Current knowledge, key uncertainties and future research directions for defining the stock structure of skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific Ocean

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Identifying the Spatial Stock Structure of Tropical Pacific Tuna Stocks

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Report outline

Tuna are the focus of significant fisheries in the Pacific Ocean, with landings of four species (skipjack tuna, yellowfin tuna, bigeye tuna and albacore tuna) constituting approximately 70% of the global tuna catch. Stock assessments for skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific Ocean currently assume eastern and western stocks, a split that reflects historical development of fishery management in the region rather than biological considerations. There is widespread agreement that uncertainties surrounding the stock structure of the four main target species could have important impacts on population dynamics models used to assess stock status and inform management options. Improved knowledge of stock structure is also essential to modelling the effects of climate change on the distribution and abundance of tuna species. This paper reviews current knowledge and understanding of the stock structure of skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific Ocean, through an exploration of available literature relating to movement, connectivity, and spatial dynamics. Informed by an expert workshop, we then outline the key questions that need to be addressed to determine the stock structure for each species, and propose some potential sampling designs by which future studies may address these uncertainties and improve understanding of stock structure of the four tuna species in the Pacific.

Introduction

Tuna (Family Scombridae, Tribe Thunnini) are ecologically important top-order predators in pelagic ocean ecosystems. They occur across tropical to sub-polar habitats and support extensive fisheries worldwide. In the Pacific Ocean, tuna support major industrial fisheries and a variety of small-scale domestic and subsistence fisheries. The principal target species are skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*), and albacore tuna (*Thunnus alalunga*). Combined, these four species comprise over 90% of industrial catches in the Pacific and approximately 70% of global catches, with approximately 3.2 million metric tonnes (mt) harvested in 2017 (SPC-OFP 2018a).

Commercial catches of tuna in the Pacific result mainly from two separate fisheries: 1) a surface fishery, that targets skipjack and juvenile yellowfin tunas using purse-seine and pole-and-line fishing methods, primarily for the canning trade, and 2) a sub-surface longline fishery, that targets mature bigeye and yellowfin tunas for the sashimi trade and other high-value markets, and albacore tuna for canning.

The majority of the catches of these four species in the Pacific Ocean comes from the waters of the Western and Central Pacific Ocean (WCPO), with an estimated 2,539,950 mt harvested commercially in 2017 (Figure 1) (SPC-OFP 2018a[1]). Around 60 per cent of this is taken within the Exclusive Economic Zones (EEZs) of Pacific Island Countries and Territories[2] (PICTs; Williams and Reid 2018), including by foreign-flagged vessels that pay fees to PICTs in order to access their EEZs. In addition, important harvests are made by artisanal and subsistence fishers in nearshore waters of PICTs for domestic consumption (Bell et al. 2015, 2018a). As a consequence, tuna fisheries make substantial contributions to government revenue, gross domestic product, employment, livelihoods and food security in several PICTs (Gillett 2016; Williams and Reid 2018; Bell et al. 2018a). Further west, large catches of tuna are also taken in the waters surrounding Indonesia and the Philippines, representing around 35% of the total WCPO catch (SPC-OFP 2018a). Smaller, and in some cases seasonal, catches of the four species are taken in the EEZs of Australia, New Zealand, China, Japan, and Vietnam (SPC-OFP 2018a).

Substantial harvests of tuna are also made in the Eastern Pacific Ocean (EPO), with an estimated 637,397 mt of skipjack, yellowfin and bigeye tunas caught in 2017 (IATTC 2018). Historically, catches in the EPO have been dominated by yellowfin tuna, with catches for this species peaking at around 440,000 t in 2002 (IATTC 2018). However, in recent years, catches of skipjack tuna have exceeded those of yellowfin tuna, with an estimated 327,979 t of skipjack tuna landed in 2017 (IATTC 2018).

Management of tuna stocks in the Pacific, which are assumed to straddle EEZs and the high seas, occurs primarily through two international conventions: the Convention on the Conservation and Management of High Migratory Fish Stocks in the Western and Central Pacific Ocean; and the Antigua Convention (which revised the Convention for the establishment of an Inter-American Tropical Tuna Commission). These conventions are operationalised by two independent tuna Regional Fisheries Management Organizations (RFMOs): the Western and Central Pacific Fisheries Commission (WCPFC) in the WCPO, and the Inter-American Tropical

[1] Based on catch estimates for the Western and Central Pacific Fisheries Commission Statistical Area.

[2] American Samoa, Cook Islands, Fiji, Federated State of Micronesia, French Polynesia, Guam, Kiribati, Marshall Islands, Nauru, New Caledonia, Niue, Northern Mariana Islands, Palau, Papua New Guinea, Pitcairn Islands, Samoa, Solomon Islands, Tokelau, Tonga, Tuvalu, Vanuatu, Wallis and Futuna.

Tuna Commission (IATTC) in the EPO. There is an overlap in the area of responsibility of the two RFMOs, bounded by 150°W, 130°W, 4°S and 50°S, with this region considered part of the WCPO in catch statistics (the WCPFC Statistical Area; Figure 1). Assessments of skipjack, yellowfin and bigeye tunas have been conducted by the Pacific Community (SPC) in the WCPO, and by the IATTC Secretariat in the EPO. The status of albacore tuna in the South Pacific is assessed by SPC and in the North Pacific by the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean (ISC).

Despite their importance to fisheries across the Pacific and globally, and the regular population assessments conducted as part of RFMO activities, a number of uncertainties associated with the population connectivity and stock structure of skipjack, yellowfin, bigeye and South Pacific albacore tunas exist. Current assessments for skipjack, yellowfin and bigeye tunas assume eastern and western stocks of each species; a split that essentially reflects the history of fishery management in the region rather than biological considerations. Similarly, regional structures in stock assessments, when present, typically represent the spatial distribution of fishing gears with differing selectivities, tag mixing assumptions, and management regimes. There is growing evidence however, that suggests that the spatial structure and dynamics of populations of the four target tuna species may be more complex than currently assumed, as highlighted across the breadth of studies reviewed herein. There is widespread agreement that complexities in stock structure, if present at levels beyond those currently incorporated in the population dynamics models used to assess stock status, will have important impacts on assessments for the four main target species. Depending on the degree of complexity present, there are also implications for models used to assess the effects of climate change on the distribution and abundance of the tropical Pacific tuna species (Lehodey et al. 2017; Senina et al. 2018). To date, such modelling has assumed that each species of tuna is a panmictic population across the tropical Pacific basin. For such models to be applied effectively in identifying potential adaptation scenarios that may be uptaken to reduce the socio-economic risks associated with changes in the distribution and abundance of tuna (Bell et al. 2018b), models need to be able to appropriately represent each self-replenishing population (stock) of tuna. Accordingly, defining the stock structure of the four species is considered a key research priority (Lewis 1990; Kolody and Hoyle 2015; Evans et al. 2016).

This review adopts the approach that to the greatest extent possible self-replenishing populations should be the basic unit of fisheries management and examines information published relating to the stock structure of skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific Ocean in this context. We first explore definitions of stock structure, in the context of highly mobile species, and examine the techniques commonly used for discerning stock structure of pelagic fishes. We then review those studies that have contributed to the current understanding of the stock structure of the four tuna species in the Pacific. Last, based on information from an expert workshop, we outline key knowledge gaps and questions to defining the stock structure of each species, and outline potential sampling design approaches and considerations that could be implemented to improve understanding of the stock structure of the four tropical tuna species in the Pacific.

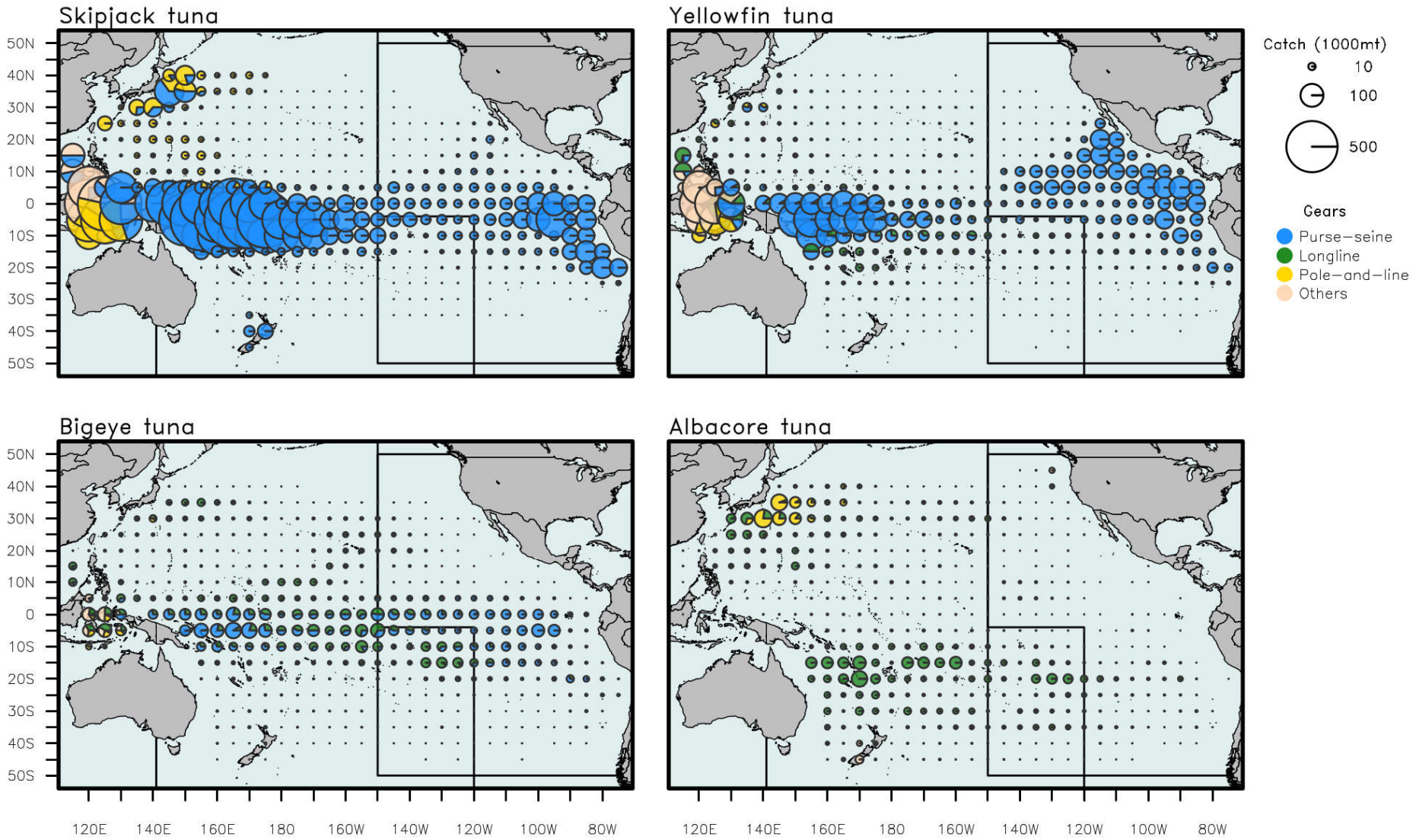


Figure 1. Distribution and magnitude of total catches for the four main tuna species in the Pacific Ocean over the most recent decade (2008–2017) by 5◦ square and fishing gear: longline (green), pole-and-line (yellow), purse seine (blue) and miscellaneous (pink).

The role of stock structure in fisheries management

Knowledge of a species' stock structure is a fundamental component of single species and ecosystem-based fisheries assessment and management. Fisheries management generally aims to achieve objectives which may include maximising production whilst avoiding the overexploitation of the units being harvested (Shaklee et al. 1990). To meet these goals fisheries managers must acquire knowledge about the number, size and spatial extent of the stock(s) being harvested. Most stock assessment models rely on the assumption that the group of individuals being assessed (a unit stock) form a discrete entity, with its own origin, demographics, and fate (Kutkuhn 1981; Begg et al. 1999a; Cadrin et al. 2005; Waldman et al. 2005). Accordingly, before any population parameters can be derived for use in stock assessment models, the boundaries that characterise the stock in question must be defined, otherwise the way a stock will respond to management decisions cannot be accurately predicted (Begg et al. 1999a). Undertaking a single stock assessment on multiple individual stocks or on only a portion of a larger stock may produce misleading results if a closed stock within the assessment boundary is assumed (Begg et al. 1999a) (Figure 2). Failure to recognise stock structure can lead to over- or under-fishing (Tuck and Possingham 2000). Where stocks may be undergoing rebuilding, differential restoration between unidentified stock components can lead to an inability to anticipate future recruitment to those stocks (Begg et al. 1999a; Kell et al. 2009).

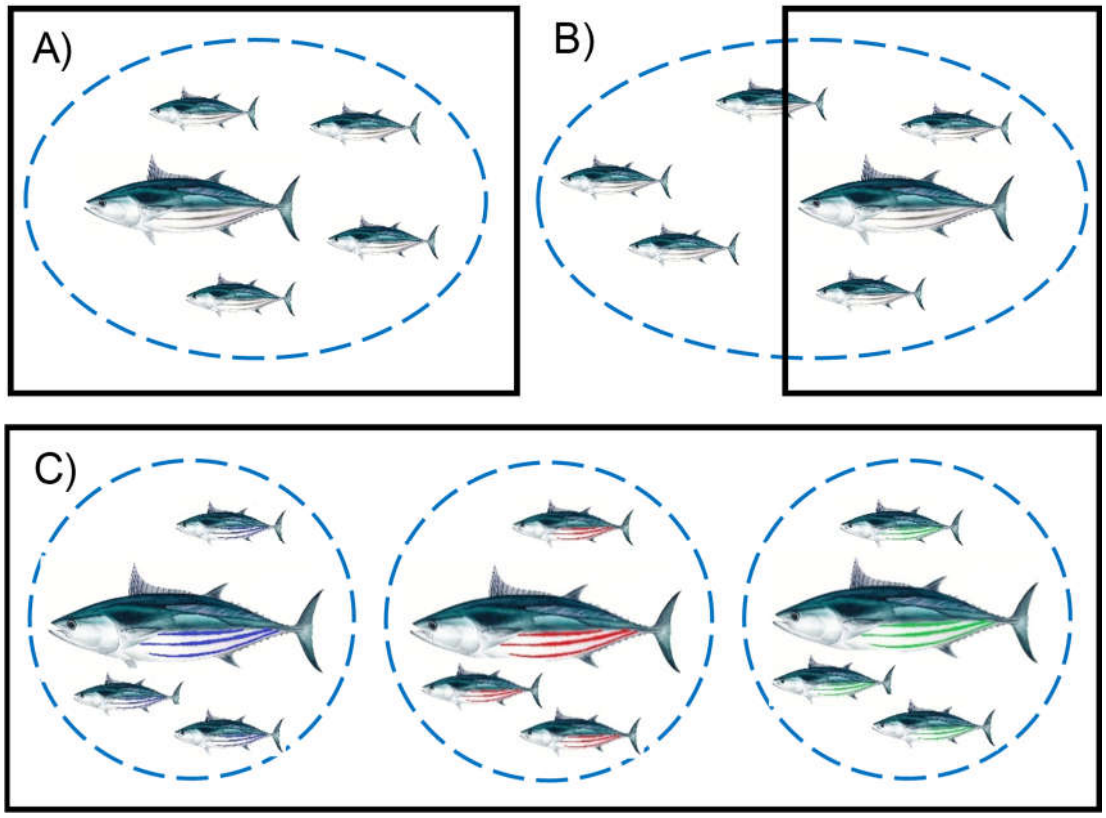


Figure 2. Diagram of scenarios in which A) assessment boundaries (black rectangles) match stock unit (dashed blue ellipses); B) assessment boundaries smaller than stock unit (i.e. the modelled stock is not closed), and C) assessment boundaries encompass multiple stock units (i.e. model assumes exchange and same biological parameters across stocks).

Hypothetical stock structure scenarios for tuna in the Pacific Ocean

The first step in defining stock boundaries for a specific species is to consider which model best describes the potential population structure (Baverstock and Moritz, 1996). Higher levels of migration and gene flow are expected to result in greater similarity within and between populations. Pelagic fishes such as tuna can exhibit complex spatial dynamics, owing to a range of processes acting on all life history stages. Past and ongoing studies aiming to identify stock structure for pelagic fish have generally attempted to address one of three main themes: i) the conditions governing spawning (timing, location and behaviour; Figure 3), ii) the extent of individual movement/mixing, including provenance, or where the individual is sourced from, and iii) the existence of natal homing, or the tendency for individuals to return to their birth location to spawn. For tunas, questions relating to these three themes are especially important. This is because tropical tunas appear to have overlapping spawning and foraging areas, combined with potentially high levels of juvenile movement, and consequently populations sampled from an area may represent a mix of fish with different natal origins. These three themes can result in different scenarios of population structure, outlined below, each with their own stock assessment implications (Table 1). For example, in a hypothetical instance in which spawning is conducted in discrete locations, with low post-larval mobility, and high degree of natal homing, there is a high risk of overfishing less productive stocks if a single stock is assumed (Table 1). Hypotheses of tuna stock structure in the Pacific Ocean that warrant consideration are summarised as follows:

1. Basin-wide Panmixia. A panmictic population is one where it is assumed that there are no mating restrictions, neither genetic nor behavioural, upon the population, and that therefore all recombination is possible (i.e. the mating between two organisms is not influenced by any environmental, hereditary, or social interaction). This hypothesis assumes a single basin-wide stock for the Pacific Ocean.

