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Defining the stock structures of key commercial tunas in the Pacific Ocean II: Sampling considerations and future directions

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ABSTRACT

Delineating the stock structure of highly-mobile, wide-ranging fishes subject to exploitation is a challenging task, yet one that is fundamental to optimal fisheries management. A case in point are stocks of skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*) and albacore tuna (*Thunnus alalunga*) in the Pacific Ocean, which support important commercial, artisanal, subsistence, and recreational fisheries, and contribute roughly 70 % of global commercial tuna catches. Although some spatial and temporal structuring is recognised within these stocks, growing evidence from a range of approaches suggests that the stock structure of each tuna species is more complex than is currently assumed in both stock assessment and climate change models, and in management regimes. In a move towards improving understanding of the stock structure of skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific Ocean, an

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international workshop was held in Nouméa, New Caledonia, in October 2018 to review knowledge about their movement and stock structure in the region, define and discuss the main knowledge gaps and uncertainties concerning their stock structure, and develop biological sampling approaches to support the provision of this information. Here, we synthesise the discussions of this latter component. For each tuna species, we identify several general sampling considerations needed to reduce uncertainty, including i) the need for broadscale sampling in space, ideally covering each species' distribution, targeting adults in spawning condition and adopting a phased approach; ii) the need for temporally-repeated sampling of the same geographical areas to assess stability in observed patterns over time; iii) the need to resolve patterns in spatial dynamics, such as those resulting from movements associated with the seasonal extensions of poleward flowing currents, from underlying stock structure, iv) the importance of adopting a multidisciplinary approach to stock identification, and v) the need for careful planning of logistics and coordination of sampling efforts across agencies. Finally, we present potential sampling designs that could be adopted to help overcome uncertainties around the initial identification of stocks and the provenance, mixing and proportional contributions of individuals in harvested assemblages, as well as how these uncertainties could be accounted for in fisheries management via the use of management strategy evaluation.

1. Introduction

Tunas support extensive fisheries across the world's oceans (Brill and Hobday, 2017; FAO, 2018). In the Pacific Ocean, catches of four species – skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*), and albacore tuna (*Thunnus alalunga*) – support important industrial, artisanal, subsistence, and, in certain locations, recreational fisheries, and comprise over 90 % of industrial tuna catches from the region and approximately 70 % of the global commercial tuna catch (SPC-OFP, 2018). Nowhere are the benefits of these species more apparent than in the Pacific Islands region, where they make significant contributions to food security, employment opportunities and government revenue (Gillett, 2016; FFA, 2017; Bell et al., 2018).

Stock assessments for skipjack, yellowfin and bigeye tunas in the Pacific Ocean currently assume the occurrence of distinct Western and Central Pacific Ocean (WCPO) and Eastern Pacific Ocean (EPO) stocks, corresponding to the respective Convention Areas of the two tuna Regional Fisheries Management Organisations (tRFMOs) tasked with their management: the Western and Central Pacific Fisheries Commission (WCPFC) and the Inter-American Tropical Tuna Commission (IATTC) (Fig. 1). For albacore tuna, two separate populations are recognised: a North Pacific population and a South Pacific population, with the most recent stock assessment assuming a single stock in the South Pacific between 140 °E and 130 °W (Tremblay-Boyer et al., 2018). In each case, these splits reflect the historical development of fisheries management in the region rather than the biology and ecology of these species. There is, however, growing evidence that the spatial structure of populations of these four tunas in the Pacific Ocean may be more complex than currently assumed (Schaefer, 2009; Moore et al., this issue), and that a better understanding of each species' stock structure could improve the reliability of population dynamics models used to assess their status and inform management (Lewis, 1990; Kolody and Hoyle, 2015; Evans et al., 2016). An improved knowledge of tuna stock structure is also essential for predicting the potential for localised population depletions and their consequences, as well as for modelling the impacts of climate change on tuna distribution and abundance and developing appropriate adaptation strategies (Lehodey et al., 2017; Senina et al., 2018; SPC, 2019).

In a move towards improving understanding of the stock structure of skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific Ocean, an international expert workshop was held in Nouméa, New Caledonia, in October 2018. The workshop focused on these four tunas due to their importance in fishery catches throughout the Pacific, their overlap in habitats (particularly as adults), their collective management under the two tRFMOs in the Pacific, and their importance to Pacific Island countries and territories (PICTs) (Moore et al., this issue). The objectives of the workshop were to: 1) review the current understanding of movement and stock structure of these four tuna species in the Pacific Ocean, and define and discuss the main related knowledge

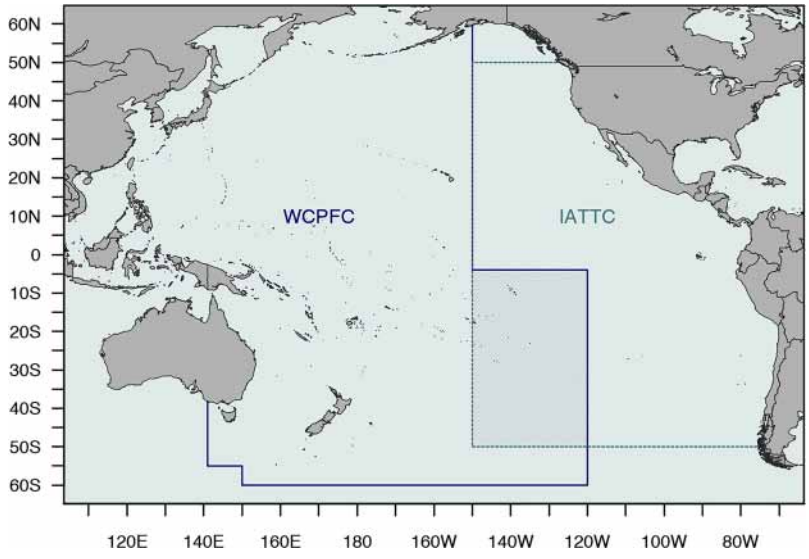

Fig. 1. Map of the Pacific Ocean showing the Western and Central Pacific Fisheries Commission (WCPFC) and Inter-American Tropical Tuna Commission (IATTC) Convention Areas. The overlap in management areas between the WCPFC and IATTC is shaded.

gaps and uncertainties; and 2) outline sampling considerations and approaches aimed at reducing these gaps and uncertainties. The workshop brought together fisheries scientists, population geneticists, ecologists, resource managers and other key stakeholders involved in monitoring, assessment and provision of management advice for tuna fisheries across the Pacific region.

Moore et al. (this issue) provide a synthesis of current knowledge and main uncertainties associated with the stock structure of skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific Ocean. Identified uncertainties related to: i) spawning dynamics; ii) the degree of spawning area fidelity and localised residency; iii) the provenance of individuals in, and proportional contributions of self-replenishing populations to, fishery catches within the Pacific Ocean; iv) linkages with adjacent 'stocks'; v) the effects of climate change on stock structure and proportional contributions of self-replenishing populations to fisheries; and vi) the implications of improved knowledge of tuna stock structure for stock assessment and climate change model assumptions and fisheries management.

Here, we provide a synthesis of the workshop discussions on the sampling considerations and approaches required to help improve understanding of the stock structure of the four tunas. Following Moore et al. (this issue), we consider a stock to represent a self-replenishing population. Under this working definition, a stock could be considered synonymous with a population, although it should be noted this is not always the case, with various definitions of stock canvassed in the literature (see Begg and Waldman, 1999; Cadrin, 2020 for examples). We first describe some of the potential scenarios by which tuna stocks may be structured in the Pacific Ocean and some of the general considerations around sampling, before outlining specific sampling strategies that could be adopted to improve understanding of stock structure, focusing these discussions on approaches to resolve uncertainties related to stock identification i.e., the initial identification of fisheries management units (self-replenishing populations in this context), and stock discrimination i.e., the proportion of individuals that each potential self-replenishing population contributes to harvests (following the terminology of Waldman, 2005). Tagging experiments have been extremely informative in elucidating tuna movements, behaviour, physiology and habitat use (e.g., Block et al., 2005; Schaefer et al., 2007; Schaefer and Fuller, 2010; Williams et al., 2015), and will continue to play an important role in future studies on the spatial structuring of the four species covered here. However, tagging was not discussed in detail at the workshop and thus we do not discuss tagging experiments here. Instead, we focus on the workshop's discussion of the considerations and strategies required to provide biological samples to better understand stock structure. Where relevant, we present what might be considered as 'perfect world' sampling strategies. However, we acknowledge that such scenarios rarely exist due to time, cost and logistical constraints and therefore also present alternate sampling strategies that could feasibly progress efforts towards addressing the uncertainties identified.

2. General sampling considerations

2.1. Defining research aims, objectives and key questions

Studies into the stock structure of exploited fishes require careful attention with respect to sampling design, planning and implementation. Studies should begin by defining the aims and objectives of the study, and a series of working questions or hypotheses to be tested (Abaunza et al., 2014), from which a corresponding set of experiments or sampling design could be developed. To help contextualise the problem to be solved, and facilitate discussion of appropriate sampling designs, the workshop considered various conceptual models of the stock structure of the four tunas, based on scenarios observed in marine fish species. These included: (1) panmixia, (2) isolation by distance, (3) regional residency of post-larval life history stages, including scenarios with extensive (3a) or limited (3b) larval movement, (4) spawning area fidelity, and (5) metapopulations, although it was acknowledged that alternatives exist. In addition, to further identify strategic areas and times where sampling should take place, a series of key research questions was developed for each of the four species (Table 1). The key conceptual models identified as relevant to the four tunas are defined below, along with a brief summary of the key evidence supporting or opposing each model. For a greater discussion on the current knowledge of the stock structures and spatial dynamics of the four tunas, the reader is referred to Moore et al. (this issue). It is noted that stock structure scenarios are likely to differ for each of the four tunas covered here, and that spatial structuring within a given species may be an intermediate between individual models, or show various models simultaneously within different geographic regions (Thomas and Kunin, 1999). As such, the intention here was not to attempt to classify a species into a particular model, but rather to consider the implications

Table 1
Key research questions for defining the stock structure of skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific Ocean developed by the workshop. EPO = Eastern Pacific Ocean, WCPO = Western and Central Pacific Ocean.

