-130ºW and 20ºS-25ºS during November-December (Kume and Joseph, 1969). While larvae were not identified in this region at the same time, they have been identified in a region to the northwest of this (145ºW-150ºW, 10ºS-15ºS) during October to December, and between 140ºW-145ºW, 15ºS-20ºS during January to March (Nishikawa et al. 1978).

Central Pacific Ocean larval surveys failed to find any striped marlin in the Hawaii region (Matsumoto and Kazama, 1974), despite the occurrence of other billfish larvae as well as striped marlin juveniles (10kg+) in this region. Overall, however, it should be noted that larval surveys have been relatively few and intermittent, and may be limited in how they relate to average billfish larval abundance and distribution.

2.4.2 Movements and migrations within the Pacific Ocean

Introduction: The abundance and distribution of adult striped marlin changes with seasons, as fish respond to feeding and reproductive urges, as well as to oceanographic changes such as SST, currents and upwellings. Squire and Suzuki (1990) summarised the overall movement trends, stating that adult marlin tend to exhibit north-south movements that correspond with feeding or reproductive activities. They move closer to the equator to spawn in spring-summer months, and to higher latitudes to access summer-autumn feeding grounds. Juvenile marlin tend to concentrate adjacent to warmer spawning-ground waters, moving to higher latitude feeding grounds as they mature. These changes in distribution of striped marlin have been identified though analyses of seasonal changes in distribution of longline CPUE, size modal analysis, and tag-recapture data (Figure 2.4). The following sections deal with striped marlin movements in the Pacific on a region-by-region basis, using where required, updated longline and tag-recapture data.

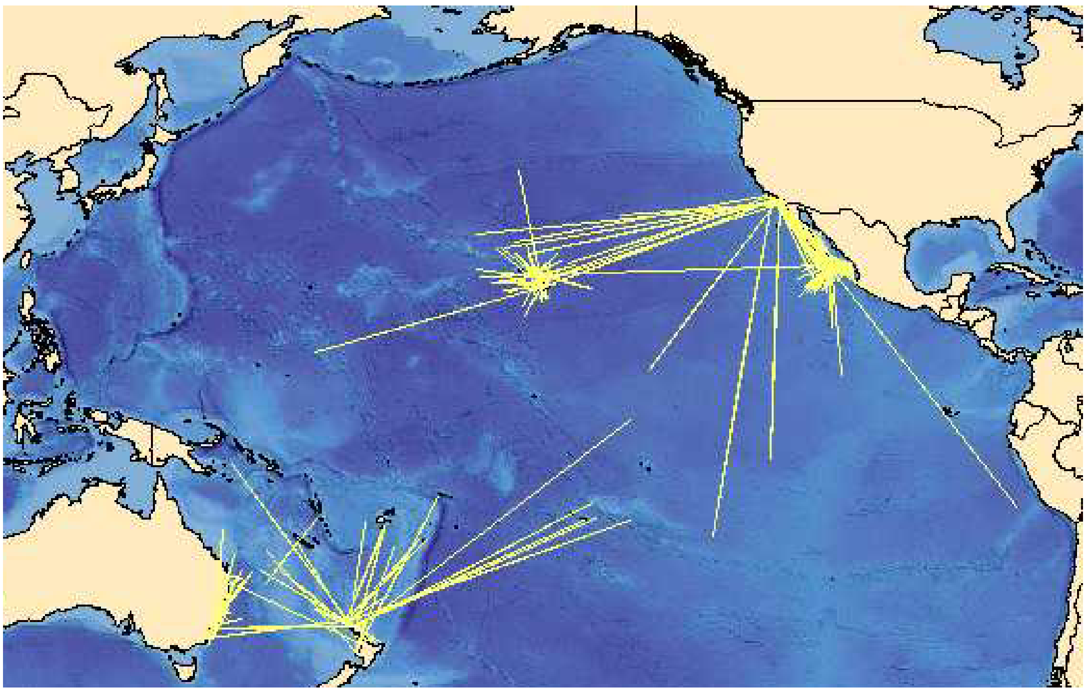

Figure 2.4 – The release and recapture positions of striped marlin tagged and recaptured in the Pacific Ocean (Data Sources: NMFS, NSW Fisheries, NIWA, TBF, 2002).

Southwest Pacific Ocean: Striped marlin caught by longline in this region show a modal size of near 190cm eye-fork length (Squire and Suzuki, 1990), with over 85% of these considered to be mature. More recent SPC observer data demonstrates most striped marlin caught by longline in this region to be in the size range 180-250 cm (lower jaw-fork length; Figure 2.3). Three basic movements of striped marlin have been identified by analysing CPUE and tagging data in the southwest Pacific Ocean region. These are:

1) Movements from the east (Fiji, New Zealand and South Central Pacific) by adult striped marlin to underwater ranges of the Lord Howe Rise and the Norfolk Ridge from September to October (Squire and Suzuki, 1990). These aggregations initially avoid the warm east Australian current, with longline catch rates analyses suggesting that these pre-spawning aggregations might associated to cooler waters surrounding elevated bottom topography (Hanamoto, 1978; Bailey et al. 1996). Fish tagged off New Zealand have tended to move either northwest into this region, north or northeast towards the central Pacific (Appendix I). Given the relative low level of reporting from the latter region, the proportion of marlin making this migration may be higher than indicated. Tagging data have also demonstrated that the majority of striped marlin released off Australia are caught within several hundred nautical miles from release points even after 6 to 9 months. In contrast, 27% (14) of the fish tagged off northern New Zealand have been recaptured more than 1000nm from the release point, some travelling as far away as Fiji and the Marquesas Islands (the maximum distance travelled before recapture being 3250nm).

2) Mature individuals are then thought to migrate north and northwest from the underwater ranges to spawn in the South Coral Sea region during November and December (predominantly in a region between 15ºS- 25ºS) while juveniles appear to stay associated with seamounts (Hanamoto, 1978).