2. Isolation by Distance. This describes the process of increasing genetic differentiation correlated with increasing geographic distance. (i.e. a continuous stock with organisms exchanging genes from geographically close areas).

3. Metapopulations. This describes a series of small sub-stocks with small amounts of connectivity between them, either through advection of eggs or larvae, or movement of post-larval life history stages (juveniles and adults). Spatial and temporal isolation mechanisms may restrict the gene flow within a population. This may result in differing levels of recruitment in an area as a result of stochastic processes leading to the reproductive activity coinciding with the oceanographic conditions conducive to spawning, fertilization, and larval survival. If favourable (or unfavorable) environmental conditions persist this may lead to sufficient selection of alleles that delineates sub-stocks. This may manifest in other traits such as differing growth rates and maturity dynamics.

4. Closed populations. Each species is structured into multiple, reproductively isolated units, with no gene flow between them.

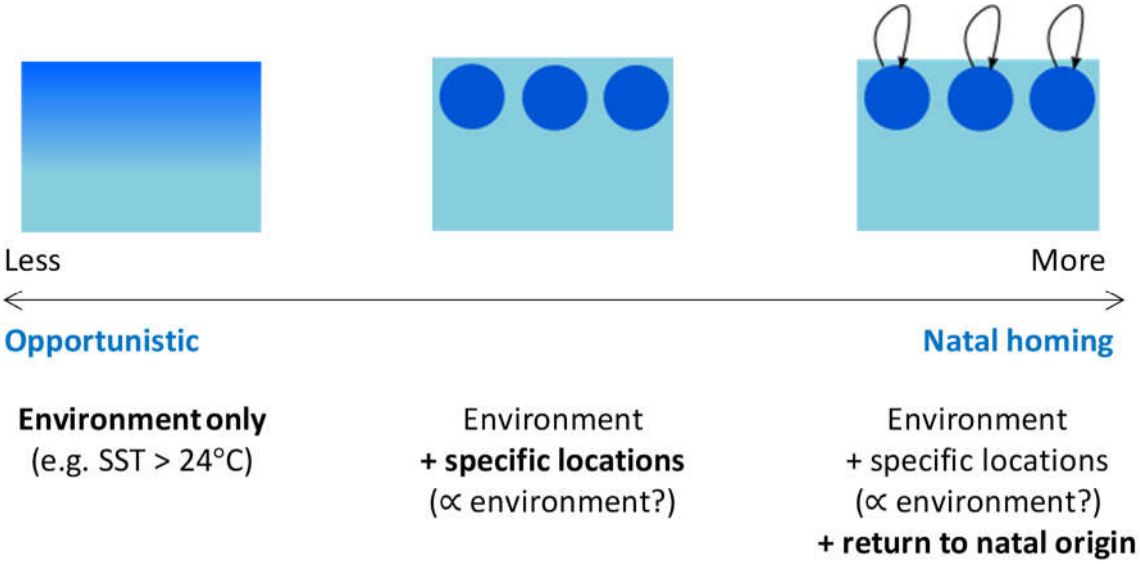
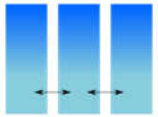
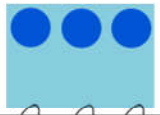
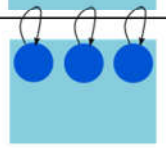
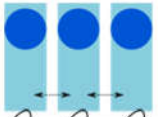
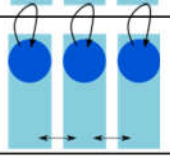


Figure 3. Schematic of the range of conditions governing spawning in tunas, ranging from less restrictive, where spawning is opportunistic and limited by environmental conditions, to slightly more restrictive, where adults spawn in specific areas, to the most restrictive, in which adults undergo homing and only spawn in their area of natal origin.

Table 1. Summary of key research themes to gain understanding of stock structure for pelagic species: spawning conditions (opportunistic vs. discrete); post-larval mobility (low vs. high) and natal homing. The combination of these themes in turn yields different scenarios of stock structures (4th column; diagrams) associated with potential stock assessment concerns (5th column). The top row outlines the main tools available to study each of the three themes. The darker blue in the diagrams indicate an area where spawning occurs within the overall range (light blue).

	Spawning behavior	Post-larval mobility	Natal homing	Stock structure scenario	Assessment concerns
Tools	- Gonad development - Larval distribution	- Tags (all types) - Molecular markers - Otolith chemistry - Parasites	- Electronic tags - Molecular markers - Chemical markers - Parasites		
	Opportunistic	High	--		Limited; must ensure assessment boundary contains the full stock
		Low	--		Higher; risk of overfishing less productive stock under single stock assessment, unless spatially-explicit assessment allows for different biological parameters across regions
	Area-specific	High	No		Limited; adult mixing should ensure productivity is the same across stocks
			Yes		Higher; risk of overfishing less productive stock, but cannot be individual assessments due to mixing of adults
		Low	No		Higher; risk of over-fishing less productive stock under single stock assessment, unless spatially-explicit assessment allows for different biological parameters across regions
			Yes		

Approaches for delineating stock structure of pelagic fishes

Molecular approaches

Molecular markers have been widely used in fisheries management to investigate the genetic structuring of populations of fishes. In addition, they have been used for species identification, provenance (e.g. for chain of custody determination) and for investigations of population connectivity (Morin et al. 2004; Pecoraro et al. 2017). The continuous development of novel techniques, combined with increasing accuracy and reliability, has seen the utility of molecular markers in fisheries management applications increase over time. In particular, the development of DNA-based markers in the early 1990s rapidly revolutionized population genetics. The invention of a technique known as polymerase chain reaction (PCR) and more recently DNA sequencing has further driven progress in approaches to investing the population genetics of marine fish species.

Allozymes were the first molecular markers used in population genetics. They were used for several decades due to their relative rapidity and ease to quantify genetic variation among populations allowing the assessment of their genetic structure (Ward et al. 1997; González-Wangüemert et al. 2007), as well as to underline evolutionary forces that promote differentiation (Carvalho and Hauser 1995). However, the limited number of loci and the low level of variability of allozymes resulted in low analytical power in terms of the comparison of allele frequencies, estimation of population differentiation and basic mixed-stock analyses (Lewontin 1974; Ryman and Utter 1987).

The development of DNA markers in the early 1990s rapidly revolutionized population genetic structure analysis by allowing determination of gene flow and allele frequencies among populations. The first widely used DNA marker was mitochondrial DNA (mtDNA), surveyed either by fragment or direct sequencing analysis. Two main characteristics make mtDNA a particularly useful marker in population studies. First, the mtDNA control region evolves rapidly, allowing for detection of genetic differentiation over relatively small geographic and short evolutionary timescales (Avise 1994). Second, mtDNA is maternally inherited, resulting in it having an effective population size one fourth of that of nuclear markers, making it a more sensitive detector of population subdivision and bottlenecks (Wilson et al. 1985). In addition, because of this maternal inheritance, it can provide insight into the extent of female dispersal and spawning dynamics (Avise 1994).

Microsatellite markers have been commonly used in population genetic studies of marine fishes due to features including hypervariability, codominant inheritance, reproducibility, high mutation rates and their multiallelic nature (Pompanon et al. 2005; Guichoux et al. 2011; Horreo et al. 2017). High mutation rates are of particular interest due to high levels of variation present in marine fish populations. Microsatellite markers are considered to be more reliable than mtDNA markers for identifying populations with recent divergence or that exhibit greater gene flow (Ogden 2008). Their high mutation rates and presence of null alleles however, may cause problems in population analysis (Morin et al. 2004; Pompanon et al. 2005), including producing unreliable estimates of divergence times and gene flow among populations (Kalinowski 2002; Morin et al. 2004; Pompanon et al. 2005). In addition, compared to allozymes and mtDNA assays, microsatellite markers are species-specific, making their development and reproducibility quite challenging (Zane et al. 2002; Pompanon et al. 2005; Guichoux et al. 2011).

In the last decade, the development of high-throughput (next-generation) sequencing technology has allowed for the sequencing of DNA more rapidly and cheaply than previously. In particular,

this technology has facilitated the identification of single nucleotide polymorphisms (SNPs). These markers consist of a single base change in a DNA sequence, with the least frequent allele having a frequency of one percent or greater and are usually bi-allelic in nature. Single nucleotide polymorphisms, which are linked to genes under selection, offer numerous advantages over mtDNA and microsatellite-based approaches in population structure studies, including the potential for higher genotyping efficiency, greater data quality and reliability, genome-wide coverage and analytical simplicity (Morin et al. 2004; Corander et al. 2013). Use of SNPs in fishery applications include investigation of population structure, determination of species identification, traceability and provenance, and estimations of population size (Morin et al. 2004; Nielsen et al. 2012; Bylemans et al. 2016; Grewe et al. 2015).

Non-molecular approaches

Tagging

A range of externally attached and internally placed tags can provide information on the movements of individuals and have been used extensively throughout the Pacific on a range of tuna species (e.g. Kleiber and Hampton 1994; Hampton and Gunn 1998; Labelle and Hampton 2003; Schaefer and Fuller 2007; Evans et al. 2008; Williams et al. 2015; Scutt Phillips et al. 2017). The simplest is a plastic, uniquely identifying, tag known as a conventional, mark-recapture tag. Information on the location at which the tagged fish was released and recaptured provide insights into dispersion of fish (e.g. Hampton and Gunn 1998). The advent of electronic tagging now provides detailed information on the behaviour of pelagic species, and aspects of their environment, on spatial and temporal scales largely independent from fisheries. The deployment of an ever-evolving array of telemetry and data logging devices on a growing number of marine species is rapidly increasing our understanding of the movement, behaviour and physiology of these species and the complex, and often highly dynamic, environments they use and respond to (e.g. Evans et al. 2013), with light-based geolocation approaches providing lower resolution of movements and GPS tags providing higher resolution of movements (see Sibert et al. 2003; Evans et al. 2011; Basson et al. 2016).

Life-history parameters

Variability in life history parameters, particularly those associated with age, growth, and reproduction, and morphological and meristic characteristics, can provide some insights into the potential structuring of pelagic fish populations (Jennings and Beverton 1991; Abaunza et al. 2008; Silva et al. 2008; Zischke et al. 2013) and the presence of geographic and / or reproductive isolation (Ihssen et al. 1981; Begg et al. 1999b).

Analysis of body shape (morphometrics), or counts of morphological structures, such as fin rays, gills rakers, or scales in rows (meristics) have long served as a basis for fish stock identification. Variations in body morphometrics and meristics are widely acknowledged to be influenced by both genetic and environmental factors, including temperature, salinity, depth, current flow and dissolved oxygen (Robinson and Wilson 1994; Foote et al. 1999).

Chemical constituents of body parts

Examination of the chemical composition of inert body tissue has the potential to offer insights into the movement and stock structure of pelagic fishes (Rooker et al. 2001, 2008; Shiao et al. 2010; Wells et al. 2015). A range of tissues have been used to provide information on movement and stock structure (as reviewed by Tzadik et al. 2017), although otoliths are the most commonly examined. As an otolith grows, elements are incorporated into its calcium carbonate structure at rates largely mediated by both environmental and endogenous factors, including ambient concentration, water temperature, salinity and diet (Fowler et al. 1995; Campana 1999). As

otoliths are metabolically inert (i.e. they are not subject to resorption, remodelling or regeneration), the deposition of elements and resulting chemical signature remains unaltered through time (Campana 1999). Consequently, otoliths retain a chronological record of the environments experienced by a fish throughout its life (Campana 1999; Secor and Rooker 2000).

Historically, studies typically examined whole otoliths dissolved in solution providing a composite chemical signal across a fish's entire life (e.g. Newman et al. 2009). However, recent advances in laser ablation and micro-milling technologies have allowed for examination of fine-scale patterns in chemistry within defined areas of individual otoliths. When assessed in conjunction with temporal references within otoliths, such as annual or daily growth increments (e.g. Rooker et al. 2008; Moore and Simpfendorfer 2014), and/or an understanding of the potential source of the chemical signature examined (e.g. Harwood et al. 2008), resulting chemical profiles can facilitate examination of ontogenetic patterns of movement and determination of natal origin and provenance thereby providing insights into potential differences between populations.

Recently, several studies have examined the chemical composition, and in particular isotopes of $\delta^{13}C$ and $\delta^{15}N$, of metabolically active tissues of pelagic fishes to examine the broad scale foraging ecology of species (see review by Graham et al. 2010). In pelagic fishes, estimates suggest isotopic signatures in metabolically active tissues such as muscle typically have turnover rates of less than one year (e.g. Madigan et al. 2012), indicating they could provide inform on short-term movements.

Parasites as biological tags

Several studies have used parasites as biological tags to elucidate movements and stock structure of pelagic fishes, including skipjack tuna (Lester et al. 1985), albacore tuna (Jones 1991), black marlin *Istiopmax indica* (formerly *Makaira indica*; Speare 1994), Spanish mackerel *Scomberomorus commerson* (Moore et al. 2003), and wahoo *Acanthocybium solandri* (Zischke et al. 2013). If it is known where a fish acquires a certain parasite, its subsequent movement can be deduced. Where the source of infection is not known, analysis of parasite fauna can at least indicate whether fish from different samples share a common environment history (Lester 1990). Where the parasite fauna of two or more individual fish, or groups of fish, is the same, those fish have either resided in a similar environment or share a common history. Where the parasite faunas are different, the history of the samples is different according to the parasite's residence time in or on the fish, with parasites with short residence times providing information on recent location history, and parasites with long residence times provide information on long-term location history (Lester and MacKenzie 2009; Lester and Moore 2015).

Ecosystem, movement and larval dispersal models

Ecosystem, movement and larval dispersal models have been used to provide insights into the dispersal, mixing and potentially the stock structure of pelagic species. In the Pacific, two such models have been developed for modelling the movement and population dynamics of tuna and other pelagic fishes: the Spatial Ecosystem and Population Dynamics Model (SEAPODYM; Lehodey et al. 2008) and the Individual-based Kinesis, Advection and Movement of Ocean Animals model (Ikamoana; Scutt Phillips et al. 2018). SEAPODYM simulates the spatial distribution of weekly or monthly age-classes of a given species through time, using an advection-diffusion-reaction modelling approach, representing the population of fish as a continuous tracer in a two-dimensional field. Species- and size-specific parameters capture individual accessibility to a three-dimensional forage-fish prey model through estimates of thermal tolerance and oxygen limitations that represent the diving behaviour of individuals (Senina et al. 2016; Lehodey et al. 2018). SEAPODYM assumes a single Pacific stock for each of the four tuna species examined in this review, but patterns in distribution do emerge as a

function of physical ocean forces, population depletion due to natural and fishing mortality, and population responses to a spatiotemporally varying spawning and foraging habitat index generated from the three-dimensional forage-fish model (Lehodey et al. 2010a).

Two distinct and non-overlapping spawning grounds can still give rise to a genetically homogenous population, if movement between these grounds is high enough across many individuals of the species. This is hard to examine using Eulerian models such as SEAPODYM, because the conditional pathway of a tracer in the advection-diffusion-reaction model used is undefined. While this tracer, which represents the density of tuna, can fluctuate spatially, it is not possible to track the source of the proportional change in tracer through space across sequential time-steps. In order to answer questions that involve such spatial tracking of individuals, the Individual-based Kinesis, Advection and Movement of Ocean Animals model (Ikamoana) was developed (Scutt Phillips et al. 2018). To date, the model has been applied to Pacific skipjack tuna using the immature and adult behavioural model of SEAPODYM, to examine connectivity between stock assessment regions and the bias present in data from tagging experiments (Scutt Phillips et al. 2018).

Current understanding of the stock structure of skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific Ocean

Skipjack tuna

Skipjack tuna are broadly distributed across the Pacific Ocean, inhabiting tropical to temperate waters from the equator to around 35° of latitude in the western Pacific, extending to around 40° of latitude with the seasonal extensions of warm poleward flowing currents. Their distribution narrows longitudinally, to approximately 10–15° of latitude from the equator east of about 145°W, extending to around 20° of latitude seasonally along the coasts of Central and South America (Sund 1981; Matsumoto et al. 1984). The bulk of biomass of skipjack tuna, however, occurs within 10° of latitude from the equator (Figure 1). Tagging and fishery catch data suggests the distribution of skipjack tuna varies with the El Niño-Southern Oscillation (ENSO), with an increase in eastwards movement from the western Pacific Ocean under El Niño conditions (Lehodey et al. 1997).