Species	Key research questions
Skipjack tuna	Is there panmixia in skipjack tuna across the equatorial Pacific Ocean?
	Is the occurrence of skipjack tuna in subtropical and temperate waters (e.g., Japan, New Zealand and other extremities of distribution) independent of the equatorial stock/stocks?
	Do skipjack tuna in the northern and southern regions of the EPO represent different stocks?
	To what degree do skipjack tuna from different self-replenishing populations, if present, mix in fisheries during non-spawning times?
Yellowfin tuna	Is there evidence for fidelity of mature yellowfin tuna to spawning areas?
	Do yellowfin tuna in the northern and southern regions of the EPO represent different stocks?
	Do yellowfin tuna from equatorial and sub-equatorial regions (e.g., Hawaii) of the WCPO represent different stocks?
	To what degree do fish from different self-replenishing populations, if present, mix in fisheries during non-spawning times?
	Is there a genetic basis for the different movement phenotypes observed from tagging data (i.e., residents, nomadic individuals)?
Bigeye tuna	Is there evidence for fidelity of mature bigeye tuna to spawning areas?
	Do bigeye tuna in the northern and southern regions of the EPO represent different stocks?
	Do bigeye tuna from equatorial and sub-equatorial regions (e.g., Hawaii) of the WCPO represent different stocks?
	To what degree do fish from different self-replenishing populations, if present, mix in fisheries during non-spawning times?
	Is there a genetic basis for the different movement phenotypes observed from tagging data (i.e., residents, individuals that undertake cyclical movements, nomadic individuals)?
Albacore tuna	Is there evidence for fidelity of mature South Pacific albacore tuna to spawning areas?
	Do fish in the eastern and western extents of the WCPFC assessment area constitute separate stocks?
	What is the stock relationship between fish to the east of the assessment area and within the assessment area?
	To what degree do fish from different self-replenishing populations, if present, mix in the fisheries during non-spawning times?
	Is there connectivity between North Pacific and South Pacific albacore tuna populations?

for sampling design, including selection of methodological approaches to use and the resulting patterns that might be anticipated under each model (see Section 2.5).

2.1.1. Panmixia

A panmictic population is one where all individuals involved in breeding are potential partners. This assumes that there are no mating restrictions within the population, such that all recombination is possible, i.e., reproduction between two individuals is not influenced by any environmental, geographical, hereditary, or social interaction. Previous genetic studies have generally ruled out Pacific-wide panmixia for yellowfin and South Pacific albacore tunas (Takagi et al., 2001; Montes et al., 2012; Grewe et al., 2015). For skipjack and bigeye tunas, the picture is a little less clear, with contrasting results observed between genetic studies (in the case of skipjack tuna), or weak evidence of structuring (in the case of bigeye tuna), and no comprehensive assessments utilising modern next-generation sequencing (NGS) approaches conducted on these species in the Pacific Ocean to date (see Moore et al., this issue).

2.1.2. Isolation by distance

This describes the process of increasing genetic differentiation correlated with increasing distance i.e., a continuous stock with exchange of genes among individuals in close proximity, although it should be noted that distance is not always synonymous with geographical distance (e.g., Reeb et al., 2000). As noted by Moore et al., (this issue), isolation by distance may be a highly plausible hypothesis for each of the fours tunas covered here. Richardson (1983) proposed an isolation by distance model for skipjack tuna in the Pacific Ocean based on spatial clines in enzyme allele frequencies, with the average radius of a genetic neighbourhood in the order of ~1080 nautical miles (nmi). Fujino (1996) similarly concluded that skipjack tuna were structured according to an isolation by distance model. Single nucleotide polymorphism (SNP) markers indicate a cline in genetic structure in bigeye tuna, and to a lesser extent, in yellowfin tuna, across sampling locations in the Indian and far western Pacific Oceans, indicative of isolation by distance (Proctor et al., 2019). Tagging data for bigeye tuna also suggests intermingling of western Pacific Ocean (WPO) 'stocks' and central Pacific Ocean (CPO) 'stocks' on either side of 180°, and of CPO and EPO 'stocks' on either side of 120 °W (Schaefer et al., 2015), consistent with isolation by distance.

2.1.3. Regional residency

Regional residency describes the existence of relatively stable, self-contained populations that exhibit minimal mixing with other populations across space, over time and through ontogeny. Depending on the level of exchange between regions, regional residency may result in a range of population structures. Under scenarios with limited or no exchange between adjacent groups, populations may represent independent, or 'closed', units, with any dispersal among them being so trivial as to have little influence on their dynamics. As noted by Moore et al. (this issue), given their largely continuous distributions in tropical waters evident from fishery data, and observations of individuals undertaking large-scale movement from tagging studies, the occurrence of fully discrete, closed populations of each of the four tunas in the WCPO and EPO is unlikely, at least without some additional structuring mechanism (e.g., fidelity to spawning areas, as discussed below). In the event that individuals reproduce with their nearest neighbours and overlap in their spatial distribution, regional residency may result in isolation by distance. Under a scenario of dispersal and mixing among largely resident populations, regional residency may tend towards metapopulation dynamics (see below).

2.1.4. Spawning area fidelity

Spawning area fidelity describes a scenario where fish spawn in the same area throughout their lives. This may be achieved by (i) fish undertaking restricted movements and thus maintaining close proximity to specific spawning areas, or (ii) fish dispersing widely during non-spawning periods and then returning to the same area to spawn (i.e., natal homing). The latter scenario is largely characteristic of bluefin tunas, with spawning area fidelity observed in southern bluefin tuna, *Thunnus maccoyii*, where adults forage across temperate latitudes and migrate to a single spawning ground in the tropical eastern Indian Ocean (Evans et al., 2012). At least partial fidelity to two main spawning grounds – the Gulf of Mexico and Mediterranean Sea – has been reported for Atlantic bluefin tuna, *Thunnus thynnus*, from tagging (Block et al., 2005), otolith chemistry (Rooker et al., 2014) and genetic (Rodríguez-Ezpeleta et al., 2019) data. Given tagging data generally suggest the majority of individual skipjack, yellowfin, and bigeye tunas undertake limited movements, fidelity to spawning areas, if it occurs, may more likely be associated with scenario (i) above, or potentially a combination of behaviours. Gunn et al. (2005) suggested that the cyclical movement observed for individual bigeye tuna in the northwest Coral Sea may be linked in part to movements from spawning sites and into areas of the Coral Sea and western Pacific Ocean at the completion of spawning. Similar cyclical movements have also been observed in an individual bigeye tuna tagged in the EPO (Schaefer and Fuller, 2010), although the cause of these movements is unknown.

2.1.5. Metapopulation(s)

This describes a series of population units with a degree of connectivity among them, maintained either through advection of eggs or larvae, or movement of post-larval life history stages (juveniles and/or adults). Under a metapopulation structure, rates of exchange among population units are sufficient to allow demographic connections to be conserved, yet low enough as to not impede the evolution of local population dynamics (Kritzer and Sale, 2004; Sale et al., 2006, and references therein). This may result in variation in demographic parameters such as growth rates, maturity profiles or spawning dynamics among units. On the basis of patterns in genetics, otolith chemistry and parasite assemblages, Buckworth et al. (2007) proposed a metapopulation structure for the confamilial narrow barred Spanish mackerel, *Scomberomorus commerson*, in the waters off northern and western Australia, with largely resident adult assemblages linked by larval dispersal. Although tagging data suggest the horizontal movements of individual skipjack, yellowfin, bigeye and South Pacific albacore tunas are relatively limited, a small, though potentially non-trivial, proportion of individuals are considered to undertake long-range movements (Moore et al., this issue). Assuming these individuals spawn and successfully reproduce over the course of these movements, the combination of such displacements and regional residency of most individuals may be sufficient to result in a metapopulation structure.

2.2. Sampling in space and time

Adequate biological sampling in space and time is paramount to both stock identification and stock discrimination. Ideally, sampling should cover the entire distributional range of a species as well as temporal periods that might result in any variability (Ward, 2000). For species with broad geographic distributions such as the four tunas covered here, this represents a significant challenge because it necessitates a significant and coordinated sampling effort across the broad spatial scales at which these species occur. Adopting a stepwise or phased approach to sampling could facilitate this process. Phased sampling has been a feature of several studies investigating the stock structure of broadly distributed species (e.g., Buckworth et al., 2007; Abaunza et al., 2008; Moore et al., 2012; Welch et al., 2015). One approach would be to conduct sampling across broad spatial scales, targeting the geographical extremities of each species' distribution, as well as other key areas such as boundaries of management jurisdictions, in the first instance, followed by progressively finer-resolution sampling across the region. Finer-scale sampling could be informed by existing

studies or from the results obtained from initial sampling efforts.