3) Longline catch rate data indicate that post-spawning aggregations then migrate south and southeast from the South Coral Sea from December onwards, with high densities been observed right down the east coast of Australia, in the Tasman Sea and off the North Island of New Zealand. Tag-recapture data and recreational catch rates support this observation of a southerly movement between 4^{th} and 1^{st} quarters. Tag-recapture data for the east coast of Australia also indicate that after the 1^{st} quarter, striped marlin then move northwards again. The north-south movement appears associated with the incursion and retraction of the warm east Australian current.

Overall, reasonably clear seasonal movements can be defined for striped marlin in the southwest Pacific region. Striped marlin tagged off the east coast of Australia have a mean displacement before recapture of less than 200nm. Those tagged off New Zealand have a mean displacement of 674 nm, suggesting that marlin around New Zealand are less residential, or show less regional fidelity (See Figure 2.4; and Appendix I). However, other possible reasons for such unexpected differences, such as influence of regional fishing pressures and reporting rates upon such statistics, or potential behavioural association with the continental shelf, are discussed in Appendix I.

Northwest Pacific Ocean: Nakamura (1949) noted that concentrations of striped marlin move in northerly direction during March and April (Spring), migrating from the South China Sea towards the waters of Japan. Squire and Suzuki's (1990) analyses of longline catch rate data also indicated that striped marlin in the northwest Pacific tended to move north and west toward Japanese waters over summer, and then south and eastwards leading into winter. Furukawa (1958) presented evidence for a southward migration into the East China Sea during winter. This trend of moving to more tropical waters during winter, and to more temperate waters during summer is also apparent in other areas of the Pacific Ocean (Squire and Suzuki, 1990; also tagging analyses, Appendix I).

Southeast Pacific Ocean: Longline catches of striped marlin in the southeast region are generally dominated by fish having a single size mode (average 180cm EFL) (Squire and Suzuki, 1990). About 75% of these fish are considered to be mature. Analyses of changes in longline CPUE by Squire and Suzuki (1990) suggest that during the 1st-2nd quarters there is a general northeastern migration towards the Galapagos and south-central American coastline from offshore southeast Pacific waters. Tagging data (Appendix I) indicate that some large adults (100kg+) are caught in the recreational fishery off Costa Rica at this time, while significant numbers of adult marlin are caught by game fishers off the Galapagos Islands in the 1st and 2nd quarters. These fish have a mean size of around 71kg in the second quarter. There then appears to be a mainly northerly movement in the 3rd quarter, as indicated by increased commercial and recreational catch rates between 0º-10ºN off the central American coast at that time. Longline catch rate data suggest that the main concentrations of striped marlin in the southeast region are located relatively close to the South American coastline over the winter (April to October) but this range then expands offshore towards the southwest in the 4th-1st quarters, possibly as mature individuals migrate to spawning grounds over the summer (from October to March) (Kume and Joseph, 1969). A southward expansion of distribution of striped marlin during summer and a retraction to the north during winter was noted by Joseph et al. (1974) in their analyses of longline catch rate data. Overall, movements of striped marlin within this region appear to be fairly complex and require a much greater level of investigation before any firm conclusions regarding movement patterns in this region can be made.

Northeast Pacific Ocean: Striped marlin caught by longline in the northeast Pacific shows a restricted size mode (average 170cm) of which 65% are mature fish (Squire and Suzuki, 1990). However, more recent research has noted that the mean size modes predominantly caught by Japanese longliners in the northeast Pacific has declined considerably in the past three decades, from around 150-205cm EFL in the 1970s, to 130-180cm EFL in the 1980s, to 100-170cm in the 1990s (Hinton and Bayliff, 2002). Whether this reflects the removal of older larger marlin by commercial fleets, or increased recruitment of younger marlin in recent years, or an effect of shifted effort/targeting, has yet to be analysed. Records of recreational catches off Baja California (a core catch and abundance region) indicate marlin in this region range in size from 20-100kg, but that most of these are medium sized fish with a monthly mean ranging between 55-64 kg depending on time of year (See Appendix I). This region is perhaps the best characterised region in terms of knowledge of actual striped marlin movements, due to an extensive tagging program there, and a number of analyses of commercial and recreational fishery catch trends for the high abundance region off Southern California and Baja California, Mexico. From these various studies, three basic observations of striped marlin movements can be made:

1) The core abundance regionin the northeast is off Baja California. There is a general pattern of south and southwestward movement from this region during the summer and early autumn (Squire Jr, 1974; Squire, 1987). This observation is supported by analyses of sport fishing catch rates, which are much lower in this region during the summer (Ortega-Garcia et al. 2001). This seasonal movement was originally thought to be a spawning based migration, based on low gonad indices in the Baja California area (Eldridge and Wares, 1974) and higher gonad indices to the southwest. The Baja California area was regarded as primarily a feeding ground for this species (Eldridge and Wares, 1974). However, recent larval surveys have demonstrated the presence of larvae in and around the mouth of the Gulf of California, during summer and autumn (Armas et al. 1999; Armas et al. 2001), suggesting that at least some adults must remain in the region to spawn. Summer also sees some movement to the north of the core region, toward southern California.

2) There is evidence from tagging data for a movement by some marlin back to the core Baja-Mazatlan region over winter, while analyses of commercial longline data

suggest a broader scale movement to the central eastern and south eastern Pacific during the northern winter (southern summer) (Squire and Suzuki, 1989). Data from tagging programs indicate that the majority of recaptured striped marlin (originally released in the northeast Pacific) are caught, even after considerable periods approaching two years, within a few hundred miles of their release point, demonstrating considerable fidelity to this northeast region. However, a certain proportion of recaptured marlin have also undertaken extensive movements, the furthest being over 3000 nautical miles into the central north Pacific, to a point southwest of Hawaii. These tagging data also demonstrate that striped marlin are capable of travelling up to 31.5 nm per day over extended periods.

3) Tagging studies confirm localised movements within the region but also indicate that some marlin will migrate much greater distances into the central-north Pacific (Hawaiian waters) and South-east Pacific Ocean (Figure 2.4; also, Appendix I). Eight of the Hawaiian recaptured marlin were originally released off Southern California. However, a greater proportion of southern Californian released fish are caught southeast off Baja California, Mexico.

