

SCIENTIFIC COMMITTEE

SEVENTEENTH REGULAR SESSION

Online meeting

11–19 August 2021

Biology, stock structure, fisheries, and status of swordfish, *Xiphias gladius*, in the Pacific Ocean - a review

WCPFC-SC17-2021/ SA-IP-08

24 July 2021

Bradley Moore¹

Report prepared for SPC (Pacific Community)

¹NIWA (National Institute of Water & Atmospheric Research Ltd)



Biology, stock structure, fisheries, and status of swordfish, *Xiphias gladius*, in the Pacific Ocean

- a review

Prepared for The Pacific Community (SPC)

December 2020

Climate, Freshwater & Ocean Science

Prepared by: Bradley R. Moore

For any information regarding this report please contact:

Dr Bradley Moore Fisheries Scientist

+64-3-545 7746 bradley.moore@niwa.co.nz

National Institute of Water & Atmospheric Research Ltd PO Box 893 Nelson 7040

Phone +64 3 548 1715

NIWA CLIENT REPORT No:	2020361WN
Report date:	December 2020
NIWA Project:	SPC21403

Quality Assurance Statement						
Junfen Deine	Reviewed by:	Jennifer Devine				
ALL	Formatting checked by:	Alex Quigley				
Reput	Approved for release by:	Rosemary Hurst				

This report should be referenced as:

Moore, B.R. (2020) Biology, stock structure, fisheries and status of swordfish, *Xiphias gladius*, in the Pacific Ocean – a review. *NIWA Client Report* 20200361WN. National Institute of Water and Atmospheric Research, Wellington, NZ. 46 p.

© All rights reserved. This publication may not be reproduced or copied in any form without the permission of the copyright owner(s). Such permission is only to be given in accordance with the terms of the client's contract with NIWA. This copyright extends to all forms of copying and any storage of material in any kind of information retrieval system.

Whilst NIWA has used all reasonable endeavours to ensure that the information contained in this document is accurate, NIWA does not give any express or implied warranty as to the completeness of the information contained herein, or that it will be suitable for any purpose(s) other than those specifically contemplated during the Project or agreed by NIWA and the Client.

Contents

Εχεςι	itive s	ummary	5
1	Intro	duction	6
2	Тахог	nomy, morphology, and physiology	8
3	Life h	istory	9
	3.1	Distribution	9
	3.2	Diet and trophic ecology	9
	3.3	Early development 1	.0
	3.4	Age and growth1	.0
	3.5	Length-length and length-weight relationships1	.4
	3.6	Natural mortality1	.4
	3.7	Stock-recruitment relationships1	.4
	3.8	Reproductive biology1	.6
	3.9	Vertical movements1	.9
	3.10	Horizontal movements and stock structure1	.9
4	Fishe	ries 2	24
	4.1	Commercial fisheries	4
	4.2	Recreational and sport fisheries2	27
5	Stock	assessment and status	28
6	Interi	national management3	0
7	Futur	e research directions	:1
	7.1	Life history	1
	7.2	Data collection to inform stock assessments	4
	7.3	Stock assessments	4
	7.4	Reference points and harvest strategies	4
8	Ackno	owledgements	5
9	Refer	ences	6

Tables

Table 1:	Summary of studies into the age and growth of swordfish, <i>Xiphias</i>	10
	giudius, in the Pacific Ocean.	12
Table 2:	Key biological input parameters used in recent assessments of	
	Pacific swordfish stocks.	18
Table 3:	Summary of previous genetic research into the population structure	
	of swordfish, Xiphias gladius, in the Pacific Ocean.	22

Figures

Figure 1:	Estimated global landings of swordfish, <i>Xiphias gladius</i> , by region, 1950–2018.	6
Figure 2:	Biological parameters used in the most recent stock assessments for swordfish, <i>Xiphias gladius</i> , in the Pacific Ocean.	15
Figure 3:	Distribution and magnitude of longline catches (mt) of swordfish, <i>Xiphias gladius</i> , by decade and 5° square from the Pacific Ocean, a) 1979–1988, b) 1989–1998, c) 1999–2008, d) 2009–2018.	25
Figure 4:	Total annual catches of swordfish, <i>Xiphias gladius</i> , in the Pacific Ocean by geographic region, 1952–2015.	26
Figure 5:	Boundaries of the spatial domains used in recent Pacific swordfish stock assessments.	28