Stability of differences among stocks over time, and thus in stock structure itself, is a fundamental criterion when identifying stocks (Fabrizio, 2005). Accordingly, sampling designs investigating stock structure should involve repeated temporal sampling of the same geographical areas (Ward, 2000). For skipjack, yellowfin, bigeye and South Pacific albacore tunas, temporally-repeated sampling over annual timescales is also essential for understanding how large-scale regional and global processes, such as the El Niño-Southern Oscillation (ENSO), affect the movement of individuals and subsequent stock structure. Tagging and fishery catch data suggest that the distribution of skipjack tuna in the Pacific Ocean varies with ENSO patterns, with a shift in the species' core distribution to the central and eastern Pacific Ocean under El Niño conditions (Lehodey et al., 1997). The effect of this potential change in distribution on underlying stock structure is a key unknown, particularly given an increase in the frequency of extreme El Niño and La Nina events has been predicted as a result of climate change (Cai et al., 2014, 2015; Wang et al., 2017). Temporally-repeated sampling would also contribute to alleviating biases such as the Allendorf-Phelps effect, whereby genetic results are influenced by the analysis of samples from the progeny of too few breeding adults (Allendorf and Phelps, 1981).

Consideration should also be given to variability on intra-annual timescales. To minimise any potential intra-annual effects, effort should be made to ensure individual sampling events across different areas occur over as short a time window as possible. This may be challenging, however, when targeting individuals in spawning condition (see below), given that spawning within a species can vary in time and space, even in equatorial waters, where spawning in skipjack, yellowfin and bigeye tunas is generally considered to occur year-round (e.g., Suzuki et al., 1978).

Migratory behaviours constitute an additional spatio-temporal component requiring particular consideration in studies of the stock structure of pelagic species such as tunas. Of the four tunas covered here, only albacore tuna is considered to be truly 'migratory', with individuals moving between specific feeding and spawning areas (Langley, 2006; Farley et al., 2013, 2014). For skipjack, yellowfin and bigeye tunas, consideration should be given to poleward extensions in distribution facilitated by seasonal latitudinal warming of sea surface temperatures (Sund et al., 1981; Blackburn and Serventy, 1981; Kiyofuji et al., 2019). Identifying the self-replenishing populations that individuals undertaking such movements have originated from and decoupling such spatial dynamics from underlying stock structure will be critical in resolving spatial structuring.

2.3. Tissues to collect and techniques to use

Approaches for delineating fish stock structure have advanced considerably in recent years and include examination of genetic markers, biochemical markers in fish otoliths or muscle, parasite assemblages, demographic parameters, otolith shape and morphometric and meristic data, as well as conventional and electronic tagging approaches (Begg and Waldman, 1999; Welch et al., 2015; see also Moore et al., this issue, for an overview of studies and approaches used for the four tunas covered here). In practice, these approaches typically provide information on movement and connectivity, from which stock structure is inferred (Begg and Waldman, 1999). Each approach is informative at different spatial and temporal scales. For example, genetic approaches have the potential to provide information about rates of mixing of fish from different regions within their lifetimes, as well as evolutionary patterns of gene flow over inter-generational timescales. Otolith chemistry and parasite assemblages, by comparison, are directly influenced by environmental factors a fish experiences as well as intrinsic factors (e.g., physiology, metabolism, growth), and so reflect processes occurring within an individual fish's lifetime (Grammer et al., 2017; Taillebois et al., 2017; Reis-Santos et al., 2018a, b).

Methodological advancements in genetic approaches in recent years have greatly increased their potential to resolve patterns of stock structure. In the last decade, the development of high-throughput NGS technology has allowed for more rapid sequencing of DNA at lower cost (Cuéllar-Pinzón et al., 2016). In particular, this technology has facilitated the identification of SNPs. By allowing for genome-wide scans, NGS approaches provide a better representation of the genome and facilitate the identification of SNP loci that are potentially under selection (so-called outlier loci). Use of such loci can increase the power to discriminate between weakly differentiated populations, by disentangling neutral evolutionary processes such as genetic drift from those influenced by selection potentially resulting in local adaptation (Corander et al., 2013; Grewe et al., 2015; Pecoraro et al., 2017). This technology has also facilitated the development of close-kin mark-recapture approaches (e.g., Bravington et al., 2016), which allow for the estimation of the population size of particular life history stages based on the likelihood of detecting parent-offspring pairs. However, these approaches require significantly more sampling than that required for the identification of stocks.

A key advantage of otolith chemistry-based approaches is their ability to provide information at selected points of time throughout a fish's life. Otoliths contain life-long, individual-level time series of chemical markers and morphological traits, and can provide valuable insights into contemporary connectivity and rates of mixing among stocks (Macdonald et al., 2013; Rooker et al., 2016). The development and continued advancement of probe-based analytical tools such as laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS), or nanoscale secondary ion mass spectrometry (NanoSIMS), allows precise targeting of specific regions within the otolith. This can include, for example, material accreted during early life (otolith core), just prior to capture (otolith edge), or encompassing the full life-history of the fish (transect from otolith core to edge), generating data that may help disentangle individual spatial dynamics and diffusive movements from underlying stock structure. Research into the assimilation of nitrogen stable isotope ratios (i.e., $\delta^{15}N$) into the organic matrix of fish otoliths has revealed strong potential for tracking trophic position and dietary changes (Rowell et al., 2010; Grønkjær et al., 2013), including over time scales as low as days (Shiao et al., 2018). Analyses of $\delta^{15}N$ and other otolith chemical markers (e.g., trace elements, $\delta^{13}C$, $\delta^{18}O$) may provide an exciting opportunity to trace movements between environments where availability of prey and ambient conditions differ, and to address open questions such as whether skipjack tuna captured in subtropical and temperate waters are independent of the equatorial stock (Table 1).

Parasites have been used to elucidate movements and stock structure in a range of fishes, including tunas (Lester et al., 1985; Jones, 1991; Lester and Moore, 2015; Moore et al., 2019). Investigations of parasite assemblages have been used to resolve recent, short-term movements, from more long-term movements, including movements from tropical to temperate waters (Lester et al., 1985). The principle of the approach is that fish that have resided in a similar environment or share a common history should have a similar parasite fauna. Where parasite faunas between groups of fish are different, the history of those fish 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 providing information on long-term location history (Lester and Moore, 2015).

Examination of stable isotope ratios in muscle tissue has also provided information on short-term patterns of residency and movement in tunas (e.g., Houssard et al., 2017), and may further help identify fine-scale movement behaviours, particularly between environments where prey and ambient conditions differ. Variability in life history parameters, particularly those associated with age, growth and reproduction, and morphological and meristic characteristics, have also been used to provide insights into the spatial structure of tunas, and the

presence of geographic and/or reproductive isolation (e.g., Schaefer, 1992; Schaefer, 2009). It is well recognised, however, that as each technique outlined above considers different aspects of a fish's evolutionary or ecological history, the choice of individual approaches depends on the specific research and management questions under consideration (Begg and Waldman, 1999).

An increasing number of studies investigating stock structure have employed a multidisciplinary approach, involving two or more complementary techniques (e.g., Buckworth et al., 2007; Abaunza et al., 2008; Welch et al., 2015; Marengo et al., 2017; Taillebois et al., 2017; Barton et al., 2018; Proctor et al., 2019). Multidisciplinary approaches are now considered 'best-practice' because they are regarded as being more effective in determining stock structure than any one technique used in isolation, in that they provide greater confidence in the results of individual techniques where consistent results are obtained (i.e., a weight of evidence approach), and allow the discrepancies of individual methods to be resolved (Begg and Waldman, 1999; Cadrin et al., 2014; Welch et al., 2015). Ideally, techniques should be applied to samples derived from the same fish specimen, which can facilitate the interpretation of the results and comparison of the performance of the individual techniques (Waldman et al., 1997). The use of a multidisciplinary approach is particularly pertinent for species with complex stock identities (Begg and Waldman, 1999), such as are likely for the four tunas covered here, and should thus form the basis for any study into their stock structure.

Studies of biological processes on wide-ranging, broadly-distributed fish species such as tuna are often extremely costly in terms of time, effort and resources, and thus an attempt should be made to ensure that the benefits of sampling are maximised. Collecting as many tissues as possible also creates the potential to use stored tissues for the development and application of new techniques in the future. Accordingly, consideration should be given to collecting a broad range of material from each sampled fish, including material that is not of direct relevance to addressing stock identification questions using current techniques (see Table 2 for examples). Ensuring collected samples are catalogued and stored in regional repositories to facilitate current and future access will be critical.

2.4. Sample sizes

Consideration of the number of individuals to sample and their distribution through space and time is of critical importance in studies examining the stock structure of fish (Abaunza et al., 2014). Inadequate sample sizes from individual spatio-temporal sampling strata (i.e., Location A in Time 1) may yield results that are unrepresentative of the larger population, potentially leading to false-positives (i.e., a Type I error) or precluding the detection of differences between units where they occur (i.e., a Type II error). On the other hand, excessive sample sizes may prevent additional sampling over time and/or space due to budget limitations.

Determination of appropriate sample sizes for investigating stock structure is largely considered an iterative process that should be evaluated as a project evolves through analytical procedures such as power analysis (Abaunza et al., 2008, 2014). Nevertheless, some guidance can be drawn from previous studies. For genetic approaches, a number of studies and recent simulations suggest that around 40–60 samples is generally sufficient to detect differences between sampling strata should they occur (Grewe et al., 1993; Abaunza et al., 2014; Proctor et al., 2019). Similarly, for otolith chemistry and parasite markers, previous studies have generally targeted $\geq$ 50 fish per stratum (e.g., Buckworth et al., 2007; Abaunza et al., 2008; Proctor et al., 2019), although actual sample sizes required depend on the degree of variation among strata. However, very few published studies adequately justify the sample sizes used, by including, for example, analyses of prospective power or of the precision of population estimates (Abaunza et al., 2014).