Analyses of finer scale movements within this region are presented in Appendix I. Overall, these observations, combined with studies that have correlated fluctuations in longline catch rates in the Baja California region with those in the rest of the EPO (Squire and Au, 1990), suggest considerable mixing within the eastern Pacific Ocean. The degree of mixing with other regions, such as the southwest Pacific, remains uncertain at this point in time. .

Central-north Pacific Ocean: According to size modal analyses of Japanese longline data, the central-north region, which encompasses Hawaii and waters south of this, shows a bimodal size distribution with almost equal proportions of very young (mode 110cm EFL) and older marlin (mode 160cm EFL)(Squire and Suzuki, 1990). More recent SPC observer data indicates that marlin caught in the central north Pacific fall in the size range 135 to 220 cm lower jaw-fork length (Figure 2.3). Juvenile marlin are thought to appear in the Hawaiian fishery (or at least become susceptible to fishing gears) at an initial size range of around 10kg, and remain in the central north Pacific Ocean for several seasons. However, upon reaching a size mode thought perhaps to correspond to first maturity, these fish disappear from the fishery (and region). Consequently it is believed that this region serves as a feeding ground for juveniles, which then migrate away to spawning grounds (Matsumoto and Kazama, 1974). This theoretical pattern of movement is as yet unproven. Analyses of changes in longline CPUE by Squire and Suzuki (1990), have suggested east-north-easterly movements in the 2nd-3rd quarters, switching back to west-south-westerly movements in the 3rd-4th quarters. Tag recapture data have shown movements into this region by marlin migrating from Californian coastal waters from late autumn/ early winter. Most of these marlin were in the 40-60kg size range. However there is no recapture evidence for movements in the opposite direction, even though reasonable numbers of striped marlin have now been tagged in Hawaiian waters.

Central-south Pacific Ocean: There is a lack of movement analyses for this region, however, longline data suggest an expansion of a high catch region from east to west during the 3rd and 4th quarters (spring and summer)(See Chapter 3). SPC observer data suggest that three distinct size modes occur in this region, (Figure 2.3), centred at 120 cm, 220 cm and 290 cm LJFL. This region exhibits the broadest modal size range of any of the regions in the SPC data and may be an ecologically important region for the species. It is a region into which numerous New Zealand tagged marlin have moved and subsequently been recaptured, as well as the recapture area for one tagged marlin from the northeast Pacific. Understanding movements of marlin in this region may prove important in understanding stock relationships in the Pacific and should be examined more closely.

Summary and conclusions: Based on analyses of spawning locations, modal size data, changes in regional CPUE and tagging data, three main conclusions can be drawn in regard to striped marlin movements within the Pacific Ocean. Firstly, there appear to be repeated regional patterns of seasonal north-south movements of mature individuals, most likely associated with their feeding and spawning needs. Secondly, there may be movements related to developmental status and maturity, with central and western regions typified by a mix of smaller juvenile and larger adult size classes, while eastern regions are characterised by intermediate size groups (Squire and Suzuki, 1990). Analyses of tag-recapture data over time indicate a fairly high level of broad regional fidelity but that a small number of striped marlin may undertake extensive trans-regional movements (Appendix I). Even though some patterns of movement are discerned, more tag data, and a much greater level of detailed analyses are required.

2.4.3 Stock structure in the Pacific Ocean

Introduction*:* The population structure of striped marlin in the Pacific has been subject to considerable debate for some time, and has yet to be conclusively resolved. There are three main hypotheses that have been put forward, postulating that Pacific striped marlin comprise either one, two or three separate stocks. Many different types of evidence have been put forward to support these hypotheses. Much of this evidence has already been discussed in relation to striped marlin classification, identification, distribution and movements. The following section discusses these observations in relation to stock structure.

Morphological analyses*:* Differences in morphometric characters (e.g., the larger size of southern fish, pectoral fin length differences) of striped marlin from the EPO, SWPO and NWPO led Morrow (1957; in Ueyanagi and Wares, 1975) and Kamimura and Honma (1958) to suspect that the Pacific may contain more than one population of this species. However, it cannot be discounted that size differences might result from differential habitat/region selection by marlin at different developmental stages or ages.

Molecular analyses: Striped marlin stock structure in the Pacific Ocean has been investigated using both allozyme analysis (Morgan 1992) and RFLP analysis of whole mtDNA (Graves and McDowell 1994). Morgan (1992) surveyed 44 allozyme loci within samples of approximately 40 – 50 striped marlin each from four areas, these being western Mexico, Ecuador, Hawaii, and eastern Australia. They found that there was slight, but statistically significant heterogeneity (genetic differences) among the four striped marlin collections. Graves and McDowell (1994) surveyed mtDNA variation using the same samples. Their analysis revealed considerable variation, and that levels of variation were similar among the four collections (average nucleotide diversity of h = 0.82). They found that while there was only relatively small mean net nucleotide sequence divergence between samples, there were highly significant differences in the distribution of genotypes among collection locations, with this particularly apparent in a comparison of Australian samples with those from the other locations. Overall, the results of the allozyme and mtDNA analyses are consistent with shallow, but statistically significant population structuring within striped marlin in the Pacific Ocean. This contrasts with similar Pacific wide studies of other pelagic species such as yellowfin tuna, which show little heterogeneity and are thought to comprise a single stock. Subsequently, some researchers have proposed that adult striped marlin may exhibit spawning site fidelity, limiting gene flow between geographically distant regions, promoting the formation of stock structuring in the Pacific (Graves, 1998).

In the time since these papers were published, the Virginia Institute of Marine Science has acquired some further samples of striped marlin and have examined some hyper variable microsatellite loci – none of this new work has yet been published. The microsatellite analyses showed considerable variation and a large amount of heterogeneity. In fact, there was so much noise (variation) that a reliable stock structure signal was not obtained. It was determined that much larger sample sizes are needed to properly estimate allele frequencies.

Future studies are also likely to focus on mtDNA. It has also been strongly suggested that attempts should be made to focus on sampling juveniles or ripe adults in known spawning areas.