Based on observations of gonad state and the distribution of larvae, spawning in skipjack tuna is considered to take place year-round in areas of both WCPO and EPO where sea surface temperatures (SSTs) generally exceed 24°C, with the greatest proportion of spawning occurring in waters between 26°C and 29°C (Nishikawa et al. 1985; Schaefer 2001a; 2001b; Servidad-Bacordo et al. 2012; Ashida and Horie 2015; Schaefer and Fuller 2018). Outside of these waters (e.g. off the coast of Mexico and central America), spawning is reported to occur seasonally (Schaefer and Orange 1956; Orange 1961; Schaefer and Fuller 2018). Off Japan, for example, Yabe (1954) found fish with high relative gonad weight >5%) from May through June and fish with spent ovaries in July and August. Larval densities of skipjack tuna are higher in the WCPO than in the EPO, suggesting the main spawning areas are in the WCPO (Ueyanagi 1969; Matsumoto et al. 1984). Mean length at 50% maturity has been estimated to be ~52 cm in the EPO and ~48 cm in the WCPO, when fish are estimated to be around 9–12 months old. The maximum age of skipjack tuna in the Pacific is not known, but is assumed to be around 8–12 years (Colette and Nauen 1983), although it is likely few fish live beyond 5 years.

Skipjack tuna are a schooling species, however, the degree to which schools maintain their temporal integrity is largely unknown, with varying hypotheses put forward based on a range of analyses. Sharp (1978) found evidence of genetic similarity between individuals in ‘core’ schools,

suggesting that some members of the school were siblings. Based on parasite data, Lester et al. (1985) estimated that schools of skipjack tuna maintain their integrity for several weeks, but not for life. Using tagging data, Bayliff (1988a) estimated that schools of skipjack tuna maintain integrity for weeks to months. Hilborn (1991) concluded that schools in the Pacific 'do not appear to remain composed of the same individuals for more than a few weeks'. On the basis of ultrasonic tagging data, Schaefer and Fuller (2013) concluded that skipjack tagged in association with drifting FADs were not a cohesive unit, and did not exhibit a high degree of permanence in structure or size.

Currently, skipjack tuna in the Pacific are assessed and managed as separate stocks in the WCPO and EPO by the WCPFC and IATTC, respectively. Within each of the convention areas of these RFMOs, a single stock is assumed. In the WCPO, the stock assessment area extends from 20°S to 50°N and is split into five sub-regions (Figure 4), based on the nature of the fishing fleets and tag mixing assumptions around tag release sites (McKechnie et al. 2016). It has been suggested that the northward region should be split to better capture skipjack tuna dynamics in the North Pacific (Kinoshita et al. 2018), but it is unlikely that there are sufficient tagging data in that zone to inform movement.

In the EPO, the last formal stock assessment was conducted in 2005 and was considered uncertain due to unreliable indices of abundance (Maunder and Harley 2005). Indicators of stock status are now used to monitor skipjack tuna in the EPO (Maunder and Deriso 2007), which implicitly assume a single stock. Spatially structured assessment models have been explored (e.g. Maunder 2012), but to date there has been insufficient information in the catch-per-unit-effort (CPUE) and length-composition data to provide reliable estimates of stock size for most sub-populations.

Molecular studies

Studies applying molecular approaches to skipjack tuna in the Pacific Ocean have to date yielded varying levels of population structure. On the basis of blood groups, two phenotypes were identified from fish caught in the waters around Hawaii (Cushing 1956). Variability in blood groups were further identified from fish caught around Hawaii, Marquesas and Tuamotu/Society Islands, suggesting isolated populations (Spague and Holloway 1962). Using blood groups and isozymes, two skipjack tuna groups were identified across the Pacific Ocean: a 'western Pacific' population, including samples from the east coast of Japan, Marcus Islands, Bonin-Marianas and Palau, and a 'central east Pacific' population, including samples from Baja California, Ecuador, Society Islands, Line Islands and Hawaii (Fujino 1970).

Based on allozyme markers, fish from around Japan and Hawaii were observed to be heterogeneous, while no differences were observed between fish from Hawaii and Palau (Fujino and Kang 1968). Variability in allozyme markers have also been used to propose at least five subpopulations with overlapping geographical boundaries in Pacific Ocean (northeastern Pacific, southeastern Pacific, New Zealand, northwestern Pacific, and Papua New Guinea / Solomon Islands) and the presence of two distinct populations in the central equatorial Pacific and in the southwestern Pacific (Sharp 1978; Richardson 1983).

Molecular approaches, combined with conventional tagging and size distribution data, were used to identify three sub-populations within the central-eastern Pacific population of Fujino (1970): the central west Pacific, the central northeast Pacific, and the central southeast Pacific (Fujino 1996). DNA isolation, mtDNA D-loop region amplification, and nucleotide sequence analyses failed to detect any genetic differentiation between skipjack samples from the WCPO and EPO (Ely et al. 2005).

Non-molecular studies

Skipjack tuna has been the primary focus of a large number of dedicated, large-scale, conventional tagging programmes conducted in both the WCPO and EPO. In the WCPO, these studies date back to the 1970s, commencing with the Skipjack Survey and Assessment Programme (SSAP; 1977–1981). Large numbers of skipjack tuna have since been tagged through the Regional Tuna Tagging Programme (RTTP; 1991–1996), which operated in waters between the Philippines east to Fiji, including off the east coast of Australia, and the Pacific Tuna Tagging Programme (PTTP; 2006–present), operating in waters 10°N–10°S; 120°E–130°W (Hampton and Gunn 1998; Leroy et al. 2015). Combined, these three programmes have tagged over 469,000 individual skipjack tuna to date, with over 65,000 recoveries reported to June 2018, including almost 47,000 recoveries of skipjack tagged in the PTTP alone (Leroy et al. 2015; SPC-OFP 2018b). Within the WCPO, these programmes have been complemented by a number of national-level tagging activities (Leroy et al. 2015). In the EPO, tagging operations have been conducted by the IATTC since the 1950s, with around 130,000 skipjack tagged to 2015, with 1,426 recoveries included in analyses of movement by Fonteneau and Hallier (2015).

Results from these programmes demonstrate that the movement dynamics of skipjack tuna are both spatially and temporally complex. In the WCPO, individual skipjack tuna have been shown to be capable of extensive movement, with several displacements well in excess of 1,000 nm from original tagging locations (Matsumoto et al. 1984). Seasonal migrations have also been inferred from conventional tagging programs. For example, fish from the western-central Pacific have been hypothesised to follow two migratory routes to feeding grounds near Japan, one from Hawaii through the Midway Islands, and a second from the Mariana-Bonin-Izu archipelagos. Both groups are then considered to return to tropical waters with the Kuroshio Current Extension in late autumn (Fujino 1996). In the western South Pacific Ocean, skipjack migrate south along the Australian coast during the austral summer, reaching as far as Tasmania before migrating back into tropical waters across the late autumn and winter.

The majority of recaptures of skipjack tuna tagged in the WCPO, however, suggest that long-distance movements are, however, uncommon, with 95% of fish tagged in the SSAP, for example, being recaptured within 1,000 nm of their original release point (Figure 4) (Hilborn and Sibert 1988). Sibert and Hampton (2003) estimated skipjack tuna tagged during the SSAP and RTTP to have a median lifetime displacement ranging from 420–470 nm. Displacements of skipjack tuna have been found to have a positive relationship with fish size (SPC-OFP 2015). Modelling of the movement dynamics of skipjack tuna suggests comparatively low rates of movement for tagged fish in the region surrounding the Solomon Islands archipelago (Kleiber and Hampton 1994; SPC-OFP 2017). Notwithstanding issues surrounding time-at-liberty, the distribution of tag release and the distribution and variability of fishing effort, observations from these programmes suggest the potential for some degree of regional fidelity in skipjack tuna.

Tagging data from the EPO suggest a similar mix of seasonally cyclical movement, large-scale displacements, and regional fidelity (Fink and Bayliff 1970; Bayliff 1984; Bayliff 1988b). On the basis of tagging data, Fink and Bayliff (1970) concluded that there appear to be two main ‘groups’ of skipjack in the EPO: a northern group, occurring around Baja California, the Gulf of California, and the Revillagigedo Islands off the coast of Mexico, and a southern group, occurring from Central America (~Panama) south to northern Chile, with some exchange between groups. The origins of the two groups are largely undefined, with some authors (e.g. Rothschild 1965) hypothesising that they both originate from spawning in the central equatorial Pacific Ocean east of 130°W. However, significant spawning is known to occur in waters of the EPO $\geq$ 24°C, and fish in spawning condition have been reported off the coasts of Panama and Ecuador (Schaefer

2001a; Schaefer and Fuller 2018), suggesting that at least some proportion of fish in both groups may result from local spawning.

In general, fish in the northern group undertake a northern and then southern movement between 20°N and 30°N coincident with the seasonal movement of the 20°C surface water isotherm (Fink and Bayliff 1970). The movements of the southern group appear to be more complex than those of the northern group, although are considered to be poorly delineated by conventional tagging data (Fink and Bayliff 1970). Young fish that appear in the Panama Bight appear to migrate either northward or southward along the coast, before returning to equatorial waters as adults to spawn (Schaefer 2001a). Movements of skipjack tuna tagged in the EPO into the WCPO have also been documented, although the proportion of fish observed to undertake such displacements is low (Bayliff 1988b), with only 27 fish of the near 130,000 tagged in the EPO having been recaptured in the WCPO, with 21 of these recaptured around Hawaii (Bayliff 1988b).

Several other features of the life history of skipjack suggest potential spatial structuring of skipjack tuna populations across the Pacific Ocean. Differences in morphometrics and growth rates of skipjack tuna between the EPO and WCPO have been reported (Hennemuth 1959; Sibert et al. 1983; Bayliff 1988b), suggesting some variability in the biology of individuals derived from the two areas. Ianelli (1993) observed differing patterns of recruitment between skipjack tuna in EPO and in the waters around Hawaii, suggesting fish from this latter region had originated under different spawning conditions than those from the EPO. Differences in growth rates of larval and juvenile skipjack tuna collected from the Western Pacific Warm Pool and the North Pacific Tropical Gyre have been observed, suggesting these fish had grown under differing environmental conditions (Ashida et al. 2018).

To date, studies of parasites of skipjack tuna have found no evidence of more than one parasitological stock of skipjack in the Pacific, although investigations have been limited to one study (Lester et al. 1985).

Few studies have been conducted on the otolith chemistry of skipjack tuna. An investigation into the ontogenetic patterns in otolith Sr:Ca ratios of skipjack tuna (32.2–58.2 cm fork length (FL)) collected from the tropical western Pacific (Marshall Islands and Palau) and off the coast of Japan reported results consistent with a mix of individual movement behaviours (Arai et al. 2005). Most skipjack sampled from the Marshall Islands had a constant otolith Sr:Ca ratio, suggesting continuous residence in tropical waters after hatching (Arai et al. 2005). One individual was found to have a transition point in its otolith Sr:Ca ratio profile, which was suggested to have resulted from this fish moving to a temperate region after hatching, and then returning to a tropical region before capture. Most of the fish from Japan were found to have transition points in their otolith Sr:Ca ratio profiles, suggesting migration northward from the tropics to temperate waters (Arai et al. 2005), consistent with what is known from tagging data (Aoki et al. 2017).

Based on tagging, size and CPUE data, the most recent stock assessment for skipjack tuna predicts that populations in the assessment regions north of 20°N (east coast of Japan and the North Pacific; Region 1) and west of 140°W (Indonesia and the Philippines; Region 4) result largely from self-recruitment, while there is considerable exchange between the regions east of 140°W framing the equator (Figure 4; McKechnie et al. 2016). Of note, the lack of north-south mixing predicted could be due to low tag reporting rates in the North Pacific from tropical release sites, which would lower the number of recorded tag recoveries in that region.

The mean optimal spawning temperatures as modelled by SEAPODYM are estimated at 28.5–29°C (Senina et al. 2016). These results generally match observations that skipjack spawn near continuously in the Western Pacific Warm Pool, where such temperatures are most consistent (e.g. Nishikawa et al. 1985). Seasonably favourable areas are estimated in the EPO by SEAPODYM as occurring during April-June, partially matching observations of spawning in the region (Schaefer and Orange 1956), the central equatorial Pacific in May-August, the north-west East China Sea in August-October, and occasional seasonality of high and low larval densities in the Bismarck Sea during May-November, and December-February, respectively.

Diffusive, non-directional movement is estimated to be high in young and adult skipjack by SEAPODYM, and is near invariant across habitat quality index values. This high degree of mixing by these age groups predicted under the SEAPODYM movement model was further quantified using Ikamoana (Scutt Phillips et al. 2018). In particular, the Western Pacific Warm Pool region appears to be an area of high transitivity for immature fish. Ikamoana demonstrated that quarterly transfer rates between the Solomon and Bismarck Sea area to the oceanic Western Pacific Warm Pool were potentially greater than 10% in both directions, with a transfer of up to 42% from the former to the under an examined La Niña time period (Scutt Phillips et al. 2018). Simulated transfer of fish between the Western Pacific Warm Pool and central equatorial Pacific under non-El Niño conditions was also high. Exchange between the EPO and the WCPO convention area appeared to be relatively low, dominated by a quarterly influx of between 5% to 15% of this outside biomass migrating into the central equatorial region (Scutt Phillips et al. 2018).

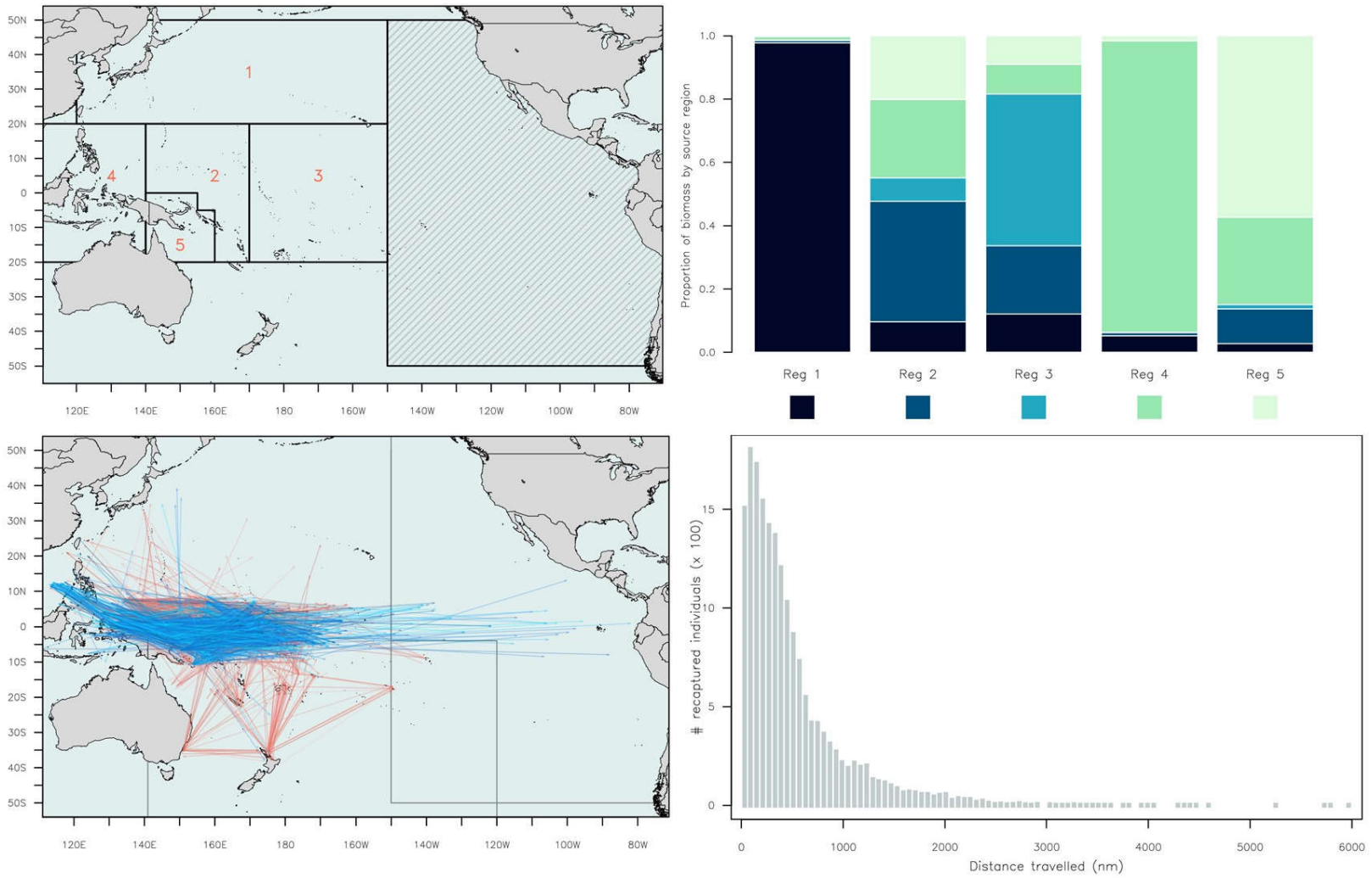


Figure 4. Top left: The geographic area and regional structure for stock assessments of skipjack tuna in the WCPO (numbered areas) and EPO (line shaded area); bottom left: movements of tagged skipjack tuna tagged during the RTTP (red arrows) and PTTP (blue arrows) recaptured > 1,000 nm from their release point; top right: proportional distribution of total biomass (by weight) in each WCPO assessment region apportioned by the source regions; bottom right: distribution of observed tag displacements for skipjack tuna at liberty for ≥ 3 months from RTTP and PTTP data. All tagging data shown is based on SPC holdings.