Given that such sampling constitutes a stratified sampling design, additional factors to consider are potential biases associated with uneven distributions of sexes within samples, and the use of analytical approaches that account for the non-random nature of samples. Samples should reflect equal proportions of both sexes to account for the potential for sex-biased behaviours, such as differences in sex ratios at certain locations. Analytical approaches need to be robust to potential within-strata biases that might be generated through the use of too few sample numbers (and in the case of genetic approaches, too few markers). As a consequence, both the approach adopted and the appropriate number of samples should be carefully considered when identifying analytical approaches to investigating population structure (Särndal et al., 1992). Where adequate numbers of samples are not available resampling approaches may need to be considered. It would be prudent, where possible, to over-sample within an individual spatio-temporal strata and then select which individual fish to analyse, rather than under-sample. Accordingly, and irrespective of whether adults or young of the year (YOY) fish are sampled on spawning grounds/natal

Table 2
Types of biological tissues commonly sampled in stock structure studies, and examples of their application in stock structure and non-stock structure related investigations.

Tissue	Application in stock structure studies	Examples of other applications
Muscle	Genetic/genomic approaches e.g., examination of mitochondrial DNA (mtDNA), single nucleotide polymorphism (SNP) markers; Medium-term residency patterns via analyses of stable isotopes (e.g., $\delta^{15}N$), methylmercury and other organometallic toxins.	Species and sex identification, assessment of speciation and phylogeny; Development of SNP-based origin traceability tools; Investigations of organometallic toxins and other contaminants e.g., methylmercury, micro-/nano-plastics for public health issues; Studies of trophic positioning (in space and time).
Fin clips	Genetic/genomic approaches e.g., examination of mtDNA, SNPs.	Species and sex identification, assessment of speciation and phylogeny.
Otoliths	Analyses of chemical constituents; Shape analyses; Examination of growth rates by strata.	Age and growth estimations; Dietary studies of predators.
Gonads	Identification of sex and reproductive state; Examination of sex ratio by strata; Examination of reproductive parameters by strata.	Estimation of reproductive parameters (e.g., maturity, timing of spawning, fecundity).
Stomachs	Examination of parasite assemblages.	Dietary studies, including those of pollutants (e.g., plastics).
Gill rakers	Examination of parasite assemblages; Gill raker counts (meristic analyses).	Species identification.
Liver and blood	Short-term movement/residency patterns via analyses of stable isotopes (e.g., $\delta^{15}N$), methylmercury and other organometallic toxins; Endocrine profiling to assess differences in maturity and timing of spawning by strata.	Investigations of organometallic toxins and other contaminants e.g., methylmercury, micro-/nano-plastics; Studies of trophic positioning (in space and time); Endocrine profiling to assess maturity and reproductive status.
Dorsal spines	Analyses of chemical constituents.	Ageing.

areas (see Section 3.1), based on current information available, for purposes of stock identification it is recommended that a sample size of at least 50–100 fish be collected per spatio-temporal stratum. Larger sample sizes may be required for stock discrimination, depending on the approach used (see Section 3.2).

The number of samples to collect per sampling event may also require careful consideration in stock structure studies, particularly if sampling individuals that might demonstrate social cohesion through time, such as schooling in skipjack tuna, or juvenile yellowfin and bigeye tunas. The degree of cohesion among schooling individuals is largely unknown for each of the four tunas, with contrasting results reported in the literature (Moore et al., this issue). Where strong cohesion might occur, sampling all of the required individuals per spatio-temporal stratum from a single sampling event, such as a fishing set, or from even a small number of sampling events, may not provide samples that are representative of the overall stock. In contrast, sampling too few individuals from individual sampling events may lengthen the period required to obtain appropriate sample sizes and may result in sampling targets not being met, particularly in locations where access to fish is variable due to seasonal limitations. Exploring numbers of samples required via power analyses may assist in identifying the number of fish that should be sampled per event.

2.5. Sampling of actively spawning fish from spawning areas

One of the fundamental aims in any sampling design for stock identification, or the identification of self-replenishing populations, is to obtain samples of fish in spawning condition from those areas in which spawning occurs, when mixing between putative stocks is likely to be minimal (Hauser and Ward, 1998; Begg, 2005; Cadrin, 2005). The first step in doing so, however, is to identify any key spawning areas (i.e., those areas characterised by a concentration of either adults that are actively releasing eggs and sperm, or by an abundance of eggs or larvae) and times when spawning occurs, so that sampling can be targeted accordingly. For skipjack, yellowfin, bigeye and South Pacific albacore tunas, spawning is generally considered to take place in waters with sea surface temperatures (SSTs) of > 24 °C (Nishikawa et al., 1985; Schaefer, 1998, 2001; Itano, 2000; Schaefer et al., 2005; Farley et al., 2013; Schaefer and Fuller, 2019). If SST alone is used to predict spawning, this would result in spawning occurring across large regions of the Pacific Ocean where and whenever temperatures meet this condition. Several authors, however, posit that actual spawning areas for tunas may be more spatially and temporally restricted than this (Reglero et al., 2014; Muhling et al., 2017), and several temporally-consistent spawning 'hot spots' have been identified for yellowfin and bigeye tunas (e.g., McPherson, 1988, 1991; Gunn et al., 2002; Servidad-Bacordo et al., 2012). Although areas where, and times when, actively spawning tuna are already known to occur could be sampled as a priority, several additional sources of data could be examined to provide further guidance on the spatio-temporal dynamics of spawning in each of the four tunas to prioritise sampling areas and times. These include: 1) examining fisheries observer data for reports of 'running ripe' tuna from fleets that target adults; 2) identifying aggregations of mature-sized tuna from catch-per-unit-effort (CPUE) and length-frequency data from datasets first filtered for known constraints such as SST; 3) histological examination of previously collected gonad material, such as existing collections within the WCPFC Tuna Tissue Bank (www.spc.int/ofp/PacificSpecimenBank; SPC-OFP, 2019); 4) examining stomach content data of predators to identify areas with high occurrence of ingestion of larval or early juvenile tunas; and 5) interrogation of movement and dispersal models such as the Spatial Ecosystem and Population Dynamics Model (SEAPODYM; Lehodey et al., 2008) or the Individual-based Kinesis, Advection and Movement of Ocean Animals model (Ikamoana; Scutt Phillips et al., 2018) for time-resolved predictions of areas of high larval densities.

The size of individual sampling areas (i.e., spatial strata) also requires consideration when targeting fish in spawning condition for stock identification. If spatial strata are too large, there may be the potential for sampling multiple stocks within the same strata at the same time, precluding the detection of fine-scale spatial structure if samples are grouped together for analysis (Anderson et al., 2019). Conversely, if spatial strata are too small, sampling opportunities within a given stratum may be limited. This might necessitate a substantial increase in sampling time and effort in order to obtain sufficient samples, increasing costs and logistical challenges. The spatial strata should be defined based on the biology and life history of the species in question, including known movement patterns and/or the extent of spawning areas, the habitat available, and the management questions being addressed. For each of the tunas covered here, spawning is considered to occur over wide geographical areas, even where spawning occurs away from tropical waters (e.g., McPherson, 1991; Farley et al., 2013; Schaefer and Fuller, 2019). Accordingly, sampling areas for skipjack, yellowfin, bigeye or South Pacific albacore tunas could afford to be relatively large (e.g., at the scale of areas, such as the northern Coral Sea), at least in the first instance, and should be reviewed after an initial phase of sampling.

For each of the candidate conceptual stock structure models described in Section 2.1, consideration was given by the workshop as to how patterns in the results of three approaches commonly used in synergy to investigate stock structure might manifest between fish in spawning condition sampled from distinct spatial strata with differing local environmental conditions. The three approaches considered were i) genetic markers such as SNPs, ii) otolith chemistry, including analyses of both otolith core and edge material, and iii) parasites, including short-term and long-term markers. Under a panmictic population scenario, genetic, otolith core chemistry and long-lived parasite markers of adult fish sampled from different spatial strata would appear largely homogenous, although some differentiation may be evident in otolith edge chemistry or short-lived parasites, reflecting the local conditions experienced by the fish prior to capture (Table 3). Under an isolation by distance model, a gradual cline in examined signals might be expected, with neighbouring groups appearing most similar with respect to genetic, otolith and parasite markers, and fish separated by the greatest distance appearing least similar (Table 3). The occurrence of resident juvenile and adult assemblages would be expected to show large differences in otolith edge chemistry and parasite faunas between areas. However, the level of genetic variation and patterns in otolith core chemistry would depend on the extent of larval dispersal. Under extensive larval dispersal, few differences between adjacent groups could be expected. Conversely, if larval dispersal was limited, greater differences in these markers could be expected (Table 3).