Distribution and movement characteristics (from longline data): Honma and Kamimura (1958 in Ueyanagi and Wares, 1975) point out that firstly, hook rates of striped marlin near the equator are extremely low, therefore implying a separation of populations into the north and south regions in the western Pacific, and secondly, that spawning grounds are separate and geographically distant. However, these factors do not necessarily preclude the mixing of striped marlin from different regions. A progressive increase in mean size of marlin caught as longliners operated further south off the western American coastline, into the southeast Pacific, and then across to New Zealand, led Howard and Ueyanagi (1965) to suggest that juvenile striped marlin from California might migrate over a period of two years to waters surrounding New Zealand. However such movements have not, to date, been backed up by tag-recapture data. While the uniquely horseshoe shaped distribution of striped marlin in the Pacific has apparently vacant central and western equatorial regions, the actual distribution of striped marlin according to longline data is still continuous, if sparse in these regions. The existence of geographically distant spawning grounds does not necessarily imply genetically separate populations, but may have arisen as a protective mechanism against failure of conditions to promote larval survival in one particular spawning ground. Overall, longline data and analyses to date are somewhat inconclusive regarding stock structure in the Pacific.

Tagging data analyses: (See tag-data analyses, Appendix I).While tagging data have demonstrated some longer distance (>1000 nm) movements by striped marlin, most recaptures show that the majority of striped marlin only undertake localised movements in their ocean regions (e.g. NEPO) (Ortiz et al. 2003). Less than 8% of tagged and recaptured striped marlin have been recaptured more than 1000 nm from their release point, suggesting only a small proportion undertake extensive movements (Appendix I). While there are no confirmed trans-ocean east-west recaptures, there is some evidence for overlap of stocks in the central eastern Pacific from tracks of marlin released off New Zealand and off North America (Figure 2.4). When compared to blue and black marlin tag-recapture data, striped marlin appear to exhibit greater regional fidelity but inter-regional movements can also occur in this species.

Summary and conclusions: It is clear that there is still considerable research required before any definitive conclusions regarding striped marlin stock structure in the Pacific can be made. However, based on the current evidence, it seems likely that there are possibly at least two stocks, with some low level of mixing amongst all Pacific regions. Evidence for slow and diffusive movements by this species suggests it is possible that regions of high abundance can be managed effectively as separate sub-populations (Squire and Au, 1990). Striped marlin do not appear to fit the “highly migratory” classification attributed to other marlin and tuna, in that there is no evidence for large scale movements of large numbers of striped marlin in short time periods that occur on an annual basis. Indeed, the majority of tag-recaptures indicate striped marlin undertake more localised regional movements in the order of a few hundred miles (although mean displacements vary somewhat with region; see Appendix I). Thus, the slower, more diffusive movements might explain the low but significant level of genetic heterogeneity between geographically distant sites. The “horseshoe” shaped distribution might also limit the speed of mixing, particularly between northwest and southwest regions. However, based on the fact that tag recaptures from marlin released in the SWPO are yet to be recorded in the eastern Pacific (and vice versa), that there appear to be widely separated spawning regions, and that slight genetic difference are apparent between samples from the southwest Pacific with the central-north and eastern Pacific, the possibility of a semi-independent south west stock cannot be discounted. Certainly this species contrasts markedly with black marlin, which show trans-oceanic movements, single central spawning grounds, no inter-regional genetic heterogeneity, and are therefore thought to constitute a single pan-Pacific stock.

Clearly, there are still a number of critical questions that require answers. Do striped marlin exhibit spawning site fidelity? If so this would shift the weight of evidence heavily in favour of the two or more populations hypothesis. It will also be important to determine what proportion of striped marlin undertake longer migrations, and what are the precise movements of the juveniles stocks. Do juveniles initially congregate and mix in one single main region, and what is the pattern of their dispersal? Satellite tracking studies of this species, as well tagging programs initiated in regions currently lacking these programs, would help to answer many of these questions. There is also a clear need for more genetic work with larger sample sizes from specifically identified areas, and preferably using ripe gonads (or larvae).

2.5 Indian Ocean - Distribution, movements and migration

2.5.1 Distribution in the Indian Ocean

Adult Distribution: Adult striped marlin tend have a more tropical, warmer distribution in the Indian Ocean than in the Pacific (Ueyanagi and Wares, 1975). This may result from a number of factors, including the smaller size of the Indian Ocean, its more limited northern extent, and its unusual current patterns (Honma and Ueyanagi, 1979). The southern bounds of striped marlin in the Indian Ocean are near 45ºS in the southwest and 35ºS in the southeast. Based on longline catch rates and distributions (Chapter 3), striped marlin in the Indian Ocean appear to be less abundant compared with the Pacific, with seasonal concentrations of striped marlin occurring in four main regions: off the east African coast (latitudes 0º-10ºS), the south and western Arabian Sea, the Bay of Bengal, and north-western Australian waters (Merret, 1971; Pillai and Ueyanagi, 1978; also, Chapter 3). Analyses of catch data (1985-1995) off Western Australia, demonstrated that while catches span the entire western coastline, maximum catch rates occur off the NW coast between latitudes 10°S-25ºS, (Exmouth to Broome) (Anon.,1997). Koga (1967 in Anon.,1997) noted that the main striped marlin concentrations in this region are centred at the boundary of currents running along the 115ºE longitude. Densities are generally higher in near shore waters than mid ocean areas. Furthermore, while densities varied, there appears to be at least some striped marlin throughout the overall distribution at all times of the year (Pillai and Ueyanagi, 1978).

Juvenile distribution: Virtually nothing is known of the distribution and movements of juveniles in the Indian Ocean. Tagging data indicates that some juvenile marlin have been caught off the NW coast of Western Australia in the second quarter (Appendix I).