Executive summary

The swordfish Xiphias qladius (Xiphiidae) is a large, highly mobile finfish occurring in tropical to temperate waters in all global oceans and large seas. The species is the focus of significant commercial fisheries around the world. This report reviews current knowledge on the biology, fisheries, status and management of Pacific swordfish populations. Although swordfish have a long history of exploitation in the Pacific, catches have increased abruptly in recent years with the development and expansion of targeted fisheries, increasing from ~25,000 in the mid-1990s to ~50,000 t per year, or around half of the global catch. Substantial increases in catches have been observed in high seas areas of the southwest Pacific Ocean (SWPO), as well as the eastern Pacific Ocean (EPO) and southeast Pacific Ocean (SEPO), while catches in the western central North Pacific Ocean (WCNPO) have been relatively stable. While stock assessments indicate that none of these four Pacific stocks are considered overfished, it is likely that the EPO stock was experiencing overfishing at the time of the last assessment. Moreover, stock assessments for swordfish in the Pacific are limited by uncertainty around key biological inputs and understanding of stock structure. Research and management priorities for Pacific swordfish include direct validation of age estimations, standardisation of methodologies associated with the estimation of age and maturity, reducing uncertainty around movements and stock structure, improving sex-specific fisheries data collection, and the development of harvest strategies to ensure the long-term sustainability and economic viability of the region's fisheries.

1 Introduction

The swordfish (*Xiphias gladius* Linnaeus, 1758), also known as broadbill swordfish, is considered a highly migratory species found in all tropical and temperate oceans and large seas from ~50°N to ~50°S. The species reaches a maximum size of ~ 445 cm total length and about 540 kg weight (Nakamura, 1985). Swordfish are sexually dimorphic in size, with females reaching a larger maximum size than males, while individuals in the Pacific Ocean reach a larger maximum size than those observed elsewhere (Ehrhardt, 1992; DeMartini et al., 2007; Arocha, 2007).

Swordfish support significant commercial fisheries worldwide, with recent global annual catches of around 110,000–120,000 tonnes (Figure 1). Historically, the majority of swordfish landed globally were taken as incidental catch from longline fisheries typically targeting albacore tuna (*Thunnus alalunga*), bigeye tuna (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*). However, in recent decades, targeted fisheries for the species have developed, owing to the species' high quality flesh and excellent palatability. An increasing proportion of the global swordfish catch is being taken from the Pacific Ocean, with almost 50% of total landings coming from this region in recent years (FAO, 2020). The species is also important to many subsistence and artisanal fisheries, and is a highly prized recreational sportfish (Nakamura, 1985; Martinez-Ortiz et al., 2015; Gillett and Tauati, 2018).



Figure 1:Estimated global landings of swordfish, Xiphias gladius, by region, 1950–2018.Data from FAO(2020).

The global distribution of swordfish and its migratory behaviour means that most stocks straddle jurisdictional boundaries, and management and conservation require international cooperation. Management of swordfish stocks lies with four of the world's five tuna Regional Fisheries Management Organisations (RFMOs): International Commission for the Conservation of Atlantic Tuna (ICCAT), Indian Ocean Tuna Commission (IOTC), Inter-American Tropical Tuna Commission (IATTC), and Western and Central Pacific Fisheries Commission (WCPFC).

Globally, management efforts for swordfish continue to be hindered by information gaps relating to the species life history, including age and growth, reproductive biology, movement and stock

structure, as well as data limitations regarding the quantification of catches (Braun et al., 2019). With catches of swordfish in the Pacific Ocean increasing, and loss of genetic diversity observed in overexploited populations elsewhere (Righi et al., 2020), the implementation of rigorous stock assessments and effective management practices is imperative. To date, however, there has been no synthesis of information on swordfish in the Pacific to help guide these practices. To address this gap, this report explores current understanding of swordfish life history and fisheries, focusing on the Pacific Ocean. Previous research into the biology, ecology, and stock structure of the species, and recent trends and the current state of swordfish fisheries, stock status and fisheries management are reviewed. Key gaps in current knowledge and suggest future research directions to fill these are then highlighted.

2 Taxonomy, morphology, and physiology

The swordfish is a member of the Xiphiidae, a monotypic family of the suborder Xiphioidei that contains the istiophorid billfish (marlin, sailfish, and spearfish). Although the fossil record is sparse, swordfish appear to date back to the Pliocene (approximately 5.33 to 2.58 million years before present) (Fierstein, 2006).