2.6. Logistics, operation and coordination

Successful stock structure studies can only be achieved if the operational, logistical and organisational aspects of the sampling design are clearly defined (Abaunza et al., 2008). However, information on these aspects of individual stock structure studies is poorly documented in the scientific literature. Having clear guidelines regarding the operational, logistical and organisational components of the sampling design is particularly relevant for skipjack, yellowfin, bigeye and South Pacific albacore tunas, given that their broad geographical distributions span the jurisdictional boundaries of numerous nations, two tRFMO Convention Areas and the high seas. Sampling over a broad spatial area, with temporal replication, will require an intensive and coordinated effort, involving staff from many different agencies and nations, including PICTs, other WCPFC and IATTC members, co-operating non-members, regional scientific authorities, and academic institutions. The collection of such a large dataset, comprising tissues of many different types, will also require participation by a range of experts in the analysis of samples and resulting data.

To minimise the possibility of introducing artificial variation

Table 3
The predicted magnitude of between-strata differences in genetic, otolith chemistry and parasite markers (as examples) of actively spawning adult fish under hypothetical stock structure models considered for skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific Ocean.

Life history hypothesis	Genetics	Otolith chemistry		Parasite assemblages	
		Core	Edge	Short-term residency	Long-term residency
1. Broadscale panmixia: *Individuals move around to feed and spawn anywhere conditions are suitable, such that all individuals involved in spawning are potential partners*	Small	Small	Small-large, depending on movement rates and regional residency times of adults	Small-large, depending on movement rates and regional residency times of adults	Small
2. Isolation by distance: *Individuals (larvae, juveniles and adults) mix and spawn with nearest-neighbours*	Clinal: small (between nearest neighbours); large (at opposite ends of distribution)	Clinal: small (between nearest neighbours); large (at opposite ends of distribution)	Clinal: small (between nearest neighbours); large (at opposite ends of distribution)	Clinal: small (between nearest neighbours); large (at opposite ends of distribution)	Clinal: small (between nearest neighbours); large (at opposite ends of distribution)
3a. Regional residency, with significant larval dispersal among areas: *Individuals (juveniles and adults) move and spawn within local area*	Small	Small	Large	Large	Large
3b. Regional residency, with limited larval dispersal among areas: *Individuals (juveniles and adults) move around and spawn within local area*	Large	Large	Large	Large	Large
4. Spawning area fidelity: *Adults move widely to feed, but return to same area to spawn (i.e., natal homing scenario)*	Large	Large	Small-large, depending on movement rates and regional residency times of adults	Small-large, depending on movement rates and regional residency times of adults	Small
5. Metapopulation(s): *Largely resident juveniles and adults linked by periodic larval dispersal and/or movement and spawning of nomadic individuals*	Small	Large (high variance)	Large (high variance)	Large (high variance)	Large (high variance)

between samples as a result of variability in sample collection, handling, management and/or storage methods between sampling teams or organisations, consistent best-practice approaches should be employed. Protocols should be developed that clearly set out the objectives of the project, facilitate standardisation where possible, support the generation of useful metadata streams and provide team members with the tools they need for achieving a successful sampling programme. For sampling of tunas, this should include protocols for obtaining fish, species identification (particularly for juveniles of yellowfin and bigeye tunas which are difficult to distinguish morphologically), standardised approaches for collecting tissues (including methods for minimising risk of cross-contamination of samples), sample labelling, preserving and packaging, and metadata collection standards, as well as transport and logistical arrangements (including permitting). Special attention should be given to the sample storage methods and best practices should be developed to ensure that sample quality is maintained on the long-term. A centralised archive and sample management site, with adequate back-up facilities, is recommended to ensure that management of samples and their associated data is carried out effectively, particularly given the high cost, effort and risk involved with obtaining and transporting biological samples. However, with the collection of samples across large spatio-temporal scales, development of a distributed network of archives might be logistically more feasible. Under either scenario, the number of times samples are transported following collection, and the facilities they pass through, should be minimised (Abaunza et al., 2008). Ensuring a comprehensive data management system is in place for archiving and tracking samples across such a distributed network will be essential for supporting an effective sampling programme.

Once samples have been collected and transported to the coordination facility (or facilities), consideration should be given to the order in which samples are processed before they are sent to the appropriate laboratory (Abaunza et al., 2008). This is particularly important where processing of tissue for one stock identification approach may impact on the utility of the sample for another. For example, although paired otoliths (sagittae) should be collected from each fish sampled, where only one otolith is available, an image of the whole otolith should be taken for shape analysis before sectioning for ageing purposes if otolith shape is also to be used as a stock identification tool. Similarly, ageing should be completed before any destructive sampling of the otolith occurs for analysis of chemical constituents. Care should also be taken to ensure laboratory effects are minimised, such as through the selection of a single processing laboratory and the use of consistent equipment during processing.

Training should be provided for project personnel at all stages of the study. This should include the development of appropriate training material that covers theoretical modules, 'hands-on' guidelines and training for collection and handling of samples as well as methods for data collection standardisation. Similarly, opportunities should be sought to build capacity of fisheries officers and scientists from WCPFC and IATTC members and participating territories throughout the life of the project, including through regional training courses, attachments to scientific service providers, or formal courses with academic institutions.

3. Sampling strategies to improve understanding of Pacific tuna stock structure

3.1. Sampling strategies to improve understanding of stock identification

Stock identification, or the initial identification of fisheries management units (in this context, self-replenishing populations) within the distributional range of a species (Waldman, 2005), forms the basis of stock structure studies. For each of the four tunas covered here, the first task in addressing the question of how many self-replenishing populations exist would be to identify whether existing samples of actively spawning fish, or eggs, larvae or YOY individuals (as proxies for spawning adults) collected from

geographically separate spawning/natal areas and stored in repositories such as the WCPFC Tuna Tissue Bank, are sufficient and appropriate, with respect to the aforementioned considerations, to provide evidence for stock structure. If sufficient materials exist (i.e., muscle and otolith samples from a minimum of 50 adult fish in spawning condition, or eggs/larvae or YOY individuals, per natal area per year from locations spanning the longitudinal distribution of each species, as a starting point), they could be used to provide a preliminary examination of potential structuring within each species. If sufficient materials are lacking, this data-collation step will still provide critical information on the nature, scope and distribution of available biological samples, and directly inform how future sampling should be conducted and optimised to fill data gaps.

In the event that additional sampling is deemed necessary, a carefully considered and intensive sampling effort will be needed. The key components of a sampling strategy to determine whether the four tunas are structured into discrete, self-replenishing populations, are summarised below, and depicted in Fig. 2. The most direct, non-tagging based, approach for identifying self-replenishing populations involves identifying adult fish in spawning condition from different spatio-temporal strata and obtaining biological samples from these individuals (see Table 2). In recognising the potential for non-spawning fish from adjacent self-replenishing populations to occur within the spatial strata being sampled, gonads should be collected to validate the sex and spawning condition of each fish sampled, using both macroscopic and histological criteria, and only those fish actively spawning should be analysed. Several recent studies have demonstrated the utility of identifying fish sex using genomic approaches and reproductive state from steroid levels in blood plasma (e.g., Zupa et al., 2017; Koyama et al., 2019; Suda et al., 2019). Muscle tissue and blood could thus be collected to explore the feasibility of using these approaches to confirm sex and reproductive condition, respectively, in the four tunas. Where peak spawning occurs at the same time in adjacent strata in close geographic proximity, or displays little seasonality (such as for skipjack tuna in equatorial waters; Schaefer and Fuller, 2019), effort should be made to ensure samples are taken over the shortest time window possible to minimise temporal variability.