Larval distribution: Larvae, or mature female striped marlin, have been reported as occurring in five main regions:

1) In the western Indian Ocean larvae have been identified near the equator, west of Madagascar, latitudes 6ºN-6ºS, from December through January. Both gonad index analyses as well as larval surveys have confirmed the East African population (Pillai and Ueyanagi, 1978)
2) Nishikawa et al (1978) claimed to have found striped marlin larvae occurring southeast of Madagascar at latitudes 20-25ºS and 55-60ºE.
3) In the Eastern Indian Ocean off the northwest coast of Australia during July to December (latitudes 10-18ºS, long 110-125ºE) (Jones and Kumaran, 1964; Ueyanagi, 1974; Nakamura, 1983). Mature females are also found in high numbers off NW Australia in the 3rd and 4th Quarters.
4) In the Banda and Timor Seas (central eastern Indian ocean) during January and February (Ueyanagi and Wares, 1975).
5) Mature females have been caught in the Bay of Bengal during the 1st and 2nd quarters (Pillai and Ueyanagi, 1978), although no larvae have been yet found in this region.

2.5.2 Migrations and movements in the Indian Ocean

Similar to the north-south movements observed for striped marlin in the Pacific Ocean, seasonal changes in longline CPUE suggests that striped marlin undertake north-south migrations along the East African coast, with marlin only located off south Africa in the summer months before moving north for winter. Increased density of striped marlin off the east coast of Africa during the northeast monsoon is thought to be associated with a post spawning feeding migration (Ueyanagi and Wares, 1975). A springtime northward movement also may occur in the western Arabian Sea (Ueyanagi and Wares, 1975). A similar north-south migration between the waters off northwest Australia (Spring/summer) and the Bay of Bengal (Autumn) has been inferred from longline data (Pillai and Ueyanagi, 1978). Tagging data also indicates a north-south seasonal movement off the coast of Western Australia (Appendix I).

As mentioned earlier, the oceanographic features that prevent striped marlin entering the Atlantic around the Cape of Good Hope, are still not understood. Simultaneous analyses of gonad indices indicate also that the central western Indian ocean marlin only use this southern region for post spawning feeding grounds (Merrett, 1971; Pillai and Ueyanagi, 1978). An FAO workshop in 1980 suggested that oceanographic conditions may occasionally exist that might allow movement to occur between the Pacific and Indian Oceans (FAO, 1980). Unfortunately, there is little or no tagging data for striped marlin in the Indian Ocean, with only three recaptures reported for fish tagged off the central-east African coast and one recapture off the west Australian coast. However, it would seem reasonable to assume from Pacific Ocean tagging data that these marlin would tend to exhibit broader regional fidelity, but also be capable of long distance migrations. Tagging studies are clearly required to confirm this.

2.5.3 Stock structure in the Indian Ocean

It was originally thought, given the continuous distribution of adult striped marlin from east to West in the Indian Ocean that this region comprised a single stock. However, abundance varies with region, and given evidence for north-south seasonal migrations on either side of this ocean, and the occurrence of separate and geographically distant spawning grounds in the east and west, it seems very possible that the Indian Ocean population comprises more than one stock of striped marlin (Pillai and Ueyanagi, 1978; Skillman, 1989). There is considerable need for population analyses of striped marlin in this region, as fishing pressure will only increase for this species in the future.

2.6 Behaviour

2.6.1 Daily movements

Larvae/Juveniles: The behaviour of larval and juvenile striped marlin remains a mystery. Surface tows for larvae have indicated that larvae may migrate vertically on a diurnal basis, moving towards the surface during the day and into deeper waters at night, but always remaining in the 0-50m range (Ueyanagi and Wares, 1975; Armas et al 2001). Difficulties in obtaining and identifying these larvae have hampered the acquisition of knowledge in this area, although it must be said that the same applies to studies of this kind for all other billfish species.

Adults: There is also still relatively little known of the behaviour of billfishes such as striped marlin, but recent advances in tracking technologies have added to our understanding of these animals. Trends in daily vertical (depth) and horizontal movements of individual striped marlin have been observed through the use of such technologies. These studies have successfully described a number of aspects of daily movement and behaviour in adult striped marlin:

1) Most striped marlin spend the majority of their time above the thermocline in the mixed layer. Furthermore, a great deal of this time is spent very close to the surface. Four tracking studies (two using acoustic and two using pop-up archival satellite tags) to date have confirmed that striped marlin spend at least 74% of their time within 10m of the surface (and 69% of time in top 5m) (Holts and Bedford 1990, Brill et al 1993; Domeier et al, 2003). Depth preferences of striped marlin have also been determined from analyses of longline data, with most striped marlin caught in the surface 60-90m in the Pacific and Indian Oceans (Boggs, 1992). Nakano et al. (1997) determined from longline data that the highest catch rates occurred for hooks set between 80-140m, with the rate of catch decreasing quickly as hook depth increased past about 260m. Some fish were caught even at the deepest set lines, but as Boggs (1992) observed, these could be caught as lines were rising or settling (sinking). His study used hook depth timers and demonstrated that most striped marlin are caught in the upper 150m, with the deepest being caught at 210m.
2) Striped marlin do make short abrupt excursions below the thermocline. While in general these excursions into colder waters are fairly brief, one striped marlin was recorded as spending over fours hours of a 24-hour period at depth, and in temperatures between 10 and 12ºC (Holts and Bedford, 1990). Furthermore, another tracking study found that two of 12 tracked fish spent 25% and 76% of their time below the thermocline. Clearly these fish are capable of tolerating deeper colder waters. Similar trends have been observed in some PSAT tagged striped marlin off New Zealand (J. Holdsworth, Blue Water Marine Research, pers.comm.). Whether time spent below thermocline might relate to size and thermal inertia in striped marlin needs to be investigated. Some observations suggest that the depth to which these fish will dive appears to be limited by depth associated temperatures, relative to surface temperature. Studies off Southern California and off Hawaii suggest that striped marlin will not dive to waters that are more than 8ºC colder than the surface temperatures to which they are acclimated (Holts and Bedford, 1990; Brill et al., 1993). An analysis of depth and temperature data from 66 PAT tagged striped marlin found that the maximum depth dived to be 192m and lowest temperature recorded at depth was 12.8ºC. The average maximum depth recorded for these fish was 102m (Domeier et al, 2003).
3) None of the tracking studies have shown a single behaviour to be repeated in all observed fish but there are clearly some behaviours which are common to many of these fish. These include periods of “breezing” in which marlin will surface, with caudal fin protruding from the water, and swim quickly in the direction of the wind, with tail fin above the surface but the dorsal fin laying flat. Marlin have also been observed to “sleep”, remaining motionless for up to 4 hours near the surface of the water. This behaviour tends to be observed more at night and in early morning but can occur during the day also.
4) Tracking studies of striped marlin off Hawaii have suggested that the daily movements of these fish are strongly influenced by the prevalent currents in the region (Brill et al, 1993)