Swordfish inhabit surface waters to depths of > 700 m, and subsequently can experience water temperatures of over 30°C to as low as 2.4°C, as well as rapid and dramatic changes in oxygen concentration, pressure, and light levels, often over short temporal periods (Carey and Robison, 1981; Takahashi et al., 2003; Evans et al., 2014). The species has evolved several morphological and physiological traits to function as apex predators in pelagic ecosystems and across marked gradients in ambient conditions, allowing them to exploit a wide range of oceanic environments (Carey and Robison, 1981; Van den Burg et al., 2005). Swordfish larvae undergo a marked change in physical appearance between ~8 and 13 mm preserved standard length (PSL), changing from a typical scombroid larval form to that more characteristic of a juvenile istiophorid (Govoni et al., 2003; Alvarado Bremer, 1994). Early life history stages appear well specialised for accelerated swimming, with low aspect ratio fins and high surface areas (Alvarado Bremer, 1994). Adult swordfish have a streamlined, elongate and cylindrical body with a prolonged, distinctive upper jaw ('bill' or "sword"), characteristic widely spaced first and second dorsal and anal fins, a thick caudal peduncle with a large median keel, and a crescent shaped-tail (Nakamura, 1985; Collette et al., 2006). Oil produced by glands near the base of the upper jaw is thought to create a hydrophobic layer that reduces friction drag and further increases swimming efficiency (Videler et al., 2016).

Like other billfishes, swordfish are ram ventilators, relying on forward momentum to ensure a continuous supply of ventilatory water flow across their gills (Wegner et al., 2010). Swordfish have larger gill surface areas than most other teleosts, reflecting the combined requirements for ram ventilation and elevated energetic demands associated with large size and heat production (Wegner et al., 2010). Moreover, swordfish appear unique from other billfishes in having branching gill filaments that increase the number of secondary lamellae, which may facilitate respiration in deeper, hypoxic environments, and thus allow this species to exploit resources unavailable to other billfishes (Wegner et al., 2010; Romeo et al., 2009). It has also been proposed that the large mass of white muscle tissue in swordfish enables them to tolerate hypoxic conditions by accumulating an oxygen debt, that can be compensated for when the fish spend time in warmer surface waters (Carey and Robison, 1981).

Relative to other billfishes, swordfish have large eyes, indicating that they are highly visual predators, adapted to maximise visual performance in low-light environments (Fritsches et al., 2005). Swordfish also have a specially adapted heating organ in the muscle next to their brain, which allows them to maintain brain and eye temperatures to $10-15^{\circ}$ C above water temperatures (Fritsches et al., 2005). In addition, swordfish hearts are relatively insensitive to temperature changes and undertake sarcoplasmic reticulum Ca²⁺ cycling to support contraction and supply blood to metabolically heated tissues at low temperatures such as those found at depth (Galli et al., 2009).

3 Life history

3.1 Distribution

Swordfish have a widespread geographical distribution in the Pacific Ocean, occurring throughout tropical, sub-tropical and temperate waters. Distribution varies latitudinally, following the seasonal extension and retraction of warmer waters into higher latitudes and variability in prey distributions (Palko et al. 1981). Tagging, fishery catch, and reproductive data indicate that swordfish feed in temperate latitudes and return to lower latitude areas for spawning (Sepulveda et al., 2018; DeMartini et al., 2000; Sosa-Nishizaki and Shimizu, 1991). This migration, however, is most commonly observed in larger individuals, which are predominantly female, with males considered to remain in tropical to sub-tropical waters year-round (Palko et al., 1981; DeMartini et al., 2000; Dewar et al., 2011).

Several studies have explored patterns of, and factors affecting, the fine-scale distribution of swordfish in the Pacific Ocean. Correlations have been found between oceanographic variables and the occurrence of swordfish. In particular, the presence, position, and strength of convergence zones and temperature fronts have been shown to be key drivers of a high catch per unit effort (Seki et al., 2002; Bigelow et al., 1999), with swordfish likely distributing along such gradients in response to prey accumulation, migration cues, or energetic efficiencies by riding currents (Olson et al., 1994). Off Hawaii, swordfish availability has also been found to increase in areas of steep topography near the archipelago and around seamounts and guyots to the north (Bigelow et al., 1999). Evidence of serial depletion on seamounts off the east coast of Australia, in the southwest Pacific Ocean (SWPO), similarly suggests a high degree of association and fidelity to these features (Campbell and Hobday, 2003).

3.2 Diet and trophic ecology

Swordfish represent a high level trophic predator in pelagic ecosystems due to their large size, jaw morphology, fast swimming speeds and ability to exploit a range of environmental conditions. Swordfish are opportunistic predators, feeding on a wide variety of fish and invertebrate species (Young et al., 2006; Rosas-Luis et al., 2016; Rosas-Luis et al., 2017; Zambrano-Zambrano et al., 2019). Small larvae feed predominantly on zooplankton, while larger larvae (~10 cm) have been found to feed almost exclusively on planktonic fish larvae, including members of the Scombridae, Istiophoridae, Coryphaenidae, Exocoetidae, and Xiphiidae, or those that periodically ascend to surface waters (e.g., Myctophidae) (Alvarado Bremer, 1994; Govoni et al., 2003). Juveniles and adults feed on fishes, cephalopods, and pelagic crustaceans (Young et al., 2006; Rosas-Luis et al., 2017; Zambrano-Zambrano et al., 2019).