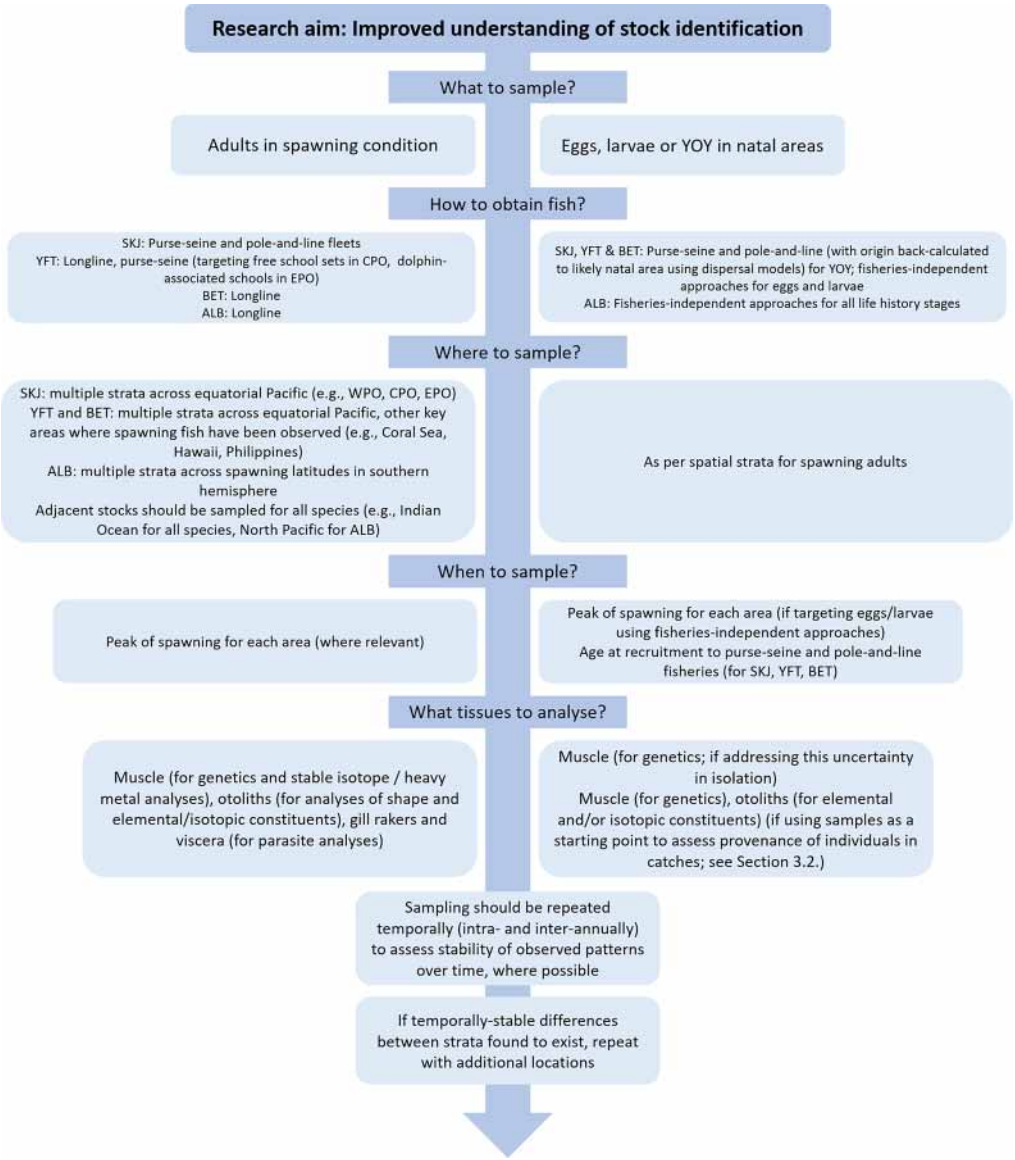

Fig. 2. Schematic diagram of a sampling design for assessing whether tuna in the Pacific Ocean are structured into self-replenishing populations (i.e., stock identification; Section 3.1). The figure depicts a proposed sampling strategy for broad-scale sampling across the Pacific Ocean (i.e., 'Phase I' in the accompanying text). YOY = young of the year, SKJ = skipjack tuna, YFT = yellowfin tuna, BET = bigeye tuna, ALB = South Pacific albacore tuna, WPO = western Pacific Ocean, CPO = central Pacific Ocean, EPO = eastern Pacific Ocean.

Where sampling of actively spawning fish is impractical, or yields insufficient samples, YOY individuals of each species could be sampled to use as indirect means of assessing the behaviour of spawning adults and structuring of self-replenishing populations (Puncher et al., 2018; Rodríguez-Ezpeleta et al., 2019). A key challenge in such cases would be to obtain fish as small/young as possible, to ensure that the location of sampling is close to or coincides with their natal area. This challenge applies particularly to South Pacific albacore tuna, which first recruit to fisheries well south of their spawning latitudes when they are around one year old (Langley, 2004; Langley and Hampton, 2005; Langley, 2006). While YOY skipjack, yellowfin and bigeye tunas may be sampled from purse-seine and pole-and-line vessels, length frequency data and daily age estimates suggest that yellowfin and bigeye tunas recruit to some of these fisheries when they are around 20–30 cm fork length (FL), at around three months old (McKechnie et al., 2017; Tremblay-Boyer et al., 2017; Proctor et al., 2019). Similarly, skipjack tuna typically recruit to purse-seine and pole-and-line fisheries in the WCPO at around 30 cm FL, when they are assumed to be ~6–7 months old (McKechnie et al., 2016). Accordingly, for all four tunas, individual fish may have moved from their natal areas in the time leading up to capture. Sampling from alternate gears, such as the gillnet, ringnet and handline fisheries of the far western equatorial region, or anchored FADs in coastal and nearshore waters of PICTs, may yield smaller/younger individual skipjack, yellowfin and bigeye tunas in some areas. Larval dispersal, particle tracking or active movement models could be used to back-calculate the origin of YOY in these fisheries to estimate putative areas of origin (e.g., Hernández et al., 2019). Fisheries-independent approaches, such as targeting eggs or larvae with plankton nets, may provide a potential alternative to obtain fish from natal areas, although this would be at high cost and effort given both the need for repeated sampling in time and space to obtain sufficient material for analysis, and the need for genetic approaches to reliably differentiate eggs and early stage larvae of tunas to species level (Nishikawa and Rimmer, 1987; Richards, 2006; Paine et al., 2008).

Irrespective of the life-history stage sampled, a phased approach to sample collection should be adopted, involving broad-scale, low-resolution sampling in the first instance (Phase I) that covers widely-spaced areas within the Pacific basin. For skipjack tuna, this could involve sampling of multiple strata spanning the spawning latitudes across the equatorial Pacific Ocean (i.e., strata within the far western, western, central and eastern Pacific Ocean areas, at least in the first instance), for example, to begin to address questions regarding panmixia across equatorial waters (Table 1). For yellowfin and bigeye tunas, this could similarly involve initial sampling of multiple strata across equatorial waters (i.e., strata within the far western, western, central and eastern Pacific Ocean areas) as well as areas where fish in spawning condition have been reported, such as the Philippines, Coral Sea, and Hawaii, at least in the first instance. For yellowfin tuna, repeated sampling of the locations examined by Grewe et al. (2015) will be important to confirm the temporal stability of the spatial patterns observed. For skipjack, yellowfin and bigeye tunas, it would be prudent to sample both northern and southern areas of the EPO, to address open questions regarding structuring between these regions (Table 1; Moore et al., this issue). For South Pacific albacore tuna, this could involve examination of adult fish in spawning condition from multiple strata distributed across spawning latitudes (10–25 °S), including within and adjacent to the WCPFC assessment area. Sampling of outlier areas (i.e., fish in spawning condition from adjacent areas within the Atlantic and Indian Oceans for all species, and from the north Pacific Ocean and southeast Pacific Ocean in the case of albacore tuna) should be conducted for each species to allow assessment of relationships with adjacent stocks. To assess the stability of observed patterns over time, spatial strata should be surveyed in two consecutive years at a minimum, and ideally longer and across different ENSO phases. Within individual strata, multiple sampling events could be conducted within the same year to test for intra-annual patterns and the potential for different stocks occurring in the same spatial strata at different times of the year, such as proposed for skipjack tuna in the waters off Hawaii and Japan (Fujino, 1996).

If temporally-consistent spatial structure is observed between areas after a first phase of broad-scale sampling, finer-scale spatial sampling targeting key areas of interest should be conducted in subsequent phases. As discussed above, the areas to be sampled in subsequent phases of sampling could be informed by previous studies or from the results obtained from initial sampling efforts (see Section 2.2). For example, for bigeye tuna, it would be prudent to include samples from additional areas beyond 10 °N and 10 °S. This would allow an assessment of the stock relationships between individuals in those areas with fish in equatorial waters (Table 1; Moore et al., this issue). Again, to assess the temporal stability of observed patterns, sampling of additional locations should be repeated in at least two consecutive years, although ideally longer, with multiple sampling events conducted over each ENSO phase.

Approaches to obtaining individual fish for biological sampling will need to vary between species and life history stages, given the differing nature of fleets and targeting practices. For each tuna species, sampling via fisheries observers or via the deployment of dedicated sampling personnel on commercial vessels provides one possible avenue for collecting samples, particularly given the need for rapid sampling within and between broadly distributed locations, and to ensure that associated catch information (including location, date, time and state of fish when landed) is available for sampled fish.

An alternative approach to obtaining fish may be to arrange for fishing companies and captains to store captured fish whole for later sampling (e.g., Williams et al., 2012). Targeted sampling of vessels fishing in specific areas and times identified as being important sampling strata could be facilitated through the vessel monitoring system (VMS) in effect in the WCPFC and IATTC Convention Areas (IATTC, 2014; WCPFC, 2014a). Cooperation from fishing companies and the crew of fishing vessels, as well as on-board observers, will be needed for this approach to be successful, including the collection of associated metadata such as the date, time and location of fishing. Sampling could then be done in port, either by trained national fisheries staff or staff from scientific agencies, or fish could be shipped to the sample management facility for processing. Dedicated research cruises could be undertaken to supplement sampling in particular areas and times of interest (Leroy et al., 2015).

With respect to specific fleets, sampling of adult skipjack tuna and immature yellowfin and bigeye tunas could be achieved using the above approaches from purse-seine and pole-and-line vessels. For adult yellowfin tuna, several avenues exist for obtaining samples, including via observers on purse-seine vessels targeting free school sets in the CPO and purse-seine catches associated with dolphins in the EPO, where typically larger individuals are landed (Minte-Vera et al., 2019), or via dedicated samplers on longline vessels that target adults across all regions. Sampling from deep handline vessels may be another viable for obtaining adult yellowfin tuna in Indonesia and the Philippines (BFAR, 2018). For adult bigeye tuna, sampling could be achieved via observers or dedicated sampling personnel on longline vessels. Sampling of adult South Pacific albacore tuna could be achieved via observers or dedicated sampling personnel on longline vessels operating between 10 °S and 25 °S during the peak spawning period (October and December; Farley et al., 2013). It should be noted, however, that observer coverage on longline vessels operating in the Pacific Ocean is currently low, typically ranging from 1 % to 4.5 % of total hooks set over most of the WCPFC Convention Area (Peatman et al., 2018), and thus significant

investment may be required to achieve sampling requirements if adopting this approach. As discussed above, fisheries-independent approaches are required to sample eggs, larvae or early YOY life history stages that have not yet recruited to the fisheries if sampling of actively spawning adults is impractical.