2.6.2 Feeding behaviour

Marlin are thought to mostly capture prey by directly grasping in their mandibles, however some food items recovered from gut analyses have been found to be speared (Ueyanagi and Wares, 1975). Recreational fishermen often observe marlin using their bill to “slash” at trolled baits, thus it seems likely that marlin might use a sideways swiping motion during normal feeding to stun or disable the prey that they are targeting. Marine turtles have been found with broken pieces of marlin bill impaled in the carapace or body, yet it seems unlikely that a marlin would view a large turtle as potential food item. It seems more likely that such injuries may occur when a marlin targets the fish that associate with turtles, and which might "hide" under a turtle when threatened, thus increasing the likelihood of collision between marlin and turtle (Goodger, 1940).

It has been hypothesised that marlin colouration has evolved specifically to aid in their predatory habits (Parker, 2001). Marlin are counter shaded with dark dorsal surface (possibly acts as camouflage from above) and silvery ventral and lower surface (for camouflage from below and side on). Such camouflage might allow marlin to get closer to prey before being seen. The sides of striped marlin are also characterised by specialised cells that reflect blue light. Black chromatophores in the skin can expand and contract, to control the extent to which the blue stripes on the side of the marlin are visible. These stripes are most vividly apparent when the marlin are feeding, and it is thought that they may serve to break up the silhouette of the marlin and confuse the prey (Parker, 2001).

Not much is know about how marlin initially locate prey, however at close quarters, vision will play a role. Recent research has shown that striped marlin are likely to have colour vision, based on analyses of anatomical features of their eyes (Fristches, 2002). It is thought that colour vision aids in object detection in the light infused top layer of the water column, but that it is relatively ineffective in low light situations, such as at night and at depth. This supports the idea that striped marlin predominantly feed in the surface layer during the day.

2.6.3 **Schooling behaviour**

Striped marlin do not form dense schools like many other species of pelagic fish, and generally occur singly or in small groups. Tracking studies by Holts and Bedford (1990) found that striped marlin may tend to aggregate in closer proximity during "sleeping" or inactive periods. The proximity between individuals also decreases when they access the same prey patches (with marlin feeding cooperatively by "balling" the baitfish and keeping the balls corralled) and productive regions, and more so during the spawning seasons (Ueyanagi and Wares, 1975). During spawning striped marlin have been observed to form trailing lines of 3-5 individuals, assumed to be a single female being courted by prospective males.

2.6.4 **Responses to predators**

There are likely to be few animals that might be capable of predating upon fully grown striped marlin, with perhaps only some species of large pelagic shark and toothed whales capable of catching and killing a marlin (Nakamura, 1985). While striped marlin are known to be capable of using their bill to spear or stun prey, it is unknown whether they might also use it in self-defence. Hooked marlin might be expected to exhibit similar behaviours to those that might accompany attacks by predators. Whether leaping and tail walking behaviours of hooked striped (and other) marlins is predator response behaviour or not is unknown. Certainly other fish species will use leaping and jumping as a means to avoid and confuse predators when being chased. Hooked striped marlin have also been known to ram fishing boats, however whether this is defensive, aggressive or accidental is unknown (Nakamura, 1985).

2.7 Size, growth and age

2.7.1 Larvae

Larvae are thought to grow very rapidly in a manner similar to other large pelagics like tuna and other billfishes. Known features of their growth and development include degeneration of head spination and development of fin formations and pigmentation (Ueyanagi and Wares, 1975). Snout elongation starts at around 7mm SL, along with extensive pigmentation. Fin ray complements are complete by 20mm SL. The dorsal fin increases height from around 10mm standard length and stands high like a sail (Ueyanagi and Wares, 1975).

2.7.2 Juveniles

The change in the shape and size of the dorsal fin is very marked in this species, with shape in larvae and juveniles being much more "sail-like" than that of the adults. By the juvenile stage, the snout is very elongate, and relative to the rest of the body, is the longest of any developmental stage for this species (Ueyanagi and Wares, 1975). Virtually nothing is known about the age and growth of striped marlin and in particular the earlier stages, as these fish only appear to become vulnerable to longline gear at around 80cm eye-fork length (Nakamura, 1985).

2.7.3 Adults

Ageing studies of striped marlin have been few, and ageing techniques for the species have yet to be conclusively validated. Therefore, life expectancy, age at size statistics, and growth rates are uncertain. However, based on size frequency analyses of longline caught fish, a maximum size of 290 cm and a maximum age of 10 years has been tentatively estimated (Koto, 1963; Ueyanagi and Wares, 1975). More recently, Melo-Barrera et al (2003) determined 10 age groups (2 to 11) from analyses of the fourth spine of the dorsal fin from recreationally caught striped marlin. A significant linear relationship was found between body length and dorsal fin radius. They calculated that striped marlin reach 45% of asymptotic length in the first year, with growth at around 4% from the third year onwards. The analyses of Merrett (1971) and Royce (1957 in Ueyanagi and Wares, 1975) of striped marlin weight frequency modal progressions in the central and western Pacific suggest an annual growth rate of 20-30 pounds and 10-20 cms. Kota (1963) north-west Pacific Ocean study found six modal length groups, being 100-120, 120-160, 160-185, 185-205, 205-220 and 220-233cm. While this indicates at least six age groups, no absolute age could be determined as no fish were caught below 100cm. However it did show that growth in length slowed as the marlin grew older. Furukawa et. al. (1958) suggest from their analyses of catch data from the East China Sea that striped marlin condition (relative fatness) increased as length increased and that, for some size modes at least, condition fluctuated on a seasonal basis, increasing in the third and fourth quarters and decreasing in the first and second quarters. Skillman and Yong (1976) also found from a length weight regression that as striped marlin became longer there was a trend toward increased relative weight gain (i.e., becoming relatively fatter).