Yellowfin tuna

Yellowfin tuna are broadly distributed across the Pacific Ocean, inhabiting tropical to temperate waters from approximately 30°N to 30°S, extending to 40° in both hemispheres seasonally (Sund 1981).The location and timing of spawning of yellowfin tuna in the Pacific have been inferred from patterns of larval distribution and histological examination of gonad condition, which suggest that spawning occurs year-round in tropical waters, and seasonally at higher latitudes when surface water temperatures are generally above 24°C (Nishikawa et al. 1985; Schaefer 1998; Itano 2000). The greatest proportion of spawning occurs in waters between 26°C and 30°C (Schaefer 1998). A number of key spawning areas have been identified, including the Banda Sea in Indonesia, the northern Coral Sea, waters to the east and south of the Philippines, northeast of the Solomon Islands, and waters around Fiji (McPherson 1988, 1991; Gunn et al. 2002; Servidad-Bacordo et al. 2012). On the basis of gonad maturity and larval distribution data, Suzuki et al. (1978) identified three 'relatively discrete areas of intensive spawning activity along the equatorial zone' – corresponding to the western Pacific (with spawning peaking in the third and fourth quarters of the year), central Pacific (with spawning peaking in the second and third quarters) and eastern Pacific (with spawning peaking in the first and second quarters). Juvenile and sub-adult yellowfin tuna show a strong schooling tendency, which becomes less pronounced with age. Mean length at 50% maturity of females is estimated to be ~108 cm in the WCPO, and around 92 cm in the EPO. Yellowfin tuna are relatively fast growing, reaching a maximum fork length (FL) of about 180 cm, and can live for at least 7 years (Lehodey and Leroy 1999).

Current stock assessments for yellowfin tuna are conducted in the WCPO and EPO separately and assume a single stock in each region. The most recent assessment for the WCPO (Tremblay-Boyer et al. 2017) incorporated a 9-region structure across the area 50°N–40°S (Figure 5). Spatial structuring of the assessment was informed by the nature of the operating fleets (longline vessels targeting larger individuals and operating primarily in temperate waters; purse-seine vessels catching smaller individuals and operating almost exclusively in equatorial waters), and tag mixing assumptions in the Coral Sea area, with additional spatial areas introduced along the longitudinal axes. Assessment models used in the EPO do not incorporate any spatial component explicitly but adopt a 'fleets-as-areas' approach, which includes the area of operation on the definition of fisheries that can have different selectivity curves and catchabilities (Minte-Vera et al. 2018).

Molecular studies

A number of studies have examined the genetic structure of yellowfin tuna in the Pacific Ocean. Using allozymes, Barrett and Tsuyuki (1967) did not identify any heterogeneity among yellowfin tuna in the EPO, while Fujino and Kang (1968) did not observe any significant heterogeneity among samples collected from the EPO, Hawaii and Line Islands. At a broader spatial scale, significant genetic differentiation between the WCPO and EPO at the Glucose Phosphate Isomerase (GPI) locus was detected by Sharp (1978), with these results supported by Ward et al. (1994). Scoles and Graves (1993) found no differences in restriction fragment length polymorphism (RFLP) mtDNA markers between yellowfin tuna from five locations in the Pacific Ocean (Australia, Papua New Guinea, Hawaii, Mexico and Ecuador), or between the Pacific Ocean locations and the Atlantic Ocean. On the basis of allozyme and RFLP mtDNA markers, Ward et al. (1997) proposed the existence of two distinct genetic populations in the Pacific Ocean: the WCPO and eastern region. In several studies (Appleyard et al. 2001; Nomura et al. 2014) the use of microsatellite markers, as for most of the earlier allozyme and mtDNA studies, did not provide any clear evidence of population heterogeneity in the Pacific Ocean. At a much smaller spatial scale, Diaz-Jaimes and Uribe-Alcocer (2003) did not detect any significant genetic

differentiation in allozymes and Random Amplification of Polymorphic DNA (RAPD) markers among yellowfin tuna around the Clipperton and Revillagigedo Islands and Baja California.

Recently, several studies have found evidence to support the hypothesis of several distinct populations of yellowfin tuna within the Pacific. Using a larger number microsatellite markers from samples taken around the same area as Diaz-Jaimes and Uribe-Alcocer (2003), Diaz-Jaimes and Uribe-Alcocer (2006) identified two discrete populations of yellowfin tuna separated by the equator, which according to the authors may have resulted from non-random sampling. Examination of mtDNA cytochrome c oxidase subunit (COI) provided evidence for the possible existence of sub-populations within the central Pacific Ocean (CPO) (Li et al. 2015), while examination of microsatellite markers revealed population structuring in yellowfin tuna between the Philippines and Bismarck Sea, Papua New Guinea (Aguila et al. 2015). Using SNPs, Grewe et al. (2015) observed heterogeneous population structure between samples from Baja California (eastern Pacific), Tokelau (central Pacific) and the Coral Sea (western Pacific), while Pecoraro et al. (2018) identified significant genetic variation between yellowfin tuna from the EPO (Mexico) and WCPO (around the Bismarck Sea and northeast of Solomon Islands).

Non-molecular studies

Large numbers of yellowfin tuna have been tagged in the WCPO using conventional tags through the SSAP, RTTP and PTTP, and other local or regional initiatives. As with skipjack tuna, analyses of tag recoveries suggest that while individual yellowfin tuna are capable of extensive movements, the majority of recaptures have been made close to release sites, suggesting limited movement and a degree of regional fidelity (Figure 5) (Itano and Williams 1992; Hampton and Gunn 1998; Sibert and Hampton 2003; Fonteneau and Hallier 2015). For example, in their analysis of conventional tagging returns from activities of the RTTP in the north-west Coral Sea, Hampton and Gunn (1998) observed recaptures as far away as Fiji, Japan, Micronesia, Papua New Guinea and Solomon Islands, suggesting individuals have the potential to mix across their range. The majority of recaptures however, were in the release area or adjacent Coral Sea (Hampton and Gunn 1998). Of the tags recovered from yellowfin tuna tagged during the RTTP, most (~90%) have been within 1,000 nm of the point of release (SPC unpublished data, cited in Hampton and Gunn 1998). Sibert and Hampton (2003) estimated yellowfin tuna tagged in the WCPO during the SSAP and RTTP to have a median lifetime displacement ranging from approximately 337–380 nm. Yellowfin tuna tagged around fish aggregating devices (FADs) and in particular FADs and seamounts within the Hawaiian archipelago have been observed to demonstrate high fidelity to these devices and features (Itano and Holland 2000).

While the majority of tags released on yellowfin tuna in the Pacific have been conventional tags, acoustic and archival tags have also been deployed in yellowfin tuna across the western Pacific, and archival tags also deployed in the CPO as part of the PTTP (SPC-OFP 2018b). Preliminary analyses of archival tag data support that of conventional tag programs with some individuals clearly capable of undertaking large scale movements, but for the majority, movement is limited (Leroy et al. 2014; Leroy et al. 2015). Archival tag returns suggest a negative relationship between dispersal distance and size of fish and a positive relationship with time at liberty (SPC-OFP 2015). Similar to skipjack tuna, modelling of the movement dynamics of yellowfin tuna suggests comparatively low rates of movement for tagged fish in the region surrounding the Solomon Islands main archipelago group (SPC-OFP 2017).

The majority of tagging in the WCPO has focused on juvenile and sub-adult yellowfin tuna, with few adults tagged. The only detailed investigation of movement of adult yellowfin tuna in the WCPO to date is that of Evans et al. (2011), who examined data from 20 pop-up satellite archival tags (PSATs) deployed on yellowfin tuna ranging 135–158 cm FL in the northern Tasman Sea /

southern Coral Sea. Similar to the results from tagging programmes on juveniles, adult yellowfin showed a limited range of movements (estimated displacements of 54–1,463 km) with all tagged fish remaining within the Coral and Tasman Seas. However, as noted by Evans et al. (2011), the findings were somewhat limited by the short attachment duration of tags (2–168 days).

Results from conventional tagging studies on yellowfin tuna in the EPO suggest movements of tagged fish at liberty for more than 30 days tend to be restricted to less than 1,000 nm of their original release positions, with little exchange of fish between northern and southern regions (Fink and Bayliff 1970; Bayliff 1979, 1984). Similarly, data from archival tags indicate that 95% of individuals tagged remained within 1,358 km of their release points, with little movement from the northern to the southern regions of the EPO (Schaefer et al. 2011; Schaefer et al. 2014), with Schaefer (2008) concluding yellowfin tuna in these regions probably represent spatially-segregated sub-stocks.

Spatial variation in life history and morphometrics has been observed for yellowfin tuna in the Pacific, suggesting potential structuring within the region. For example, length at 50% (L_{50}) maturity for female yellowfin tuna has been shown to differ between fish in the WCPO and EPO, ranging from 96.5–99.5 cm FL for females in Indonesia and Philippines, 107.9–120.0 FL for females in the Coral Sea, 98.1–112.5 cm FL for females from the WCPO and 79.1–98.1 cm FL for females in the EPO (Schaefer 1998; Itano 2000). Regional differences in growth have also been observed, with fish from Indonesia and the Philippines having slower growth rates than those in the wider WCPO (Hoyle et al. 2009), suggesting a non-random distribution, although it is unclear to what degree this variation results from methodological differences in the preparation and interpretation of otoliths (Farley et al. 2018a). In the EPO, morphometric and meristic analyses suggest significant differences between fish sampled north and south of 15°N. Schaefer (1992) found that yellowfin caught around Manta (Ecuador) have deeper bodies, and have on average one more gill-raker, than those sampled around the Revillagigedo Islands off the coast of Mexico.

Moore et al. (in press) examined parasite fauna of juvenile yellowfin tuna collected from locations within the Indonesian EEZ and two outlier locations - Maldives in the Indian Ocean and Solomon Islands in the western Pacific. Their results suggest little mixing of fish between Indonesia waters and the two outlier locations. Within the Indonesian EEZ, parasite data, and particularly abundances and prevalences of didymozoid species, suggested little movement from the western Pacific into the Indonesian archipelago or from the Indonesia archipelago to the eastern Indian Ocean.

Several studies have used otolith chemistry to determine the relationships between the chemical markers in natal regions of otoliths (assumed to represent spawning regions) from differing areas to determine nursery origins of yellowfin tuna in the Pacific. Gunn et al. (2002) examined otolith microchemistry to investigate the probable origins of yellowfin tuna caught off the east coast of Australia. Otoliths of the majority of fish caught in the Tasman Sea most closely resembled those originating from the Coral Sea than any other sampling site. Combined with broader understanding of biology, fisheries data, oceanography and tagging, the results suggest that in some years at least, yellowfin tuna caught in the Tasman Sea derive predominantly from the Coral Sea, with lower numbers originating from the broader western Pacific (Gunn et al. 2002).

Wells et al. (2012) used stable isotopes in otoliths as natural tracers to predict the nursery origin of yellowfin tuna around the Hawaiian Islands. They examined $\delta^{13}C$ and $\delta^{18}O$ in otolith cores of juveniles (within their first two months of age) collected from nursery areas throughout the WCPO in 2008–2009, including Hawaii, the Line Islands of Kiribati, Marshall Islands, Solomon Islands

and the Philippines, and of sub-adults (age-1) collected from Hawaii in 2009 and 2010, to investigate nursery-specific contribution rates. Mixed-stock analysis revealed that the majority of sub-adults in the Hawaiian fishery had core chemistries suggestive of originating from nursery areas within Hawaii, while < 10% had core chemistries that indicated they had originated from equatorial nurseries outside of Hawaii (Wells et al. 2012).

Using trace elements in addition to stable isotopes, the same otoliths examined by Wells et al. (2012) were reanalysed along with additional samples from 1–2 year-old fish caught in the Marshall Islands by Rooker et al. (2016). Results suggested that fish caught in Marshall Islands waters were almost entirely derived from local production, with only a minor contribution of recruits from the central equatorial Pacific, and that all yellowfin tuna from Hawaii were deemed to have originated locally (Rooker et al. 2016).

Houssard et al. (2017) examined stable isotope ratios of nitrogen to assess the trophic position of yellowfin tuna in the WCPO. Strong spatial trends were evident in muscle $\delta^{15}N$ values, suggesting restricted movement of individuals and high regional residency, at least over the scale of their muscle nitrogen turnover rate (i.e. half-life = 167 days).

The latest stock assessment estimated that yellowfin tuna in the two northernmost assessment regions (north of 20°N) and those from the westernmost assessment region (around Indonesia and the Philippines) result largely from self-recruitment, (Figure 5). The two southernmost regions (south of 10°S) were also estimated to result largely from self-recruitment but also had some exchange of biomass with the neighbouring equatorial regions (Figure 5; Tremblay-Boyer et al. 2017). In contrast, the remaining tropical regions were estimated to have half to two-thirds of their biomass initially recruited in other regions along the equatorial axis. The same caveats applied to recruitment of skipjack tuna from the assessment model also apply to yellowfin tuna, with potentially low tag reporting rates from tropical tagging programs in the North Pacific, as well as fewer tagging data available outside of the equator to inform movement between temperate regions (Tremblay-Boyer et al. 2017).

Simulation studies using SEAPODYM indicate a distribution of yellowfin larvae that is strongly contrasted between the two sides of the Pacific Ocean. Large areas of high larval density are estimated in the Western Pacific Warm Pool around the Solomon Islands and Papua New Guinea during the beginning of the third quarter, and within the East China Sea during August-September, with smaller high density areas in the EPO around the Peru and Costa Rica, peaking in March-April (Senina et al. 2015; Lehodey et al. 2017). Assessments of connectivity of yellowfin tuna across the WCPO using SEAPODYM suggest, in the absence of fishing, a near-even exchange of biomass between Papua New Guinea and Indonesia, with recruits moving east but not west. Papua New Guinea was also identified as a key source of recruits for the WCPO, evidenced by a 23.6% reduction in adult biomass in the WCPO when recruitment from Papua New Guinea was removed (Senina et al. 2015).

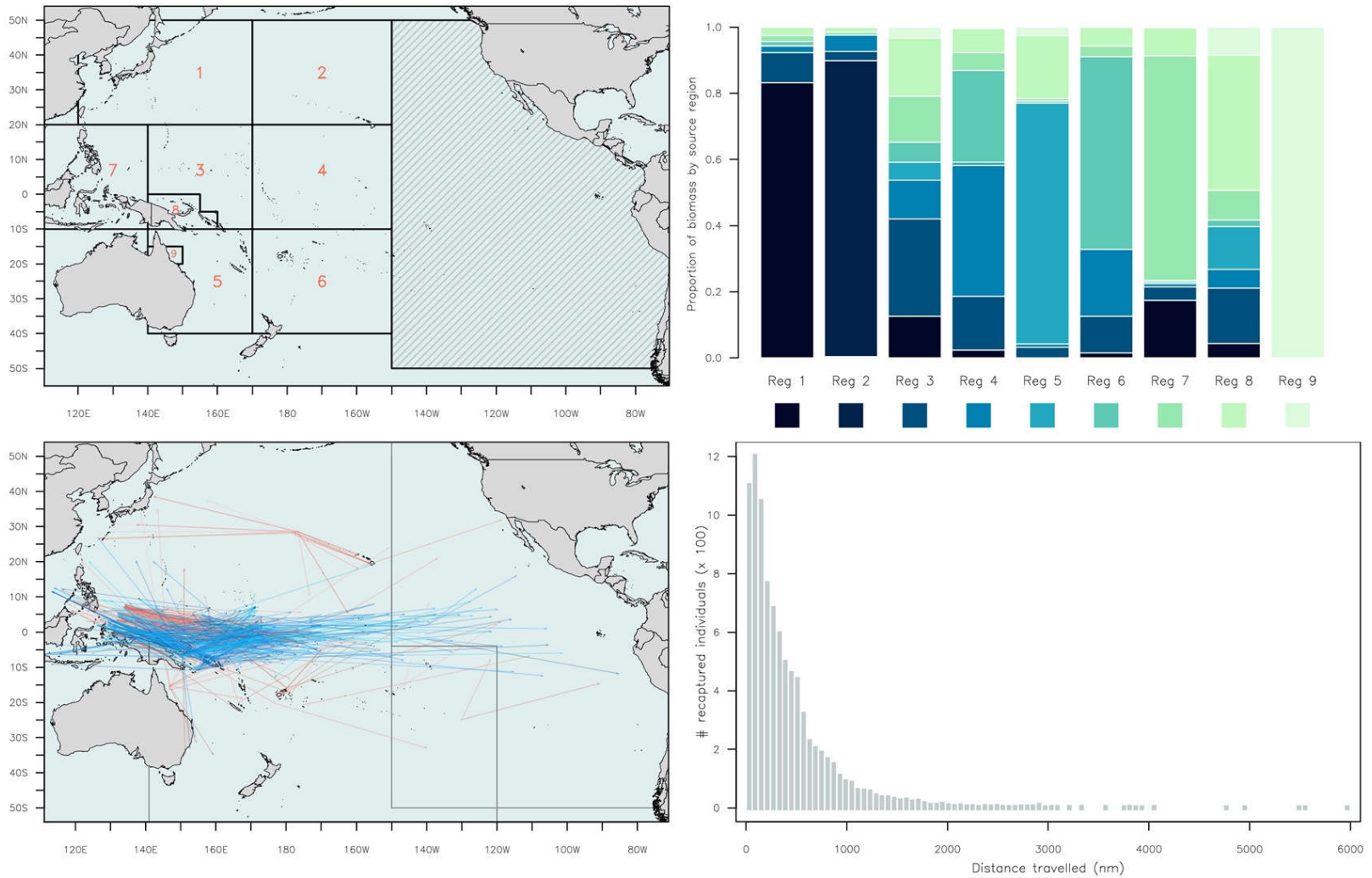


Figure 5. Top left: The geographic area and regional structure for stock assessments of yellowfin tuna in the WCPO (numbered areas) and EPO (line shaded area); bottom left: movements of tagged yellowfin tuna tagged during the RTTP (red arrows) and PTTP (blue arrows) recaptured > 1,000 nm from their release point; top right: proportional distribution of total biomass (by weight) in each WCPO assessment region apportioned by the source regions; bottom right: distribution of observed tag displacements for yellowfin tuna at liberty for ≥ 3 months from RTTP and PTTP data. All tagging data shown is based on SPC holdings.