The choice of techniques to be used to identify stocks, and thus the tissues to be analysed from each sampled fish, will depend largely on the life history stage that is sampled in the first instance. Because genomic approaches provide the most direct evidence of self-sustaining populations, genetic material should be analysed as a priority from all sampled individuals. If adult fish in spawning condition are sampled, a range of additional biological material should be analysed, including muscle samples for stable isotope analyses, otoliths for chemical and shape analyses as well as ageing, and gill rakers and viscera for examination of parasites (see Table 2 and Section 2). Although non-genetic approaches such as analyses of the chemical constituents of otoliths and parasite assemblages do not provide direct evidence of gene flow, and hence the existence of self-replenishing populations *per se*, they could be used to validate patterns observed from genetic approaches in adults, *sensu* a multidisciplinary approach (Begg and Waldman, 1999). Collection of material in addition to that used for genetic analyses, in particular the chemical constituents of otoliths, would also be valuable for examining the provenance of individuals in, and proportion contributions of self-replenishing populations to, fishery catches (see Section 3.2.1). While muscle samples and fin clips have both been proven to be effective for use in genetic studies, we recommend muscle tissues be collected as a priority, particularly given their value in other analyses (Table 2). Moreover, fin clips can be of limited value if not collected properly, with a risk of collecting insufficient material for genetic analyses and greater potential for cross contamination between individuals. Gonads should be collected from individuals of each of the four tuna species as a priority to confirm spawning condition and the sex of samples using histology, which could potentially be validated through examination of sex steroid levels in blood plasma or via genomic approaches, respectively, should these approaches prove feasible for the four tunas.

Increased deployment of electronic tags in key spawning areas may provide an additional line of evidence for the presence of self-replenishing populations and the degree of spawning area fidelity of each tuna species, and help resolve and validate patterns in signals observed through other methods. This will require care to ensure spawning fish are effectively targeted for the deployment of these tags, and potential modifications to the standard gears and fishing methods currently used in tagging programmes for these species.

If sampling of adults is deemed impractical, and eggs, larvae or YOY fish are sampled as a proxy, it is likely that only genetic markers (e.g., SNPs) will be useful for investigating uncertainties relating to the number of self-replenishing populations. However, if the collected material is to be used as a starting point to also address stock discrimination (see Section 3.2), additional biological material, and in particular otoliths for chemical analysis, should be collected given their value in providing baseline signatures of natal areas in mixed-stock analyses (e.g., Rooker et al., 2016).

3.2. Sampling strategies to improve understanding of stock discrimination

Understanding the provenance of individuals in, and proportional contributions of self-replenishing populations to, harvests (i.e., stock discrimination; Waldman, 2005) is critical in the assessment and management of mixed-stock fisheries. For skipjack, yellowfin, bigeye and South Pacific albacore tunas, this is particularly important given that i) fishing mortality is unevenly distributed across the region, ii) there is the potential for fisheries to exploit individuals from several self-replenishing populations, if present, more-or-less simultaneously, iii) different self-replenishing populations, if present, may have differing levels of productivity, and iv) there is potential for local depletion, particularly for less productive stocks, if they are structured in such a way that they are subject to higher fishing mortality (Moore et al., this issue). Addressing these key features of populations requires an initial understanding of the number and locations of self-replenishing populations. This information will provide a starting point from which to evaluate the natal origins of new recruits to the fishery as well as the degree of mixing, and could be achieved using the design proposed in Section 3.1. For each species, mixing of juveniles/sub-adults and adults should be examined to determine if it varies with ontogenetic and/or environmental influences. Below, we present two potential options, both based around mixed-stock analysis designs, for determining the degree of mixing of juveniles/sub-adults, and non-spawning adults, of each species, depending on what life history stages are sampled initially for stock identification purposes (i.e., spawning adults or eggs, larvae or YOY individuals in spawning/natal areas) (Fig. 3). In both options, the collection of fish for sampling could be achieved using the approaches outlined in Section 3.1. Sampling locations could similarly be located at or adjacent to those locations sampled for the initial identification of stocks, at least in a Phase I, with additional areas of interest (e.g., areas of high catches not initially sampled) included in subsequent phases.

3.2.1. Options based on initial sampling of adults in spawning condition

If sampling of adults in spawning condition is conducted to assess how fish are structured during spawning, and temporally stable self-replenishing populations are found to exist, sampling of non-spawning fish should be conducted. Here, multiple sampling events of non-spawning fish could be conducted over an annual cycle, to assess how mixing varies throughout the year.

As with Section 3.1, the types of tissue to be analysed from each fish and choice of techniques to be used to assess the extent of mixing will depend largely on the life history stage being examined (see Fig. 3). For example, for assessing the extent of mixing of adult fish following spawning, the same type of material found to differentiate between spawning adults (see Fig. 2) should be examined. Material that does not provide evidence of variability between spawning adults from different strata would similarly be of limited value to discern mixing of fish during non-spawning periods. This approach would provide direct evidence of mixing of adults (i.e., tracking of fish from the spawning unit over time).

To assess the extent to which juvenile/sub-adult fish from different spawning units mix in the event that only adult fish are sampled during spawning, genetic markers such as SNPs could be examined. Screening of sampled juvenile/sub-adult individuals for the same genetic markers found to differentiate spawning adults would facilitate assignment to their likely reproductive unit of origin. Due to the lack of a direct baseline (resulting from a lack of sampling eggs, larvae or YOY fish on the natal grounds in this option), natal environmental signal-based techniques such as otolith chemistry may be less useful in this instance. This is largely because environmental signatures in juveniles/sub-adults (e.g., core chemistries of otoliths) may not necessarily reflect those of the adult fish from which they were derived, even if originating from the same general spawning area, due to inter-annual differences in environmental variables (in particular ambient chemistry, temperature and salinity) (Campana, 1999; Gillanders, 2002; Elsdon and Gillanders, 2004).

3.2.2. Options based on initial sampling of eggs, larvae or YOY individuals in spawning/natal areas

If sampling of eggs, larvae or YOY fish on their natal grounds was conducted, and clear, temporally stable, differences between natal areas were found using the sampling design proposed in Section 3.1,

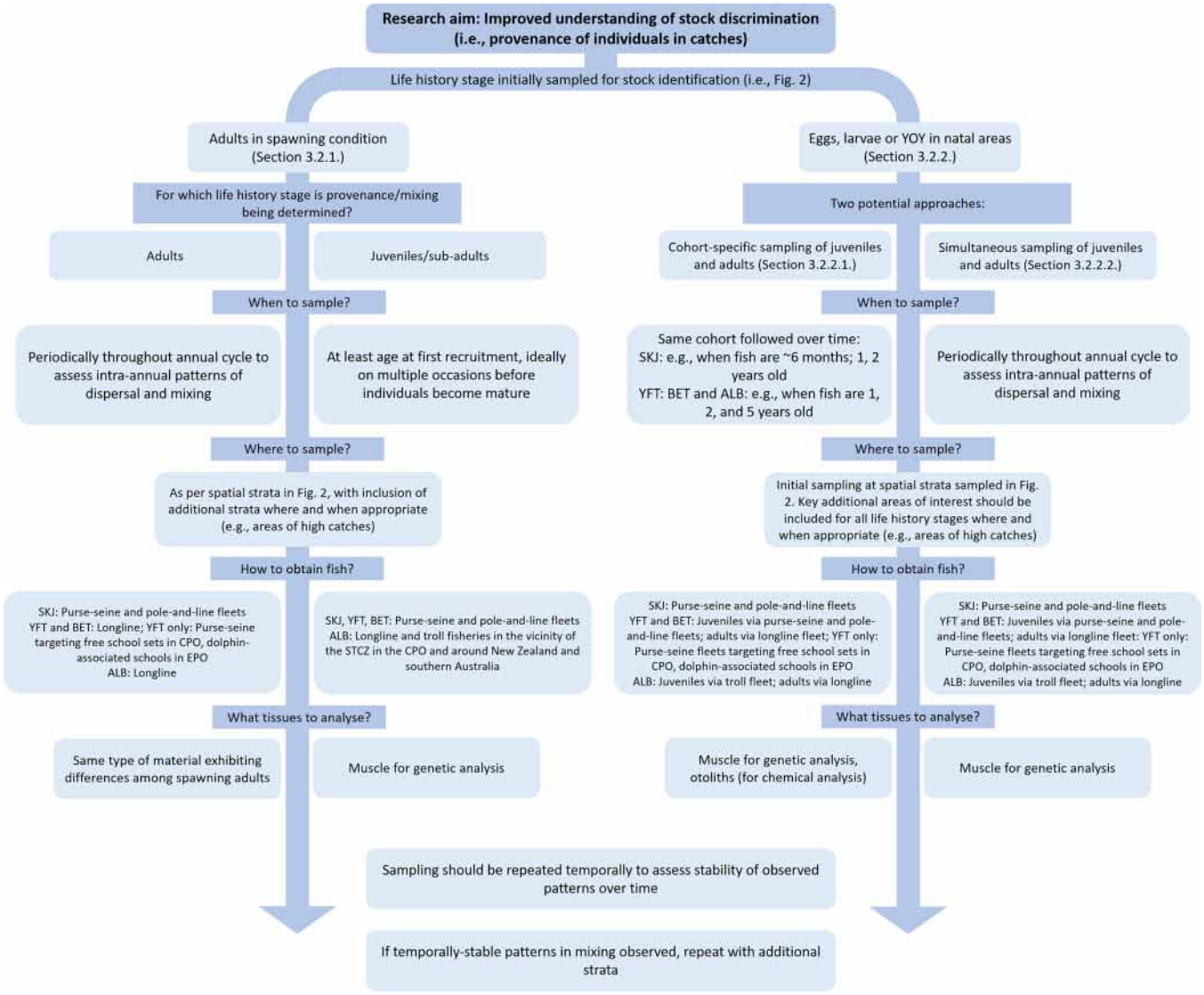

Fig. 3. Schematic diagram of a sampling design for assessing the provenance of individuals in, and proportional contributions of self-replenishing populations to, harvests (i.e., stock discrimination; see Section 3.2). The figure depicts a proposed sampling strategy for broad-scale sampling across the Pacific Ocean (i.e., 'Phase I' in the accompanying text). YOY = young of the year, SKJ = skipjack tuna, YFT = yellowfin tuna, BET = bigeye tuna, ALB = South Pacific albacore tuna, CPO = central Pacific Ocean, EPO = eastern Pacific Ocean, STCZ = subtropical convergence zone.