Analyses of Hawaiian longline data using growth models have suggested that at 2 years of age, striped marlin are around 180cm (bill-fork length) and 23kg, at three years they are 215cm and 43kg and after 4 years, they are around 227cm and 52kg (male) and 59kg (female) (Skillman and Yong, 1976). However, a study of growth using dorsal spines and otoliths by Davie and Hall (1990) in New Zealand found the following age-weight relationships: 3 years (92.8kg), 5 years (108.6kg) and 7 years (125.6kg), which suggests that they may be faster growing in these waters than in other areas, or that earlier studies were less accurate. Radtke (1983) notes that the analysis of length modes to estimate age and growth of billfishes is not reliable because it is often difficult to separate the modes in the upper age classes. However, otolith studies in billfish are rather difficult due to their small size and the difficulty in obtaining them. This paper analysed 80 striped marlin otoliths and found that in the weight range of 18-62kg, marlin otoliths ridge count ranged from 3-6 (possibly indicating 3-6 years age range). However the spine and otolith studies have yet to be validated in any way.

Marlin species are among the fastest growing teleost species. For example, the Pacific blue marlin has been shown to have growth rates that outstrip even those of yellowfin and skipjack tunas (Brill, 1996). Whether striped marlin growth rates match those of Pacific blue marlin is unknown. The largest known striped marlin ever caught weighed 243.6kg, and was taken off New Zealand by game fishermen in 1995 (J.Holdsworth; Blue Water Marine Research, pers. Comm.). The largest specimen caught off Australia weighed 191kg, and was taken off NSW in 1992 (Pepperell, 1999). Larger specimens may be more easily confused with blue marlin, as they appear less laterally compressed (i.e., fatter) than younger or smaller adults. Growth does not appear to be allometric as such, with studies indicating that features such as pelvic and first dorsal fins cease growth after reaching a certain length (Morrow 1957; Ueyanagi and Wares, 1975). Size at first maturity in the Coral Sea was calculated as being near 29kg by Hanamoto (1977).

In the Indian Ocean, analyses of tagging databases suggests that striped marlin caught off east Africa average between 50-60 kg, while those caught off the west coast of Australia range from 10-110kg, depending on latitude and season. Japanese longline data indicated a size range of 91-230cm (eye-fork length) in the Indian Ocean with most between 155-185 cm (Pillai and Ueyanagi, 1978). Sexual maturity was attained at around 140-150cm (27-40kg) for striped marlin in the Indian Ocean (though evidence was limited in this study). Larger marlin are caught in the southern Indian Ocean (size mode 201-210 cm) and smaller marlin are relatively common in the eastern Indian Ocean (131-140 cm EFL).

2.8 Diet

Striped marlin are opportunistic generalist epipelagic predators. In other words, they have a very varied diet, which while being relatively non-selective, mostly consists of species that inhabit the surface layers of the pelagic ecosystem. Squid form an important part of the diet of striped marlin in many regions of both oceans, and the orange colour of striped marlin flesh from some regions is attributed to a large intake of squid. This is due to squid having a diet of crustaceans (e.g. prawns), resulting in a bioaccumulation of carotene from these species in the marlins muscle tissue (Pepperell, 1999). However, generally the diet consists of a mix of fish and squid, with the relative proportions of these changing with season and region (Ueyanagi and Wares, 1975). Studies off New Zealand (Morrow 1952; Baker, 1966), Peru (La Monte, 1955), East Africa (Williams 1967), and in the central north Pacific Ocean all found squid to be a major component of striped marlin diet. However in the Australia-New Zealand region they also target saury, jacks, lancetfish and clupeids which include species like herring and sardine (Reviewed in Abitia-Cardenas et al. 1997). However, to emphasise the generalist nature of striped marlin diet, a study of stomach contents in 347 striped marlin caught in the EPO identified 17 prey species from 12 families, with scombrids being found in over 50% of these fish, but only accounting for 11% of number of fish per marlin. Bramids were highest in terms of total number of prey items. The authors speculated that striped marlin reduce competition with other pelagic predators by utilising their greater speed to target faster swimming scombrids. However, other studies have demonstrated that striped marlin will also feed on demersal (bottom dwelling) species (Abitia-Cardenas et al. 1997). In general the diet of striped marlin contains more surface dwelling prey species (epipelagic) than those of most other billfish and large tunas.

Many different studies of striped marlin gut contents have been conducted in various regions throughout their distribution and in different seasons. These have determined that most of the variation in diet occurs with region or season, rather than with size or sex of fish (Evans and Wares, 1972). Furthermore, prey species availability varies between years and striped marlin appear to easily switch to alternate prey species when this occurs. Abitia-Cardenas et al. (1997) demonstrated in their study of striped marlin diet off Mexico, that, while in 1988 the summer diet was dominated by squid, the following summer it was dominated by fish.

Examining diets of co-occurring billfish species can also indicate the extent to which these species compete for food (Galvan-Magana, 2003). A study of striped marlin, blue marlin and sailfish off Mexico found that striped marlin targeted mainly surface schools of sardine and blue mackerel, while blue marlin and sailfish targeted mostly bullet mackerel (Galvan-Magana, 2003). In this study it translated to the striped marlin trophic range being closer to the coast than the other two species. Another study of seven pelagic species including striped marlin analysed stomach contents and discussed the depth ranges of their prey species, relating it to how pelagic predators might compete for resources. Striped marlin were identified as “wide range feeders from surface to midwater”, similar to yellowfin tuna. Overall the study suggested that by different pelagic predators targeting prey species that occur at different depths, there would be reduced trophic competition between these predatory species (Moteki et al. 2001)

Many other species might compete for the same resources that adult striped marlin target, with species such as other billfish, sharks, tunas and dolphins likely to have overlapping trophic ranges. However, striped marlin tend to feed on more epipelagic species than do many of the tunas and swordfish, which tend to target mesopelagic prey.