Bigeye tuna

Bigeye tuna are broadly distributed across the Pacific Ocean, inhabiting tropical to temperate waters from approximately 45°N to 40°S in the western Pacific, and from approximately 40°N to 30°S in the eastern Pacific (Calkins 1980). On the basis of gonad condition of mature fish and observed distributions of larvae, spawning of bigeye tuna is considered to occur year-round in tropical equatorial waters of the Pacific Ocean and seasonally in subtropical waters when water temperatures exceed 24°C (Schaefer 2001a; Schaefer et al. 2005). Farley et al. (2018) observed spawning capable females (only) between 12°N and 12°N and between 137°E and 130°W, in water temperatures between 27.7°C and 30.3°C, suggesting central equatorial waters may be an area spawning region for bigeye tuna. Nishikawa et al. (1985) suggest the region between Japan and the Philippines is particularly important spawning area for bigeye in the western Pacific Ocean, with spawning occurring in that region during spring and early summer. Spawning aggregations have also been reported in the Coral Sea (McPherson 1988; Farley et al. 2003). As with yellowfin tuna, juvenile and sub-adult bigeye tuna show a strong schooling tendency which becomes less pronounced with age. Mean length at 50% maturity of females has been estimated to be ~118 cm in the CPO and EPO. Bigeye tuna are considered to be slower growing than yellowfin tuna, reaching a maximum age of around 16 years (Farley et al. 2006), and a maximum FL of 180 cm in the WCPO (Farley et al. 2018b) and 200 cm in the EPO (Aires-da-Silva et al. 2015).

Current stock assessments for bigeye tuna are conducted in the WCPO and EPO separately and assume single stock within each of those areas. Similar to yellowfin tuna, stock assessments for bigeye tuna in the WCPO incorporate a 9-region structure across the region 40°S–50°N (Figure 6). This spatial structuring is informed by the nature of the operating fleets (longline vessels targeting larger individuals and operating primarily in more temperate waters; purse-seine vessels catching smaller individuals and operating almost exclusively in equatorial waters) and tag mixing assumptions in the Coral Sea area, with additional splits along the longitudinal axes (McKechnie et al. 2017a). Introducing shifts to the regional structure (e.g. shifting the northern edge of the equatorial region from 20°N to 10°N) has been found to produce varying outcomes (McKechnie et al. 2017b; Vincent et al. 2018), suggesting the assessment is sensitive to the configuration of regional structure. The EPO assessments for bigeye tuna do not include a sub-regional population structure explicitly, but similarly to yellowfin tuna adopt a ‘fleets-as-areas’ approach, which includes the area of operation on the definition of fisheries that can have different selectivity curves and catchabilities (Xu et al. 2018).

A Pacific-wide assessment for bigeye tuna encompassing both the WCPO and the EPO was conducted in 2015 and included sub-regional splits that matched the WCPO and the EPO assessments at the time. This assessment assumed ‘EPO-style growth patterns across the Pacific. The resulting predictions of stock status aggregated over the sub-regions within each RFMO convention area were in agreement with the assessments conducted in each of the regions, so it was concluded that it was appropriate to proceed with separate assessments in the WCPO and the EPO (McKechnie et al. 2015).

Molecular studies

To date, molecular studies based in allozymes, mtDNA and microsatellites have generally found little evidence of structuring in bigeye tuna in the Pacific Ocean, suggesting broad scale panmixia among bigeye tuna in the region (Fujino and Kang 1968; Bremer et al. 1998; Chow et al. 2000; Wu et al. 2014). However, Grewe and Hampton (1998) found some evidence of restricted gene flow between Philippines and Ecuador, their two most widely separated sampling areas. Further

differentiation, however, was limited by small sample sizes, and Grewe and Hampton (1998) recommended larger sample sizes and additional loci be examined to adequately determine the population structure of bigeye tuna in the Pacific.

Non-molecular studies

Similar to yellowfin tuna, large numbers of bigeye tuna have been tagged under a number of tagging programmes across the Pacific. The bulk of tagging studies, particularly in the WCPO, have focused on juveniles and sub-adults, typically less than 70 cm FL (Leroy et al. 2015). Recaptures of conventional tags on bigeye tuna across the WCPO have revealed a range of movements, with some individuals dispersing large distances (e.g. two bigeye tuna were recaptured over 2,500 nm from their release points in the CPO 2.5 and 3.5 years after release), but the vast majority dispersing less than 1,000 nm from release points (Figure 6) (Miyabe 1994; Hampton and Gunn 1998; Gunn et al. 2005). Conventionally-tagged fish released in the CPO that were at liberty for $\geq$ 30 days were predominantly recaptured within approximately 1,000 nm of their original release point (although these percentages varied between release sites) with most limited to 10° of latitude from the equator, suggesting constrained latitudinal dispersion (Schaefer et al. 2015). Dispersal across all release sites was predominantly eastward in nature and there was substantial mixing of bigeye tuna between release longitudes (140˚W, 150˚W, 170˚W and 180˚). Bigeye tuna tagged around fish aggregating devices and in particular FADs and seamounts within the Hawaiian archipelago have been observed to demonstrate high fidelity to these devices and features (Itano and Holland 2000).

Archival tagging studies conducted in the WCPO primarily on juveniles support the findings of conventional tagging programmes, with a range of movements observed. Bigeye tuna tagged in the Coral Sea demonstrated local residence, cyclical movements between the Coral Sea and western Pacific Ocean, and potentially broad-scale longitudinal dispersal eastwards into the wider WCPO (Gunn et al. 2005; Evans et al. 2008). Bigeye tuna tagged in the Bismarck and Solomon Seas similarly have demonstrated limited movements (Leroy et al. 2014; Abascal et al. 2018). Across the CPO, depending on the release location, tagged bigeye tuna demonstrated varying degrees of regional fidelity. Bigeye tuna tagged at 155°W demonstrated fairly strong regional fidelity to release location, while those released at 140°W and 170°W demonstrated less regional fidelity, but more eastward movements (Schaefer et al. 2015). Most of the fish tagged were juveniles.

Similar to the WCPO, regional fidelity and limited latitudinal movement has been observed in bigeye tuna tagged in the equatorial EPO at 95°W (Schaefer and Fuller 2009), while those released at 140°W showed marked eastward movement (Schaefer et al. 2015). Bigeye tuna at liberty for $\geq$ 30 days were predominantly recaptured within approximately 1,000 nm of their original release point with limited latitudinal displacement (Schaefer and Fuller 2009). Dispersal was predominantly westward in nature and the distance dispersed appeared to be positively related to fish size and time at liberty (Schaefer and Fuller 2009). Archival tag data retrieved from bigeye tuna tagged in the EPO also indicated strong regional fidelity, with restricted westward movements (Schaefer and Fuller 2009). Of note, of the 96 bigeye tuna tagged in the EPO with archival tags that were analysed by Schaefer and Fuller (2010), one individual at liberty for 4.1 years undertook two very similar cyclical movements during its third and fourth years at liberty, moving into the CPO between ~150°W and ~160°W in November-December, before returning to ~84°W in early May in each year. potentially indicating spawning area fidelity. As with the WCPO studies, most of the fish were juveniles when initially tagged.

On the basis of archival tagging data from the three regions, Schaefer et al. (2015) proposed that bigeye tuna demonstrated three types of movement behaviours: (1) fish that are residents within

an area (<1,000 nm of release location), (2) fish that are residents, yet undertake cyclical excursions outside the area of residency, and (3) fish that are nomadic and do not demonstrate type 1 or type 2 movement patterns. They further proposed, on the degree of mixing observed in association with these behaviours, three putative stocks of bigeye tuna in the equatorial Pacific Ocean – eastern, central, and western stocks – with stock boundaries at about 120°W and 180°, and constrained between 10°N and 10°S. On the basis on constrained latitudinal movement evident in each region, they suggested that six additional stocks should be considered; three northward and three southward of the equatorial stocks.

Recent analyses of a large collection of bigeye tuna otoliths across the WCPO and EPO have resulted in a revised growth curve for the species (Farley et al. 2018b). Spatial analysis of length-at-age data from these otoliths suggest significant differences in the growth rates of bigeye tuna across the Pacific, with greater length-at-age in the far eastern and far western Pacific, compared to central longitudes (Farley et al. 2017; Farley et al. 2018b). Examination of spatial patterns in otolith weight-at-length data revealed very similar spatial patterns (Farley et al. 2018b). There is ongoing work to clarify whether this growth difference between the two regions is a result of separate populations or due to methodological differences in the preparation and interpretation of otoliths (Farley et al. 2018b). Farley et al. (2017) identified four broad areas in the WCPO with differing growth profiles, corresponding roughly to areas i) west of ~140°E (encompassing Indonesia and Philippines, ii) east of ~140°E to ~150°W and north to ~5°N, iii) north of 5°N, and iv) east of ~150°W (encompassing French Polynesia samples).

Moore et al. (in press) examined parasite fauna of bigeye tuna collected from locations within the Indonesian EEZ and two outlier locations - Maldives and Solomon Islands. Consistent with their results for yellowfin tuna, parasites suggested little mixing of bigeye tuna between Indonesia waters and the two outlier locations. Within the Indonesian EEZ, the parasite data again suggested little movement from the western Pacific into the Indonesian archipelago or from the Indonesia archipelago to the eastern Indian Ocean.

Studies of the otolith chemistry of bigeye tuna in the Pacific have been limited. Comparisons of stable isotopes ($\delta^{13}C$ and $\delta^{18}O$) and chemical signatures of the natal regions of otoliths from young of the year collected from four regions throughout the WCPO revealed spatial variability, particularly in the depletion of $\delta^{18}O$ (Rooker et al. 2016). When compared with the stable isotope and chemical signatures of natal regions of otoliths from 1–2 year-old bigeye tuna from the Marshall Islands and Hawaii, Rooker et al. (2016) concluded that bigeye tuna from the Marshall Islands were almost entirely derived from local production, with a minor contribution of recruits from the central equatorial Pacific. In contrast, a large fraction of bigeye tuna from Hawaii were deemed to have originated from the central equatorial region (Rooker et al. 2016), contrasting with the results from tagging studies that suggested limited dispersal of bigeye tuna from Hawaiian waters (Itano and Holland 2000) and constrained latitudinal dispersion of bigeye tuna within equatorial waters (Schaefer et al. 2015).

Examination of muscle chemistry also suggests some structuring in bigeye tuna in the Pacific. Similar to their findings for yellowfin tuna, Houssard et al. (2017) observed strong spatial trends in muscle $\delta^{15}N$ values for bigeye tuna sampled across the WCPO, suggesting restricted movement of individuals and a degree of regional residency regional residency, at least over the scale of their muscle nitrogen turnover rate (i.e. half-life = 167 days).

For the WCPO, the most recent stock assessment estimates some north-south exchange between equatorial regions and the North Pacific, as well as a movement of recruits from west to east in the North Pacific (Figure 6). The same general trend as with the other tropical tuna

species is otherwise predicted, i.e. mixing throughout the equatorial regions but higher retention of recruits in the westernmost tropical region. Bigeye tuna in the southernmost assessment regions were estimated to result mostly from self-recruitment self-recruited, with a small proportion of recruits predicted to move west to east (Figure 6; McKechnie et al. 2017a).

Recent outputs from SEAPODYM estimate an optimum mean spawning temperature of 26.8°C for bigeye tuna, resulting in peak larval distributions between 26° to 28°C (Lehodey et al. 2017). Model simulations estimate a large spawning area in the central equatorial region, with juvenile bigeye tuna concentrated mainly in the wider tropical central Pacific, and adults extending from this zone into more temperate latitudes following the Kuroshio extension to the north and Eastern Australian Current to the south. Bigeye tuna movement parameters appear to have varied considerably across parameter optimisations (e.g. Lehodey et al. 2017; Senina et al. 2018), suggesting very low to moderate diffusion in response to habitat quality, potentially affecting mixing.

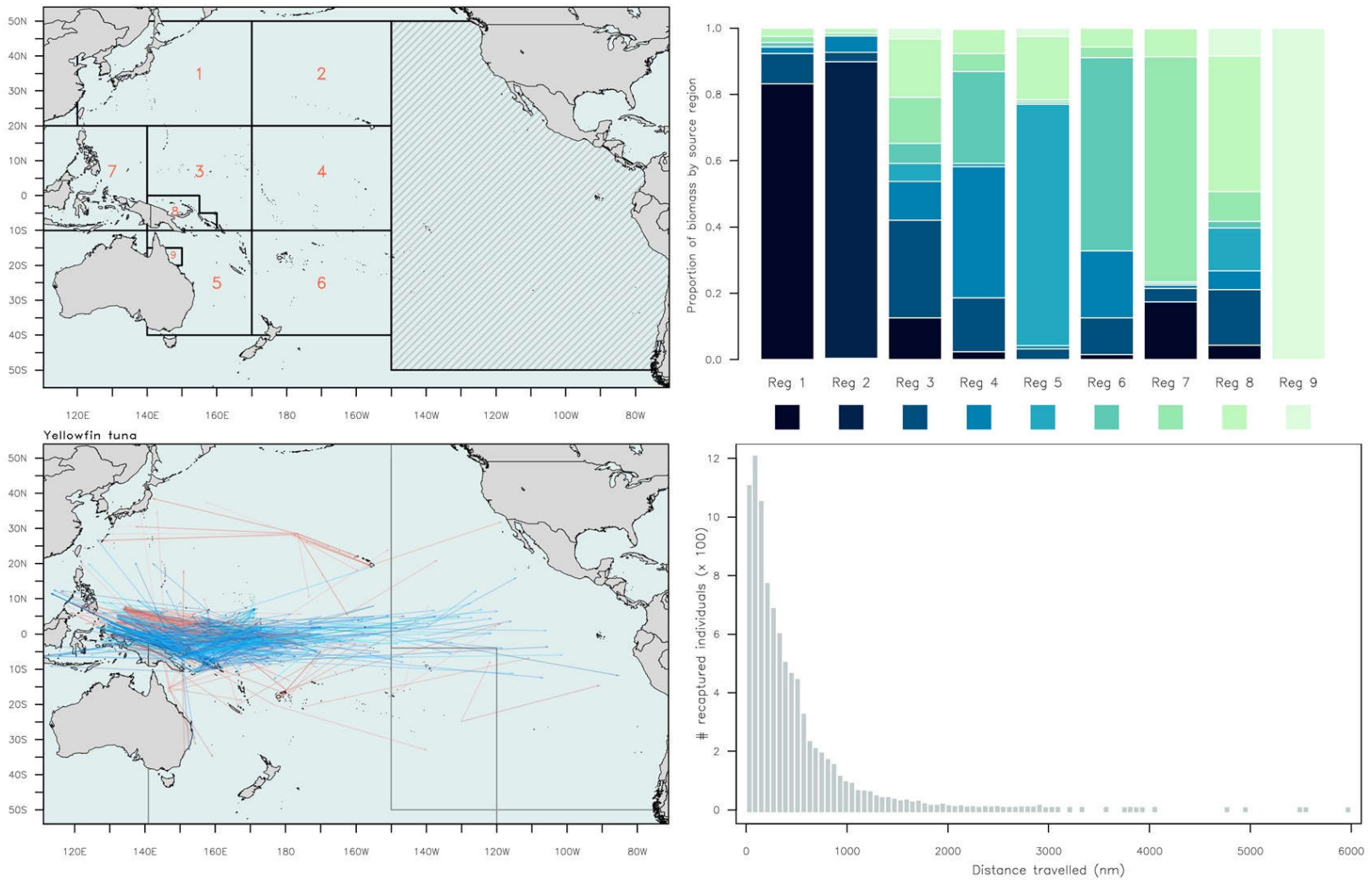


Figure 6. Top left: The geographic area and regional structure for stock assessments of bigeye tuna in the WCPO (numbered areas) and EPO (line shaded area); bottom left: movements of tagged bigeye tuna tagged during the RTTP (red arrows) and PTTP (blue arrows) recaptured > 1,000 nm from their release point; top right: proportional distribution of total biomass (by weight) in each WCPO assessment region apportioned by the source regions; bottom right: distribution of observed tag displacements for bigeye tuna at liberty for ≥ 3 months from RTTP and PTTP data. All tagging data shown is based on SPC holdings.