two potential approaches could be used to assess movement and mixing of juveniles and non-spawning adult fish:

3.2.2.1. Cohort-specific sampling of juveniles and adults. In this approach, the same cohort would be regularly sampled over time to assess movement and mixing as fish age and mature, similar to the design conducted for yellowfin and bigeye tunas by Rooker et al. (2016), albeit over larger spatial and temporal scales. For example, if larvae/YOY yellowfin tuna were initially sampled from different natal areas in Year 0, and distinct natal area signatures were found to exist, juveniles from the same cohort could be sampled the following year (i.e., Year 1) and again in Year 2 (i.e., when fish are around 1 and 2 years of age, respectively), while adults resulting from this cohort could be sampled in Year 5 (at five years of age), for example. As per Section 3.1, a range of tissues, including muscle tissue (for genetic analyses) and otoliths (for elemental and/or isotopic analyses of the otolith core region) could be analysed from each larval/YOY fish captured from putative natal areas. Subsequent samples of juveniles/sub-adults, and adults, should then be analysed for the same markers that have been used to identify differences between putative natal areas. Techniques that only provide information on short-term patterns of movement, such as examination of stable isotope signatures in muscle tissue or analysis of parasites considered to have short residence times in or on the fish, may be less appropriate because natal signatures may be altered by the time subsequent sampling of older life history stages is conducted. Results derived from analyses of the juvenile/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 and trace their subsequent mixing via a mixed-stock analysis. This approach would provide direct evidence of mixing across all life history stages, in that patterns of mixing are examined in the same cohort across time. A significant advantage of this approach is that multiple stock discrimination techniques could be used, increasing the likelihood of successfully assigning a fish to a particular stock and maximising the potential to trace patterns of movement and mixing through ontogeny (Begg and Waldman, 1999). Conversely, the requirement to identify particular cohorts would be a considerable challenge, necessitating the collection and subsequent examination of a large number of individuals to obtain sufficient samples for analysis.

3.2.2.2. Simultaneous sampling of juveniles and adults. Following an initial characterisation of the genetic signatures of eggs, larvae or YOY life history stages in putative natal areas, sampling of juveniles/sub-adults and adults within the same annual cycle could be conducted. As with Section 3.2.1, multiple sampling events could be conducted over an annual cycle to examine intra-annual patterns in dispersal and mixing. Genetic markers such as SNPs would provide an ideal tool for assessing movement and mixing in such cases. This approach would provide indirect evidence of mixing across all life history stages (in that patterns of mixing in one or multiple cohorts are inferred from another cohort). Again, due to the lack of a direct baseline (resulting from sampling different cohorts) and potential for inter-annual or inter-cohort variation, natal environmental signal-based techniques such as analyses of otolith chemistry or parasite faunas may be less useful in this instance.

3.3. Management strategy evaluation as a tool to identify the impact of incorrectly specified stock structure on fishery management

Increased knowledge about stock structure should ultimately affect the population dynamics models of tuna stocks that are used to inform management. As such, research should also be undertaken to assess the impact of uncertainty or mis-specification in the configuration of stock structures on the management of the four tuna species.

Management strategy evaluation (MSE) is widely considered to be the most appropriate way of assessing the robustness of management procedures to important sources of uncertainty (Butterworth et al., 2010; Punt et al., 2016). Rather than trying to find the single best assessment, the approach aims to identify the management procedure (or strategy) that performs best across a range of alternative biological and fishery scenarios. MSEs are currently under development for application in the WCPFC Convention Area for the four tunas covered here that will allow for pre-agreed decisions for management action to be tested for robustness to plausible hypotheses of environmentally-driven movement (WCPFC, 2014b; Scott et al., 2019a, 2019b), using operating models that assume a single stock. A similar MSE approach could be used to test the robustness of fisheries management to alternative stock structure scenarios.

MSEs can also be used to evaluate 'the value of information', i.e., the sources or types of uncertainty that are most influential to the performance of an assessment or management approach (Punt et al., 2016). In the case of skipjack, yellowfin, bigeye and South Pacific albacore tunas, an MSE simulation framework could be developed to assess how and under what conditions estimates of stock status are sensitive to a mis-specification of stock structure. Performed across the four tuna species covered here, this could inform the allocation of funding priorities if the estimated stock status and resulting management performance for some species are predicted to be more sensitive to stock structure definition than others.

Adapting an MSE framework to test alternative stock structure hypotheses would require the operating model to be sufficiently spatially and temporally resolved to represent the individual hypotheses, both in terms of the assumed population dynamics of the species and the spatio-temporal dynamics of the fisheries (Carruthers et al., 2016). To facilitate this process, a narrow set of plausible hypotheses regarding the stock structure of each tuna could be selected, informed by existing knowledge. These could be used within a preliminary MSE simulation framework, the results of which could help inform the design of staged sampling programmes to address those hypotheses and further refine plausible stock structure alternatives. Once further uncertainties about stock structure have been resolved, a more comprehensive MSE framework could be developed. This more comprehensive MSE would aim to find the management procedure most likely to achieve management objectives under key scenarios based on the remaining uncertainty about stock structure. Following development of the MSE simulation framework, scenarios for factors likely to be sensitive to spatial structuring should be explored, such as variation in fishing pressure among stocks on one hand, and variation in their intrinsic resilience to fishing on the other (e.g., Powers and Porch, 2004; Kell et al., 2009; Bastardie et al., 2016). Eventually, the data used to identify stock structure may be used for conditioning the operating model and, where appropriate, for weighting the model scenarios, although this would take considerable effort to develop.

A traditional MSE would aim to identify management procedures that are robust to alternative stock structure hypotheses, such that all plausible models considered to be realistic representations of stock structure dynamics would have to be included in the operating model. This objective would be challenging to implement on short to medium time-frames. The iterative approach we outline here, phasing instead an initial MSE aimed at assessing the sensitivity of population status to stock structure and inform research priorities, with, on a longer time-frame, a more comprehensive MSE once further knowledge on stock structure has been acquired, forms a promising avenue to ensure that the robustness of management procedures to alternative stock structures is appropriately tested.

4. Conclusions

Identifying the stock structure of highly-mobile, wide-ranging fishes such as tunas is a challenging task, yet one that is fundamental to maintaining sustainable fisheries. For skipjack, yellowfin, bigeye and South Pacific albacore tunas, an improved understanding of stock structure, via the sampling approaches and considerations outlined, will have far reaching outcomes. Importantly, once the stock structure of each tuna species has been resolved, it will be possible to fine-tune management arrangements and the associated evaluation of management strategies for each self-replenishing population (unit stock). In parallel, an improved understanding of stock structure will also reduce the uncertainty of the predicted response of tuna stocks to greenhouse gas emission scenarios, leading to improved climate models for each stock. This would then enable integrated assessments of the effects of climate change on the expected redistribution of each tuna species to be compiled, improving confidence in the vulnerability assessments used to guide the adaptation of tuna fisheries to climate change. Finally, it is envisioned that the sampling considerations and designs presented here could also serve as a blueprint to resolve uncertainties around the stock structure of other pelagic species in the region and elsewhere.

The workshop identified a practical approach for undertaking the considerable work involved in identifying the stock structure of each tuna species. Given the challenges associated with sampling over wide geographic areas, initial investments should focus on undertaking a phased approach to sampling, involving broad-scale sampling in the first instance, ideally targeting adults in spawning condition, with subsequent sampling focused on key areas of interest, informed by existing and/or initial results. Temporally-repeated sampling should be undertaken to assess stability in observed patterns over time, particularly in relation to the effects of large-scale regional and global oceanographic processes on tuna movement and their resulting stock structure. Coupled with a multi-pronged approach to sampling and data analysis that borrows strengths across fields and technologies, this strategy will generate quantitative information that reduces uncertainty around the ecological and evolutionary scales at which Pacific tuna stocks are structured.

The costs involved in coordinating the collection, storage and analysis of material needed to complete the sampling design for each species, and in verifying the resulting stock structures with tagging

programmes, are likely to be substantial. A concern is that the cost is likely to be beyond the financial resources available to the regional agencies responsible for the research needed to underpin sustainable tuna fisheries. Given the significant improvements that the delineation of stock structure will bring to the models used to assess the effects of climate change on the world's largest tuna fishery, the investments outlined here are clearly a priority for agencies committed to assisting the Pacific Islands region adapt the use of its most valuable natural resource to climate change. The extraordinary dependence of PICTs on tuna for government revenue, employment opportunities and food security (Gillett, 2016; FFA, 2017), the global significance of these resources, and the potential for climate-driven redistribution of tuna species to disrupt these benefits (SPC, 2019), provide a strong rationale for these foundational investments.

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