Evidence for the time of day that striped marlin feed is somewhat conflicting, with some studies (eg, of digestive state of food in gut) suggesting that they feed in the morning and middle of the day while others suggest that they may feed at any time of day or night (reviewed in Ueyanagi and Wares, 1975). It is quite likely that feeding time may vary with region, season, and the vertical and horizontal movement patterns of their prey species in the area. However, an analysis of Australian domestic longline catch rate data (Chapter 8) demonstrated that catch rates were highest for day time sets, suggesting a tendency towards daytime feeding in this species. This is supported by recent evidence for colour vision in striped marlin which is most effective in high light environments, such as the surface layer during the day (Fritsches, 2002).

2.9 Reproduction

Striped marlin appear not to show a great degree of sexual dimorphism, with both sexes tending to grow to about the same size. Some studies have found evidence for sexual dimorphism (with females reaching larger sizes) but other studies have not found any difference at all (Merrett, 1971; Kume and Joseph 1969b; Ueyanagi and Wares, 1975 and references therein). Not much is known in regard to age at first maturity for striped marlin, as age at specific size is still largely unknown. However, more is known about size at first maturity. There is some evidence to suggest that striped marlin in the Indian Ocean might attain maturity earlier than those in the Pacific, based on the fact that mature marlin have been identified in the 140-150cm (eye-fork length) size class in the Indian Ocean, whereas mature individuals are first apparent in size classes 160cm or greater in the Pacific Ocean. However, Hanamoto (1977) noted that minimum size of spawning striped marlin in the South Coral Sea was 143cm eye-fork length; so clearly further research is required into this area.

Maturation in males is more difficult to determine than in females as the testis only increase slightly in size during the maturation cycle (Merrett 1970). Conversely maturation in females in more obvious, with large increase in size of gonads.

Striped marlin are highly fecund, with estimates of total egg production per female ranging between 11 and 29 million (Merrett, 1971; Eldridge and Wares 1974). The eggs are spherical (around 1-1.5mm diameter), transparent and buoyant with a single oil globule (Morrow 1964). Fertilisation is external. Based on size frequency distribution of eggs in females, Eldridge and Wares (1974) suggest that spawning occurs once per season. Interestingly recent studies on white and blue marlin have suggested that spawning may be serial in these species. Further research is needed in relation to the reproductive biology of striped marlin. In both hemispheres the spawning season coincides with summer, peaking around May-June in the northern hemisphere and around November-December in the southern hemisphere (Kume and Joseph, 1969). Longline catches have indicated that sex ratios tend to change in the spawning season, and are dominated by males, but after this period the sex ratios show a bias to females (Ueyanagi and Wares, 1975). During the spawning period, striped marlin have been noticed to "pair-off", and these temporary partnerships appear to be fairly strong, with fishermen noting that even when a marlin is hooked, the partner will tend to stay close by until the fish is hauled from the water (Eldridge and Wares, 1974).

2.10 Summary and conclusions

Striped marlin, *Tetrapturus audax*, is a pelagic billfish species that is distributed throughout the Pacific and Indian Oceans (See Figure 2.2). Satellite and archival tagging studies have demonstrated that this species spends the majority of its time inhabiting the surface layer in the water column (Holts and Bedford, 1990; Brill et al 1993; Domeier 2003). Although this species is highly fecund (Merrett, 1971; Eldridge and Wares, 1974) and fast growing (Brill, 1996; Skillman and Yong, 1976), some biological parameters suggest a degree of vulnerability to overexploitation. Available evidence suggests that striped marlin may not mature until between two to three years of age or at around 145 cm eye-fork length (e.g. Pillai and Ueyanagi, 1978), but observer data from the central Pacific show that these fish are vulnerable to longline gear at around 100 cm lower jaw-fork length (Figure 2.3), well before they have the chance to contribute to the reproductive adult population. In addition, analyses of global tagging data suggest that this species may not be as "highly migratory" as once thought. Mean displacements vary between regions but of all striped marlin released off Australia, 98% of subsequent recaptures are caught within 1000 nm of their release point (Appendix I), and the majority of these within 500 nm, suggesting some level of broader regional fidelity being exhibited by this species. Presently, fisheries biologists know little about the key age, growth, mortality and reproductive parameters of striped marlin. This severely hinders understanding of the species vulnerability to overexploitation and the assessment of stock status, with flow on effects for the ability of fisheries managers to manage this resource.

The stock structure of striped marlin in the Indian and Pacific Oceans is still uncertain. Understanding stock structure of fish species generally relies on knowledge of genetic relationships between regions; mixing between regions; and distribution and possible areas of low abundance or absence that can indicate populations separations. Almost no data of this type has been collected for striped marlin in the Indian Ocean. Evidence for separated spawning grounds and north-south shifts in CPUE in the east and western regions of the Indian Ocean may suggest two stocks (Pillai and Ueyanagi, 1978; Skillman, 1989), but this conclusion is very tentative. Consequently, virtually nothing is known of its stock structure in this region. The implications of a lack of knowledge concerning the biology and stock structure of striped marlin in the Indian Ocean for fisheries management of the species is discussed in Chapter 10.

The level of knowledge pertaining to stock structure in the Pacific Ocean is much greater (but still developing). The majority of tag-recaptures indicate striped marlin undertake more localised regional movements in the order of a few hundred miles (Appendix I). Longline data indicate a "horseshoe" shaped distribution might limit the speed of mixing, particularly between northwest and southwest regions (Figure 2.2). Based on the fact that tag recaptures from marlin released in the SWPO are yet to be recorded in the eastern Pacific (and vice versa) (Figure 2.4), that there appear to be widely separated spawning regions (Figure 2.2), and that slight genetic difference are apparent between samples from the southwest Pacific with the central-north and eastern Pacific, the possibility of a semi-independent south west Pacific stock cannot be discounted. The implications of these findings for fisheries management of striped marlin in the waters off eastern Australia are discussed in Chapter 10.

To overcome uncertainties regarding stock structure, satellite and archival tagging studies, as well as conventional tagging programs are required to determine if striped marlin exhibit spawning site fidelity, and the movements of the juvenile sub-population. There is also a clear need for further genetic work.