South Pacific albacore tuna

Albacore tuna are widely distributed in the Pacific Ocean between approximately 50°N and 40°S, although fisheries catch and tagging data suggest limited occurrence in equatorial waters between 5°N and 5°S (Lewis 1990; Williams et al. 2012; Nikolic et al. 2017). Historically, two stocks have been recognised in the Pacific, located in the North Pacific Ocean and the South Pacific Ocean. However, several recent studies report apparent genetic homogeneity in fish caught in the northern and southern hemispheres, casting some doubt on separation of stocks in the two areas (e.g. Montes et al. 2012; Albaina et al. 2013).

In contrast to tropical tunas, South Pacific albacore tuna have a relatively discrete spawning season, with spawning occuring in tropical and sub-tropical waters between 10°S and 25°S between September and May, with a peak between October and December (Ramon and Bailey 1996; Farley et al. 2013). Females in spawning condition have been observed over a broad area of longitude. Juveniles (45–50 cm FL) are thought to move south from their spawning grounds into the surface waters around New Zealand and in the vicinity of the subtropical convergence zone in the central Pacific, where they are caught by longline and troll-fisheries when they are around one year old. As they age, South Pacific albacore tuna gradually disperse into lower latitudes being distributed throughout waters north of 30°S as adults (Tremblay-Boyer et al. 2018). Longline catch data indicates that adult South Pacific albacore tuna migrate seasonally between tropical and subtropical waters, moving south during early summer, and north during winter (Langley 2004; Langley and Hampton 2005), coincident with the seasonal shift in the 20–28°C sea surface temperature isotherm (Langley 2006). Latitudinal variability in maturity at age and fatty acid trophic markers support assumptions derived from fisheries catches on latitudinal separation of age groups (Farley et al. 2014; Parrish et al. 2015). Mean length at 50% maturity of females has been estimated to be ~87 cm in the WCPO, when fish are around 4.5. years of age. Albacore tuna in the South Pacific can live for at least 14 years, and reach a maximum FL of 103 cm (Williams et al. 2012).

While South Pacific-wide assessments were performed historically, the most recent stock assessments for South Pacific albacore tuna assume a single discrete stock west of 130°W and from 50°S to the equator between 140°E and 150°W, and from 50°S to 5°S between 150°W and 130°W (Figure 7; Tremblay-Boyer et al. 2018). The eastern Pacific component of the stock has not been included in recent assessments, due to low catches and poor data quality, although increasing catches in recent years have resulted in requests for a Pacific-wide assessment of the species (Pilling and Brouwer 2018). Spatial structuring of the assessment model used in the WCPO has varied through time with the structure informed by biological hypotheses of seasonal movement, spatial structuring of the population by age, and patterns of fishing activity. The distribution of recruitment in the assessment was constrained in the most recent assessment to the two southernmost regions based on the distribution of newly-recruited fish in the catch, precluding model predictions on the source of recruits to adult biomass.

Molecular studies

Few studies have used molecular approaches to examine the presence of population structuring within South Pacific albacore tuna. Those studies that have been conducted have reported evidence of genetic differentiation between the western Pacific Ocean (Australia) and EPO (Chile and Peru; Takagi et al. 2001) and the western Pacific Ocean (between New Caledonia and Vanuatu) and central Pacific Ocean (French Polynesia; Montes et al. 2012).

Non-molecular studies

Albacore tuna are considered more challenging to tag than other species of commercial tuna and as a result, comparatively fewer conventional tags have been released on albacore tuna in the Pacific Ocean in comparison to skipjack, bigeye and yellowfin tunas. Nevertheless, some tagging of South Pacific albacore tuna has been undertaken by SPC's Oceanic Fisheries Programme, primarily to inform stock assessments for this species with respect to growth, movement, and mortality. Although recapture rates have been low (1%), those that have been made support connectivity between high and low latitudes and highlight the potential for individual fish to undertake long-range dispersion, with some individuals being recaptured several thousands of kilometres from their release sites (Figure 7) (Labelle and Hampton 2003; SPC-OFP 2017; SPC-OFP 2018b). There have been few releases of electronic tags on albacore tuna, with only 19 pop-up satellite archival tags deployed on albacore tuna in New Caledonia, Tonga and New Zealand waters (Williams et al. 2015). Although tag deployments of recaptured individuals were limited in duration (≤ 50 days), displacements varied between release sites, with those fish tagged in New Zealand waters displacing further than those tagged in New Caledonian and Tongan waters (Williams et al. 2015).

Spatial variability in growth has been reported within South Pacific albacore tuna, with both females and males reaching greater length-at-age at easterly longitudes than at westerly longitudes (Williams et al. 2012). Longitudinal differences have also been observed in gonad development, with mature albacore tuna in the east having heavier gonads in relation to their length than those in the west (Farley et al. 2013). Together, these results suggest some structuring at broad spatial scales within the WCPO.

Jones (1991) examined parasites of albacore tuna from locations in the south-western Pacific. From the abundances of 10 species of didymozoid he concluded that juvenile albacore tuna moved south from the tropics to New Zealand and then return north to spawn with the onset of sexual maturity, a result that is consistent with tagging and fishery catch data. In addition, a decline in prevalence and abundance of two other parasites, *Anisakis simplex* and *Hepatoxylon trichiuri* between New Zealand and the central South Pacific and the presence of only dead *H. trichiuri* in the central South Pacific led Jones (1991) to conclude that fish were moving longitudinally along the subtropical convergence zone.

Studies of the otolith microchemistry of albacore tuna have been limited, with only one study examining the chemical signatures of the natal region of otoliths from fish captured around New Caledonia, New Zealand and French Polynesia (Macdonald et al. 2013). Albacore tuna caught off New Caledonia and New Zealand were found to have similar chemical signatures, suggesting they had originated from areas of similar water chemistry. In contrast, those from French Polynesia were significantly different, suggesting they had originated from a separate larval source (Macdonald et al. 2013). Although the locations of larval origins were not identified, these results suggest the potential for some degree of spatial structuring of spawning populations of albacore tuna within the South Pacific.

Simulations using SEAPODYM estimate an optimal spawning SST for South Pacific albacore tuna of 28°C, with the northward spawning migration peaking in early May (Senina et al. 2018). Optimal temperatures for foraging habitats for the species were estimated as ranging from 11.8–23.5°C. Little evidence on connectivity and stock structure per se is available from SEAPODYM, with the model predicting broad scale movement of albacore tuna corresponding with a seasonal shift of the 23° to 28°C SST isotherm location (Senina et al. 2018).

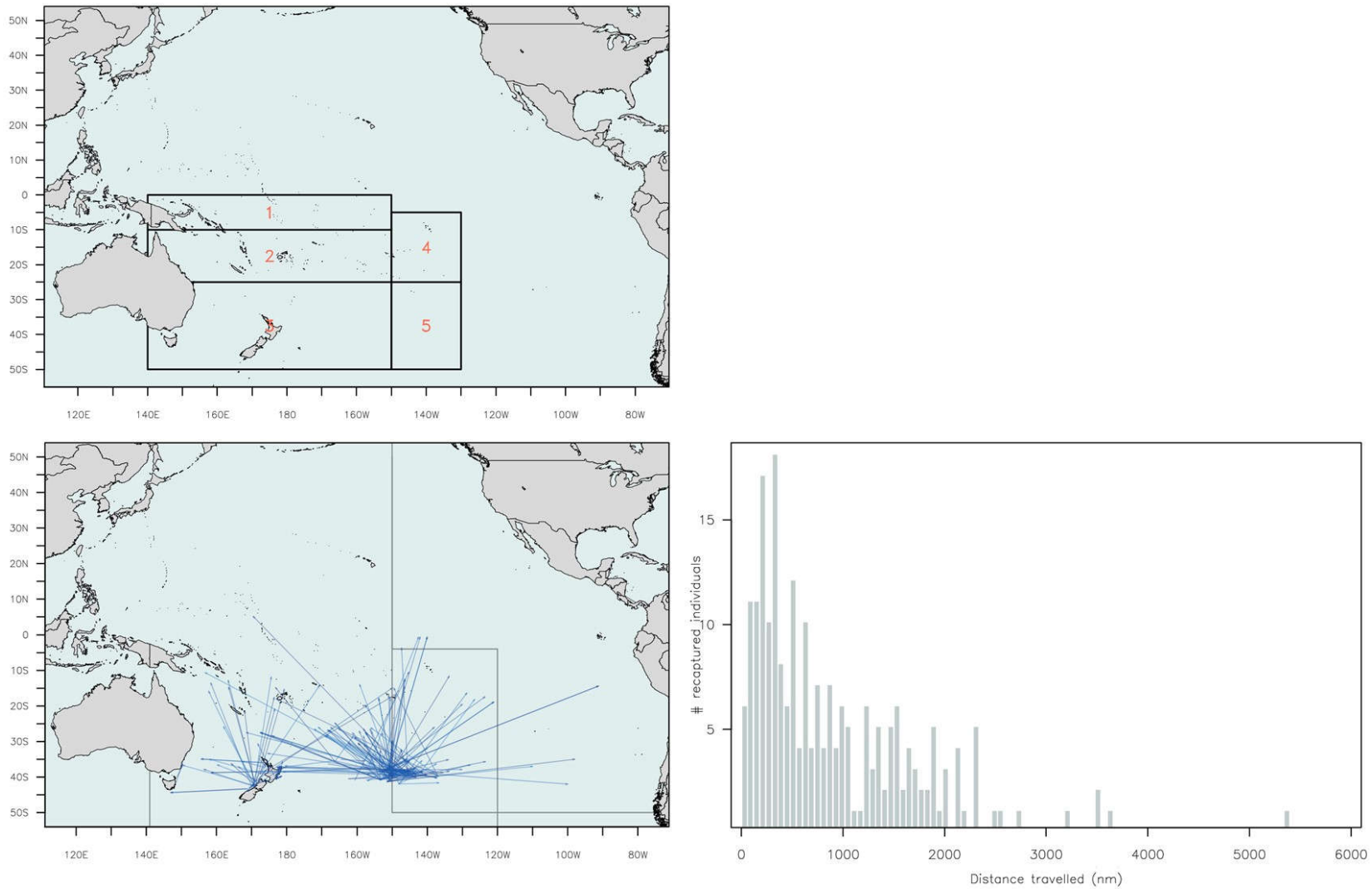


Figure 7. Top left: The geographic area and regional structure for stock assessments for South Pacific albacore tuna in the WCPO (numbered areas); bottom left: movements of tagged albacore tuna tagged during the RTTP (red arrows) and PTTP (blue arrows); bottom right: distribution of observed tag displacements for albacore tuna at liberty for $\geq$ 3 months from RTTP and PTTP data. All tagging data shown is based on SPC holdings. Note predictions of total biomass distributions are not available from the assessment model (see text).

Key uncertainties and future directions to understanding the stock structure of skipjack, yellowfin, bigeye and South Pacific albacore tunas

Recent findings from research studies across the Pacific Ocean have increased our knowledge of the spatial dynamics of the four main target tuna species. They suggest a complex stock structure rather than panmixia, at least for yellowfin, bigeye and South Pacific albacore tunas. However, to date no single study, or combination of studies, have clearly defined the stock structure of any of the four species at scales relevant to regional management. Studies conducted in the Pacific to date have typically been constrained by effects of scale (both spatial and temporal), sampling design, limitations of the techniques, availability of samples or data, and potentially the behaviour of the tuna species themselves. For example, while a large amount of tagging data exists, particularly for skipjack tuna and yellowfin tuna, most tagging studies have been focused on juvenile fish, and spatially limited, with releases largely conducted in areas of high abundance and concentrated fishing effort. This is partly because these studies were not designed solely to provide information on movement and mixing, but to assess a range of parameters for use in stock assessments, including estimations of growth rates, natural and fishing mortality, and abundance (Leroy et al. 2015). Furthermore, inferences of movement and mixing are inherently biased by the point-to-point nature of resulting data, the number of recaptures and the time at liberty of those individuals, the distribution of tagging and recapture effort, varying tag reporting rates and uncertainties around the population representativeness of tagged individuals (Ward and Caton 1992; Leroy et al. 2015). Historically, most genetic studies have used markers that are extremely sensitive to the movement of individuals between populations (Slatkin 1987), or that have low levels of genetic differentiation resulting from large populations sizes, such as estimated for skipjack, yellowfin, bigeye and South Pacific albacore tunas (Palumbi 2003; Ely et al. 2003). Some genetic studies have shown that genetically-distinct assemblages may occur in the same area (e.g. skipjack tuna off the coast of Japan; Fujino 1990), potentially as small spatial units (Sharp 1978). Grouping such assemblages together in location-based analyses may mask any differentiation. Elsewhere, studies have been limited by sample sizes (e.g. Grewe and Hampton 1998), or by widely-separated sampling locations (e.g. Grewe et al. 2015; Pecoraro et al. 2018).

As a consequence, several key uncertainties regarding the stock structure exist for each species, outlined below. In the following section, we outline some specific questions designed to address these uncertainties for each species, and outline potential sampling strategies that may help answer them.

1. *Fidelity to spawning areas*. The degree of fidelity of individuals to spawning areas is still largely unknown, and likely to vary between species. In instances where discrete spawning areas have been identified (in particular for yellowfin tuna and bigeye tuna), it is currently unknown whether individuals maintain a general close proximity to, or, for apparently transient fish, return to, the same particular spawning area each year, and, if they do, whether these movements represent fish returning to their natal spawning areas. Most tagging studies in the Pacific have focused on juveniles and as a result, understanding of adult movement, including the degree of spawning area fidelity, is limited. Although some efforts have been made to examine movement of adults via electronic tagging approaches (e.g. Schaefer et al. 2007; Evans et al. 2011; Schaefer et al. 2011), current data are largely inadequate for assessing any potential spawning area fidelity.

2. *Natal origins, the degree of mixing of post-juvenile fish and proportional contributions of each spawning unit to fishery catches.* A key challenge for management of tuna fisheries in the Pacific is an understanding of the proportion each potential spawning unit contributes to harvested assemblages. This is particularly of relevance given that i) fishery mortality is unevenly distributed across the Pacific, ii) there is the potential for fisheries to exploit individuals from several spawning units more-or-less simultaneously, iii) different spawning units likely have differing levels of productivity and iv) there is a potential for local depletion. While some studies have tackled this issue across small spatial scales (e.g. Gunn et al. 2002; Wells et al. 2012; Rooker et al. 2016), scaling this work up to scales relevant for regional fisheries management has not yet been undertaken.

3. *The management implications of an improved understanding of tuna stock structure - i.e. in the event that multiple stocks of each species are present, would management be done differently?* The spatial scale and structure of Pacific tuna assessments have been defined on the basis of management boundaries, the nature of the fishing fleets exploiting each stock, and settings required to achieve a robust model. While better knowledge of stock structure can improve assessments, the need to develop management systems that are robust to the uncertainties in our understanding of the biology, stock structure and environmental drivers such as climate change is important. The WCPFC is currently in the process of developing management procedures for the main tuna species that will allow for pre-agreed decisions for management action to be tested for robustness to plausible hypotheses of stock structure and connectivity, such as those raised in this paper. The process can also examine the value of new information in terms of its potential to improve decision making, thereby providing further support for undertaking research activities. Prior to the commencement of a sampling program for each of the four species, it would first be prudent to undertake simulations to determine whether different stock structure hypotheses actually make a difference to the stock assessment outputs and management of stocks before embarking on expensive sampling activities and analyses.

4. *Effects of climate change on overall stock structure and proportional contributions of spawning units to fisheries.* Recent modelling using SEAPODYM suggests that under climate change alone, a change in the distribution of skipjack and yellowfin tuna is likely to occur. This will result in increases in abundance in some areas and decreases in abundance in others (Lehodey et al. 2013; Dueri et al. 2014; Senina et al. 2016; Bell et al. 2018b). Understanding how these changes will affect processes mediating the dynamics, and overall structure, of tropical tuna stocks, in the Pacific is a key challenge to climate change and stock assessment modelling, and is contingent of obtaining a better understanding of the uncertainties described above.

Overcoming uncertainties about the stock structure of Pacific tunas: suggestions for future research

Careful sampling design is critical to any assessment of the spatial dynamics of broadly distributed species. Here, we outline several key questions relating to better defining the stock structure of the four tuna species and potential sampling design approaches and contingencies that could be adopted to answer these questions, informed by expert input. We start by addressing two considerations that have relevance across all of the proposed methodological approaches to answer key questions.

Sample size considerations

Consideration of sample sizes is of critical importance in stock structure studies Inadequate sample sizes may preclude the detection of differences where they occur (i.e a Type II error), while excessive sample sizes may prevent additional sampling in different strata, locations or periods due to budget limitations. For analysis of parasites and otolith chemistry, previous studies have generally targeted around 50 fish per sample. For population genetics, larger sample sizes are recommended (i.e. around 50–100 individuals per sample). Overall, it would be more advantageous to over-sample and choose which fish to analyse than under-sample, although sample sizes should ideally be determined via experiment-specific simulation and power analyses[3]. Until these analyses are complete, we recommend a sample size of at least 100 fish per spatio-temporal stratum (i.e. fish from Location A in Sampling Period B).

Multidisciplinary approaches to determining stock structure

In general, a multidisciplinary approach, incorporating two or more complementary techniques, is recommended as the most suitable approach for addressing questions regarding stock structure and mixing of the four tuna species in the Pacific. The use of a multidisciplinary approach is generally regarded as more effective in determining stock structure than any one technique alone, because it not only gives greater confidence to the results of any one technique where consistent results are obtained (i.e. a weight of evidence approach), but also allows for the limitations of each technique to be resolved, effectively increasing the chances of identifying differences between spatially-distinct populations (Begg and Waldman 1999). A key advantage of using a multi-technique approach to identify stock structure is that each method is informative about the fish's life history at different spatial and temporal scales. For example, genetic approaches have the potential to inform about rates of mixing of fish from different regions as well as evolutionary patterns of gene flow, whereas parasites and otolith microchemistry are directly influenced by the environment and so could inform on the patterns of movement during a fish's lifetime. The use of these complementary techniques in a multidisciplinary study increases the chance of detecting separate stocks where they exist (Moore 2011; Welch et al. 2015) and our recommended approach to answer the questions outlined below thus by default uses, at the very least, a genetic sample combined with at least otolith chemistry.

Skipjack tuna

Key questions regarding the stock structure of skipjack tuna in the Pacific that warrant addressing include:

1. Is there panmixia in skipjack tuna across the equatorial Pacific?
2. Is the occurrence of skipjack tuna in subtropical and temperate waters independent of the equatorial stock?

Question 1: Is there panmixia in skipjack tuna across the equatorial Pacific?

Addressing this question requires simultaneous sampling of similarly-sized fish (e.g. 40 cm FL) at locations across the species' equatorial distribution.

Where and when to sample: Sampling should be conducted over the full geographical range of skipjack tuna in the equatorial Pacific i.e. Indonesia to Ecuador, and including the high seas. Outlier locations (i.e. locations within the Atlantic and Indian Oceans) should be included for contrast, and to aid determination of provenance for traceability purposes. Sampling should adopt a phased approach across both spatial and temporal scales. Broad-scale, low resolution

[3] Such analyses are currently being conducted for the four tuna species reviewed here for a stock structure study in the Indian Ocean, and results from these analyses may help provide guidance here.

sampling should be conducted in Phase I (e.g. covering widely spaced locations across the equatorial region). Should no structuring be observed, no further spatial sampling should be conducted. If spatial structuring is observed, finer-scale spatial sampling, targeting key areas of interest, should be conducted in Phase II. Repeated sampling of the locations sampled in Phase I should also be conducted in Phase II to assess the temporal stability of examined signal(s). Repeated sampling of all locations sampled in Phases I and II should be conducted in a third phase to further assess the temporal stability of examined signal(s). To avoid the potential for repeated sampling of the same group of fish at different locations, sampling of locations in each phase should be conducted across a restricted temporal window (e.g. within a four-week period), to ensure that spawning individuals have not had time to move between locations. In order to reduce the effects of ENSO, sampling should be conducted during ENSO-neutral periods. Repeated sampling during El Niño or La Niña events would then allow for examination of their effect on stock structure of skipjack tuna.

*How to obtain sample*s: In both the WCPO and EPO, sampling could be achieved via observers or dedicated sampling personnel on purse seine and pole-and-line vessels.

What to collect: A multidisciplinary approach, involving modern molecular markers such as SNPs, otolith chemistry and shape, and parasites as biologicals tags, may prove the most useful for determining the existence of panmixia in skipjack tuna in the Pacific. At least 100 fish should be collected per stratum (i.e. a spatially or temporally distinct group of fish – i.e. fish from Location A in Phase II), and fish should be sampled for a range of biological material (i.e. muscle samples for genetics and stable isotope analyses, otoliths for chemical and shape analyses as well as ageing, gonads, and gill rakers and viscera for parasite analyses). Given the small size and low cost of skipjack tuna relative to other tropical tunas, it may be possible to purchase entire fish for sampling. If purchasing whole fish is not possible for budget or operational reasons, priority should be given to collecting biological material that has multiple uses, in particular muscle and otoliths. If sampling from purse-seine vessels, it would be better, to avoid issues of kinship, to sample a few individuals per set, and sample multiple sets per location, than sampling all individuals from a single set.

Question 2: Is the occurrence of skipjack tuna in subtropical/temperate waters independent of the equatorial stock?

Preliminary investigations using otolith chemistry (Arai et al. 2005) and parasites (Lester et al. 1985) indicate that skipjack tuna at the extremities of their distribution have spent some time in tropical waters, however, their relationships with individuals within the tropics is poorly understood. Spawning of skipjack at the extremities of their distribution has also been reported (e.g. Yabe 1954), leading some to conclude fish in these areas potentially form separate stocks to those in equatorial waters.

Where and when to sample: Addressing this question requires simultaneous sampling of skipjack from the subtropical/temperate waters and the equatorial Pacific. Sampling will need to be conducted twice per year (i.e. during each of the austral and northern hemisphere summers, when skipjack are present at the extremities of their range), with samples taken from equatorial waters in each sampling event.

How to obtain samples: Sampling to address this question could be achieved via observers in both EPO and WCPO, particularly on purse seine, pole-and-line, and troll vessels. In certain locations (e.g. east coast of Australia, New Zealand), it may be necessary to sample from the recreational fleet and charter vessels.

What to collect: A multidisciplinary approach, involving modern molecular markers such as SNPs, otolith chemistry and shape, and parasites as biologicals tags, may prove the most useful for determining relationships between skipjack tuna across latitudes. Approaches that allow for resolution of movement from one environment to another, such as otolith chemistry and parasites as biological tags (i.e. to assess whether fish have moved from the tropics, and not just that they are related to fish from the tropics), may prove the most useful in this instance. As above, given the small size and low cost of skipjack tuna relative to other tropical tunas, it may be possible to purchase entire fish for sampling. If purchasing whole fish is not possible, again priority should be given to collecting biological material that has multiple uses, in particular muscle and otoliths.

Yellowfin tuna and bigeye tuna

Specific questions regarding the stock structure of yellowfin tuna and bigeye tuna in the Pacific that warrant addressing include:

1. Do mature yellowfin tuna or bigeye tuna show fidelity to spawning locations?
2. Is there connectivity between equatorial and sub-equatorial spawning groups of yellowfin tuna or bigeye tuna, including Hawaii?
3. Is there mixing of non-spawning populations/stocks of yellowfin tuna or bigeye tuna?
4. Is there a genetic basis for the different movement phenotypes observed (i.e. resident, transitory, migratory/homing)?

Question 1: Do mature yellowfin tuna or bigeye tuna show fidelity to spawning areas?

Determining whether yellowfin tuna or bigeye show fidelity to spawning areas and the degree of reproductive stock structure across the Pacific distribution of yellowfin tuna and bigeye tuna preferentially requires an examination of adult fish in spawning condition from different spawning areas, with samples collected on an annual basis during peak spawning times over multiple spawning seasons. Should sampling of adults be impractical, or yield insufficient samples, young-of-the-year (YOY) individuals may be sampled to use as proxy for patterns of behaviour of spawning adults, although a key challenge in this instance would be to obtain fish as small as possible to ensure that we can assume that the location of sampling is close or coincides with their natal area. Larval dispersal or active movement models could be used to back-calculate the origin of YOY to estimate putative areas of origin. Distinct, temporally stable, spawning-area signals suggest that fish are using the same area for spawning, while non-distinct spawning-area signals suggest that fish may be moving between and utilising different spawning areas during their lives.

The first task to addressing whether mature yellowfin tuna or bigeye tuna show fidelity to spawning areas would be to identify existing samples of actively spawning fish, or YOY individuals, stored with the WCPFC tuna tissue bank, to determine whether there is sufficient material on hand to provide evidence for population structure. If sufficient material exists (i.e. muscle and otolith samples from ~100 fish in spawning condition per spawning area per year), these could be used to provide a preliminary examination of potential structuring within each species during the spawning season.

If existing material is insufficient, a dedicated sampling program will be required. Areas of spawning activity to target sampling towards should first be identified. Areas and times known to contain fish in running ripe state (e.g. Philippines, Coral Sea, and areas across the equatorial band) should be targeted as a priority while several additional lines of evidence could be examined to determine other areas where fish in spawning condition may occur, including:

- Observer data from the commercial purse-seine and longline fleets for fish in spawning state;
- Catch and effort data (high catches during peak spawning periods may indicate an aggregation of spawning fish, while spatio-temporal patterns in length/weight data from the longline fishery, the purse-seine fishery associated with dolphins in the EPO, or free school sets in the CPO, may indicate when large fish congregate in a particular area);
- Current collections of gonad material stored in the WCPFC tuna tissue bank (via histology);
- Areas with high occurrence of larval or early juvenile tunas in stomach contents of predators, including other tunas;
- Areas of high larval recruitment success as estimated by SEAPODYM.

Where and when to sample: Sampling should be phased across both spatial and temporal scales. Broad-scale, low resolution sampling should be conducted in Phase I (e.g. covering widely-spaced areas spanning the Pacific distribution of yellowfin tuna and bigeye tuna, such as Coral Sea, Indonesia, western equatorial Pacific, central equatorial Pacific, Hawaii, and the EPO). Outlier areas (i.e. areas within the Atlantic and Indian Oceans) should be included for contrast, and to aid determination of provenance for traceability purposes. Should no structuring be observed between areas in Phase I, no further spatial sampling may be required. If spatial structuring is observed, finer-scale spatial sampling targeting key areas of interest between the Phase I areas should be conducted in Phase II. Repeated sampling of areas sampled in Phase I should also be conducted in Phase II to assess the temporal stability of examined signal(s). Repeated sampling of all areas sampled in Phases I and II should be conducted in a third phase to further assess the temporal stability of examined signal(s). As best as possible, spawning areas should be sampled at around the same time (i.e. within a four-week window), to ensure that spawning individuals have not had time to move between areas and therefore limit the possibility that fish are sampled twice. Given that peak spawning times vary between areas, the best way to achieve this will need careful consideration.

How and what to sample: In both the WCPO and EPO, sampling could be achieved via observers or dedicated sampling personnel. To obtain adult yellowfin tuna and bigeye tuna, sampling could be conducted by observers on purse-seine vessels targeting free school sets in the CPO and the purse-seine catches associated with dolphins in the EPO, or via dedicated samplers on longline vessels. Port sampling of longline catches may also be possible within several countries and territories in the WCPO. Sampling of YOY yellowfin tuna and bigeye tuna may be achieved via observers on purse seine or pole-and-line vessels. Opportunities to collaborate with / leverage off other ongoing or planned projects, such as the recent ACIAR-funded population biology project in Indonesia (targeting skipjack, yellowfin and bigeye tunas), should be sought.

What to collect: What biological material to collect depends largely on the life history stage is being sampled. If spawning adults are sampled, sampling should ideally cover a range of biological material, including muscle samples for genetics and stable isotope analyses, otoliths for chemical and shape analyses as well as ageing, and gonads, but if required, priority should be given to material that has multiple uses, in particular muscle and otoliths. Gonads should also be collected as a priority to confirm spawning condition via histology. If sampling of adults is deemed not possible or practical, and YOY fish are sampled as a proxy, it is likely that only genetic signals (e.g. SNPs) may be worth investigating if addressing Question 1 in isolation. However, if the collected material is to be used as a starting point to address mixing outside of the spawning season or of immature fish (see Question 3 below), other biological material, including otoliths and material for parasite analysis (stomachs, gill rakers), should also be

collected given their value in providing baseline signatures of natal areas in mixed stock analyses.

Question 2: Is there connectivity between equatorial and sub-equatorial spawning groups of yellowfin tuna or bigeye tuna, including Hawaii?

Although currently considered a single stock in the WCPO for assessment and management purposes, there is preliminary evidence to suggest that yellowfin tuna or bigeye tuna in sub-equatorial regions such as Hawaii may constitute separate reproductive units to those in equatorial regions of the WCPO (Schaefer et al. 2015; Rooker et al. 2016; P. Grewe, unpublished data). Accordingly, structured studies are required to formally assess the relationships between fish spawning in equatorial regions (i.e. those between 10°N and 10°S) and sub-equatorial waters. Relationships between spawning units of both yellowfin tuna and bigeye tuna within these regions could be addressed using the design outlined above, provided adequate sampling locations are included in sub-equatorial and adjacent equatorial waters. As discussed above, care would have to be taken to ensure that fish are sampled simultaneously during the respective peak spawning time for the respective sampling areas, noting that given differences in the timing of peak spawning between areas this will likely require that each area be sampled on multiple occasions in an annual cycle.

Question 3: Is there mixing of non-spawning populations/stocks of yellowfin tuna or bigeye tuna?

Addressing this question requires an initial understanding of how yellowfin tuna and bigeye tuna are structured during the spawning season, and the natal origins of new recruits to the fishery, as a starting point from which to evaluate the degree of mixing. This could be achieved using the same design proposed for Question 1 above. Subsequent mixing of both adults and juveniles/sub-adults should be examined to account for any variation in mixing as a result of ontogenetic and/or environmental influences. Two potential options for determining mixing of juveniles/sub-adult or non-spawning adults for yellowfin tuna and bigeye tuna are proposed below, depending on what life history stages are sampled initially (i.e. adults on spawning grounds or larvae/YOY individuals in natal areas):

I. Options based on initial sampling of adults on spawning grounds

If sampling of adults on spawning grounds was conducted to assess how fish are structured during spawning, such as using the design proposed for Question 1 above, and clear, temporally stable, differences in signal(s) between different spawning areas found to exist, a second temporal sampling should be conducted. To assess movement and mixing of adults, this second sampling should ideally occur as far outside of the spawning season for each area as possible, to allow the maximum time for fish to mix between spawning events. To assess movement and mixing of juvenile/sub-adult fish, this should occur when fish are around 6–12 months old i.e. when fish recruit to commercial purse seine and pole-and-line fisheries.

In this option, the choice of techniques to use to assess mixing would largely depend on the life history stage being examined. For assessing movements and mixing of adult fish following spawning, the same material as that examined in adults at spawning areas should be examined (i.e. a complementary approach incorporating at least modern molecular markers such as SNPs, and otolith elemental and isotopic signatures, otolith shape, and potentially isotopic signatures in muscle tissue). This approach would provide direct evidence of mixing of adults (i.e. as animals from the same cohort and spawning unit are tracked over time). For juveniles/sub-adults, genetic markets such as SNP markers should be examined to classify juveniles/sub-adults back to their likely spawning unit of origin based on their relatedness to sampled adults, providing an indirect account of mixing (in that animals from a

different cohort to that originally sampled are being examined). Due to the lack of a direct baseline natal environmental signal (resulting from a lack of sampling larvae or YOY fish on the natal grounds in this option), techniques such as otolith chemistry may be less useful in this instance, as core signatures in juveniles/sub-adult may not necessarily reflect those in adult fish, even if originating from the same area, due to inter-annual differences in environmental variables (in particular ambient chemistry, temperature and salinity; Campana 1999; Elsdon and Gillanders 2004).

II. Options based on the initial sampling of larvae or YOY individuals in natal areas
If sampling of larvae or YOY fish (as small as possible) on their natal grounds was achieved, and clear, temporally stable, differences in signal(s) between fish from different natal areas were found to exist, two potential approaches could be used to assess movement and mixing of juveniles/sub-adults and adult fish outside of the spawning season:

A) *Immediate sampling of juveniles/sub-adults and adults*. Following characterisation of genetic signatures of larval/YOY fish in their natal areas, sampling of juveniles/sub-adults and adults within the same annual cycle could be conducted. Sampling should be conducted at least six months from the peak spawning season in each area, to enable adults time to move away from spawning areas and potentially mix. Genetic markers such as SNPs would provide an ideal tool for assessing movement and mixing using this approach. This approach would provide indirect evidence of mixing across all life history stages (in that patterns of mixing in one cohort are inferred from another cohort).

B) *Cohort-specific sampling of juveniles and adults*. In this approach, the same cohort would be sampled over time to assess movement and mixing as fish age and mature, following the approach conducted for yellowfin tuna and bigeye tuna by Rooker et al. (2016). For example, if larvae/YOY fish were initially sampled from different natal areas in 2020, and distinct natal area signatures found to exist, juveniles from the same cohort should be sampled in 2021 and again in 2022 (i.e. when they are 1 and 2 years of age, respectively), while adults resulting from this cohort should be sampled in 2025 (at five years of age). A multidisciplinary approach, involving complementary techniques such as examination of SNPs and otolith chemistry, would likely prove the most useful for assessing the degree of mixing in this approach. Larval/YOY fish should be sampled for genetic material (for SNP analyses) and otoliths (for elemental and/or isotopic analyses of the otolith core region). Subsequent samples of juveniles/sub-adults, and adults, should then be surveyed for the same markers. Techniques such as examination of parasites or isotopic signatures in muscle tissue may be less appropriate in this instance, particularly in larval fish, as these individuals will likely not have had sufficient time to accumulate a distinct natal-area signature, or, in the case of muscle isotopic signatures, the natal signature may be altered by the time subsequent sampling of older life history stages is conducted. Genetic and otolith elemental or isotopic signals observed in the juveniles/sub-adult and adult samples should be examined with reference to those of the larval/YOY fish to re-classify fish back to their natal area of origin, for example via a mixed-stock analysis (see boxed text). This approach would thus provide direct evidence of mixing across all life history stages (in that patterns of mixing are examined in the same cohort across time).

How to sample: As per questions 1 and 2 above, as best as possible, locations should be sampled at around the same time and over a short temporal period (i.e. within four weeks) in

each successive year, to reduce the possibility that the same group of fish has moved between locations and thus is sampled on multiple occasions, and to ensure patterns between years are comparable. Sampling, including both of adults during spawning or larval/YOY in their natal areas, and subsequent sampling of non-spawning components, should be repeated over multiple (e.g. three successive) years, to assess the temporal stability of the examined signal(s).

For both options I and II above, samples of adult yellowfin tuna or bigeye tuna both within and outside of the spawning seasons could be obtained by observers on purse-seine vessels targeting free school sets in the CPO and the purse-seine fishery associated with dolphins in the EPO, or via dedicated samplers on longline vessels. Port sampling of adult yellowfin tuna and bigeye tuna from longline catches may also be possible within several countries and territories in the WCPO. Sampling of YOY and juveniles/sub-adult yellowfin tuna and bigeye tuna may be achieved via observers on purse seine or pole-and-line vessels. A key challenge here would be to obtain YOY as young as possible from the commercial fleet, to ensure they are as close to their natal areas as possible (and that no mixing between reproductive units had occurred). Larval dispersal or movement models could be used to investigate how likely YOY are associated with the areas in which they are caught, or to back-calculate dispersion of sampled YOY to estimate their putative areas of origin. Fisheries-independent approaches would be required to sample larvae. Given the need for simultaneous, repeated sampling, this would be at high cost and effort.

Question 4: Is there a genetic basis for the different movement phenotypes observed (i.e. resident, transitory, nomadic)?

For each yellowfin tuna or bigeye tuna tagged during tagging operations, and particularly those tagged with archival tags, a biopsy of muscle tissue should be taken. Examining displacements from tagging data in conjunction with genetic signals would then facilitate whether observed movement patterns have a genetic basis, and potentially whether individuals of some stocks are more mobile than others.

South Pacific albacore tuna

Specific questions regarding the stock structure of South Pacific albacore tuna that warrant addressing include:

1. Are there separate reproductive stocks of albacore across the South Pacific with discrete spawning areas?
2. Do South Pacific albacore tuna show fidelity to these spawning areas?
3. Is there mixing of South Pacific albacore tuna during non-spawning periods?
4. Is there connectivity between reproductive populations of North Pacific and South Pacific albacore tuna?

Question 1: Are there separate reproductive stocks of albacore across the South Pacific with discrete spawning areas? and
Question 2: Do South Pacific albacore tuna show fidelity to these spawning areas?

Determining whether there are separate reproductive stocks of albacore tuna across the spawning latitudes in the South Pacific and whether mature South Pacific albacore tuna show fidelity to discrete spawning areas will require examination of adult fish (i.e. > 90 cm FL) in spawning condition from different areas distributed across spawning latitudes (10–25°S), with samples collected on an annual basis over multiple spawning seasons. Distinct and temporally stable spawning-area signals at the time of spawning suggest that fish are using the same area for spawning, while non-distinct spawning-area signals suggest that fish may move between and

utilise different spawning areas during their lives. Should sampling of adult South Pacific albacore tuna not be practical, or insufficient sample sizes be obtained, sampling of larvae or YOY fish as small as possible (so they are as close to their natal areas as possible) could be conducted to infer adult movement and behaviour. However, it should be noted that as YOY albacore tuna < 45 cm FL are not commercially harvested, such sampling would have to be based on fisheries-independent approaches, which can be more costly.

The first task to addressing these two questions would be to identify existing samples of actively spawning fish, or collections of larvae or YOY individuals stored with the WCPFC tuna tissue bank, to determine whether there is sufficient material on hand to provide evidence for population structure. If sufficient material exists (i.e. samples from ~100 fish per spawning area per year), these could then be used to provide a preliminary examination of potential structuring within the South Pacific albacore population during the spawning season.

If existing material is insufficient, additional sampling will be required. Previous reproductive work (e.g. Farley et al. 2013) could be used to determine spatial areas and months to direct sampling effort. In addition, several other lines of evidence could be examined to determine areas to sample to obtain fish in spawning condition, including:

- Observer data from the commercial longline fleet for fish in spawning state;
- Catch and effort data (high catches during the spawning period may indicate an aggregation of spawning fish);
- Areas with high occurrence of larval or early juvenile albacore tuna in stomach contents of predators, including other tunas;
- Areas of high larval recruitment success as estimated by SEAPODYM.

As with the three tropical tunas, sampling should adopt a phased approach at both spatial and temporal scales. Broad-scale, low-resolution sampling of spawning adults should be conducted in Phase I to determine whether there are spatial differences in the signal(s) examined, covering widely spaced areas across the spawning latitudes, such as the western Pacific (e.g. Coral Sea), central Pacific (e.g. French Polynesia) and eastern Pacific (e.g. around 120°W and 90°W), during peak spawning season (October to December). Should spatial structuring be observed, finer-scale sampling, targeting key areas of interest should be conducted in Phase II. Also in Phase II, repeated sampling of areas sampled in Phase I should be conducted to assess the temporal stability of the examined signal(s). Repeated sampling of all areas sampled in Phases I and II should be conducted in a third phase to further explore the stability of the examined signal(s) at all sampling areas. As best as possible, spawning areas should be sampled at around the same time (i.e. within a four-week window), to ensure that spawning individuals have not had time to move between areas and therefore limit the possibility that fish are sampled twice.

What to sample: A multidisciplinary approach, involving modern molecular markers such as SNPs, otolith chemistry and shape analysis, and parasites as biologicals tags, may prove the most useful for elucidating whether there are separate reproductive stocks and the existence of spawning area fidelity for South Pacific albacore. At least 100 fish should be sampled per stratum, with muscle, otolith, gill raker and stomach samples collected from each adult fish. If sampling adult fish, gonads should be collected from each fish to validate spawning condition via histology. Archival tagging would also provide evidence of albacore behaviour, and potential for natal homing if tags could be deployed over multiple years. However, as noted above, albacore are very difficult to tag, with high mortality and low tag recapture rates, so a very large population would need to be tagged, at a high cost.

How to sample: In both the WCPO and EPO, sampling of adult fish could be achieved by placing observers and dedicated sampling personnel on longline vessels operating between ~10–25°S within the peak spawning season (October to December). Sampling of larvae or YOY fish, if necessary, could be achieved via fisheries-independent sampling at selected areas within the same latitudes during the peak spawning season.

Question 3: Is there mixing of South Pacific albacore tuna during non-spawning periods?
As with yellowfin tuna and bigeye tuna, addressing this question in South Pacific albacore tuna requires an initial understanding of how South Pacific albacore tuna are structured during the spawning season, and the natal origins of new recruits to the fishery, to provide a starting point from which to evaluate the degree of mixing. Mixing of both adults inhabiting tropical waters, and juveniles/sub-adults inhibiting temperate waters, should be examined to account for any variation in mixing as a result of ontogenetic and/or environmental influences. Two potential options exist for determining mixing of juveniles or adults outside of the spawning season for South Pacific albacore tuna, depending on what life history stages are initially sampled (i.e. adults on spawning grounds or larvae/YOY individuals in natal areas):

I. Options based on initial sampling of adults on spawning grounds
If sampling of adults on the spawning grounds was conducted to assess how fish are structured during spawning, such as using the design proposed for Question 1 above, and clear, temporally stable, differences in signal(s) between different spawning areas found to exist, a second temporal sampling should be conducted. To assess movement and mixing of adults, this second sampling should ideally occur as far outside of the spawning season as possible (i.e. around May-June for the South Pacific population) to allow fish the maximum time to mix between spawning events. To assess movement and mixing of juvenile/sub-adult fish, this should occur when fish are around 12 months old i.e. when fish recruit to commercial and recreational troll fisheries in temperate waters.

In this option, the choice of techniques used to assess mixing would largely depend on the life history stage being examined. For assessing movements and mixing of adult fish following spawning, the same material as that examined in adults at spawning areas should be examined (i.e. modern molecular markers such as SNPs, otolith chemistry and parasite loadings). If attempting to track mixing of juveniles based on signals evident from adult fish on spawning areas, SNP markers should be examined to trace fish back to their spawning unit of origin based on their relatedness to sampled adults. Due to the lack of a direct baseline natal environmental signal (resulting from a lack of sampling larvae or YOY fish on the natal grounds in this approach), techniques such as otolith chemistry may prove less useful in this instance.

II. Options based on the initial sampling of larvae or YOY individuals in natal areas.
If sampling of larvae or YOY fish (as small as possible) on their natal grounds was conducted, and clear, temporally stable, differences in signal(s) of South Pacific albacore between different spawning locations / natal areas were found to exist using the sampling design proposed for Question 1, two potential approaches could be used to assess movement and mixing of juveniles and adult fish outside of the spawning season:

A) *Immediate sampling of juveniles and adults (using genetic markers):* Following characterisation of genetic signatures of fish in their natal areas, sampling of juveniles/sub-adults and adults within the same annual cycle could be conducted. Sampling should be conducted at least six months from the peak spawning season, to enable adults time to move away from spawning areas and potentially mix.

Genetic markers such as SNPs would provide an ideal tool for assessing movement and mixing using this approach.

B) *Cohort-specific sampling of juveniles and adults (using multiple markers):* In this approach, the same cohort would be sampled over time, to assess movement and mixing as fish age and mature, following the approach conducted for yellowfin tuna and bigeye tuna by Rooker et al. (2016). For example, if larvae/YOY fish were initially sampled from different natal areas in 2020, and distinct natal area signatures found to exist, juveniles from the same cohort should be sampled in 2021 and again in 2022 (i.e. when they are 1 and 2 years of age, respectively, while adults resulting from this cohort should be sampled in 2025 (at five years of age). A multidisciplinary approach, involving complementary techniques such as examination of SNPs and otolith chemistry, would likely prove the most useful for assessing the degree of mixing in this approach. Larval/YOY fish should be sampled for genetic material (for SNP analyses) and otoliths (for elemental and/or isotopic analyses of the otolith core region). Subsequent samples of juveniles/sub-adults in temperate waters, and adults in tropical and sub-tropical waters, should then be surveyed for the same markers. Techniques such as examination of parasites or fatty acid profiles may be less appropriate in this instance, particularly in larval fish, as these individuals may not have had sufficient time for a distinct natal-area signature to develop in the fish, or the natal signature may be altered by the time subsequent sampling of older life history stages is conducted. Genetic and otolith elemental or isotopic signals observed in the juveniles/sub-adult and adult samples should be examined to re-classify fish back to their natal area of origin based on their natal profile (i.e. the signature evident in YOY fish on the spawning ground), for example via a mixed-stock analysis (see boxed text).

How to sample: For both options I and II (A and B) above, as best as possible, locations should be sampled at around the same time and over a short temporal period (i.e. within four weeks) in each successive year, to reduce the possibility that the same group of fish has moved between locations and thus is sampled on multiple occasions, and to ensure patterns between years are comparable. Sampling of adults during peak spawning, or larval/YOY in their natal areas, and subsequent of post-recruitment life history stages, should be repeated over multiple (e.g. three successive) years, to assess the temporal stability of the examined signal(s).

In both the WCPO and EPO, sampling of adult fish could be achieved by observers and dedicated sampling personnel on longline vessels operating between ~10–25°S. Sampling of juveniles/sub-adults could be achieved from commercial troll fisheries and potentially recreational fishers in Australian and New Zealand waters. As discussed above, sampling of larvae or YOY South Pacific albacore tuna, if deemed necessary, would require fisheries-independent sampling. Given the need for simultaneous, repeated sampling, this would be at high cost and effort. If sampling YOY fish, an additional challenge would be to ensure fish are as close to their natal areas as possible. Again, larval transport or movement models could be used to identify areas most likely to host high larval densities for a given natal area.

Question 4: Is there connectivity between reproductive populations of North Pacific and South Pacific albacore tuna?

Historically, the South Pacific albacore tuna population was considered to be distinct from that of the North Pacific. However, recent evidence, suggests that some gene flow may occur between these regions (Montes et al. 2012; Albaina et al. 2013). Relationships between these two putative populations should be able to be addressed using the design outlined above provided adequate

sampling locations across both the North Pacific and South Pacific are included. However, spawning times are reported to be different between the North Pacific population and the South Pacific population, with spawning in the North Pacific extending from March to September, and likely peaking between March and April (Chen et al. 2010). Accordingly, at least two sampling periods will be required in each year (i.e. one during the peak spawning period in each hemisphere), with both North Pacific and South Pacific areas sampled in each sampling period.

Mixed stock analysis for assessing natal origins and mixing of tropical tunas

One potentially viable approach for testing specific hypotheses on natal origins and the degree of mixing of sub-adult and adult fish is via a mixed stock analysis framework. The first step in a mixed stock analysis to determine natal origins of the four tuna species would be to sample larvae or fish as young as possible (so they are as close to their original spawning areas as possible) from as many spawning sites or nursery areas as can feasibility be conducted, to identify characteristic 'natal' profiles based on, for example, genetic profiles, chemical constituents of otoliths, or parasites). In an ideal world, this sampling should cover as many known areas of spawning as possible. If distinct natal profiles are identified, the second step is to sample sub-adult and adults in the fishery to re-classify these back to their natal origin based of their natal profile (Figure 1).

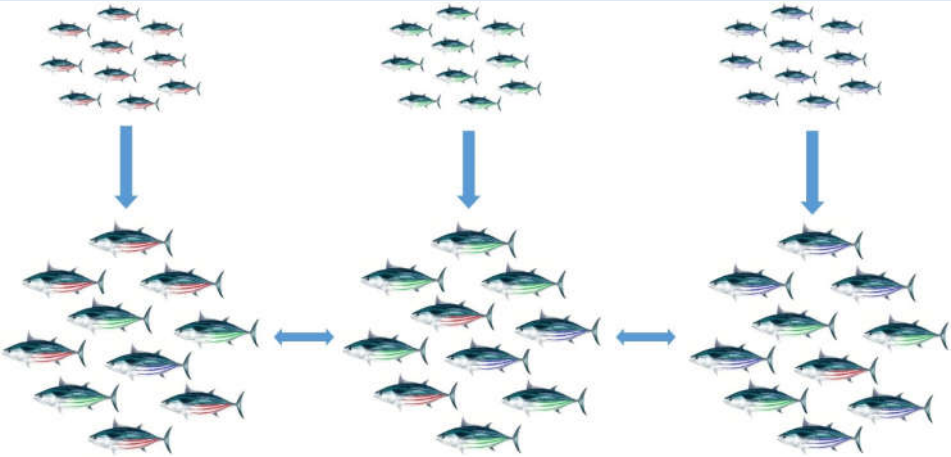


Figure 1. Theoretical depiction of a mixed-stock analyses in skipjack tuna. Here, juveniles from three nursey areas, and three mixed adult assemblages, have been surveyed for a hypothetical genetic marker influencing stripe colour, allowing an examination of natal origins and degree of mixing of adult fish.

For a marker to be used successfully in a mixed stock analysis, it must be i) uniquely representative of the spawning ground / nursery site, and ii) stable over the interval between natal characterisation and sub adult / adult mixing, and ideally for the fish's entire life (Lester 1990; Campana 1999). Modern molecular markers such as SNPs provide ideal candidates for use in a mixed-stock analysis because they are i) present in every individual, ii) not modified in the interval between natal characterisation and the mixing of adults, iii) relatively cost effective, meaning a large number of individuals can be screened, iv) logistically feasible to implement, v) most likely to be able to detect differentiation between discrete spawning groups, and iv) able to be used to prove additional insight, including provenance determination for chain-of-custody analyses, and determination of effective population sizes (Laconcha et al. 2015). Additionally, otolith chemistry and parasites have both been used successfully in mixed stock analyses to assess natal origins and relative contributions of nursery areas to adult assemblages (e.g. MacKenzie 1985; Rooker et al. 2008).

Conclusions

While current assessments typically assume single stocks of skipjack, yellowfin, bigeye and South Pacific albacore tunas within each of the WPCFC and IATTC convention areas, several lines of evidence reviewed here suggest the potential occurrence of multiple stocks within the Pacific Ocean basin at varying spatial scales. In order to better define the stock structure of skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific, and to better understand the underlying biological mechanisms by which observed spatial structuring occurs, key uncertainties surrounding spawning locations and behaviour (including the degree of fidelity to natal spawning grounds), and the origins and mixing of post-juvenile assemblages, and proportional contributions of spawning units to mixed fisheries assemblages, need be addressed. Emerging technologies, in particular modern molecular markers such as SNPs, combined with complementary approaches such as otolith microchemistry or parasites as biological tags, may prove useful for testing specific hypotheses regarding uncertainties around spatial structuring of reproductive units and proportional contributions of spawning units to fished populations, as well as providing a framework to answering questions beyond those relating to stock structure, such as provenance determination for chain of custody documentation. However, before embarking on a large, expensive sampling program, it is recommended that management strategy simulations, assessing various hypothetical scenarios of stock structure, be evaluated to determine whether an improved understanding of stock structure would result in improved management of stocks.

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