The large size and aggressive nature of swordfish likely limits the number of species that prey upon them, with large sharks their main predator (Joyce et al., 2002; Maia et al., 2006; Romeo et al., 2020). Predation of early life history stages is higher than adults, with larval and juvenile swordfish being a common prey item for other pelagic species, including larger swordfish, other billfishes, tunas, mahi mahi, and sharks (Joyce et al., 2002; Lopez et al., 2010).

Being an apex predator with a high metabolic rate, swordfish have an elevated rate of food intake. Accordingly, they can bioaccumulate large amounts of lipid soluble pollutants, such as mercury (Hg) (Branco et al., 2007; Esposito et al., 2018). The implementation of strict regulations regarding mercury content in swordfish and associated reductions in public demand lead to an abrupt drop in catches between 1970–1971 in all global oceans and major seas (Figure 1) (Sonu, 1997). These regulations were relaxed in the late-1970s and global catches increased thereafter. A recent study found median Hg concentrations in Pacific swordfish populations were generally comparable with those elsewhere, and were below limits sets by European Union legislation (although concentrations in some individuals exceeded these limits) (Esposito et al., 2018).

3.3 Early development

There have been few studies into the early life history of swordfish in the Pacific Ocean. Where studies have been conducted, they point to relatively rapid growth and development. Larvae hatch approximately three days after fertilisation, when they are ~4 mm total length (Yasuda et al. 1978, cited in Govoni et al., 2003; Alvarado Bremer, 1994). Yolk and oil globule absorption occurs approximately five days after hatching (Govoni et al., 2003). In the western North Atlantic, growth of larval swordfish occurs in two distinct phases, with early larval stages (< 13 mm PSL and < 14 days old) growing slowly (~0.3 mm per day), and later stage larvae (between 13 to 115 mm PSL and > 14 days old) growing rapidly (~5.9 mm per day) (Govoni et al., 2003). These differences in growth rate are associated with an abrupt (within 3 days) change in jaw and alimentary canal structure, and associated changes in diet from zooplankton to larval fishes (Govoni et al., 2003).

3.4 Age and growth

A number of studies have examined age and growth of adult and sub-adult swordfish in the Pacific Ocean. The majority of these have used fin rays¹ to estimate age (Table 1), which have historically been considered to provide the most reliable estimate of swordfish age (Young et al., 2008). Results from these studies indicate that initial growth is rapid, with individuals capable of reaching over a metre in length in their first year of life, with females reaching a greater length-at-age than males, particularly at and beyond the ages associated with maturation (Sun et al., 2002; Cerna, 2009; Farley et al., 2016). The oldest ages estimated from fin rays for Pacific swordfish are 18 years for females and 15 years for males, both from the SWPO (Table 1).

Marked variation in growth as estimated from fin rays is evident between geographic regions (Table 1). Swordfish in the southeast Pacific Ocean (SEPO) have faster growth rates and attain larger maximum sizes than those in the northwest Pacific Ocean (NWPO) and SWPO (Table 1) (Cerna, 2009). While similar patterns between the eastern Pacific Ocean (EPO) and western and central Pacific Ocean (WCPO) have been observed in other pelagic species (e.g., bigeye tuna; Schaefer and Fuller, 2006), it is unclear whether these patterns reflect spatial differences in growth, methodological differences in the preparation and interpretation of fin rays, or a combination of these factors.

Historically, fewer studies have used otoliths to estimate annual ages of swordfish, potentially as a result of difficulties in collection and preparation due to their small size and fragility. To date, the most comprehensive study examining the use of otoliths to estimate the age of Pacific swordfish is that of Farley et al. (2016). These researchers compared paired age estimates from fin rays and sagittal otoliths from 311 fish obtained from the east coast of Australia during the study of Young and Drake (2004). Farley et al. (2016) found that fin rays and otoliths provided similar estimates of age for individuals up to 7 years of age for females and 4 years of age for males, after which age estimates from fin rays were lower compared to those from otoliths, with otolith-based age estimations therefore indicating that fish live longer and grow slower than fin rays. They also found that the

¹ Previous fin-ray based ageing studies on swordfish have used the terms fin spines, fin rays, or spiny fin rays to describe these calcified structures. For consistency, the term fin ray is used throughout this report to describe all fin-supporting elements.

proportion of otoliths found to be unreadable was lower than for fin rays, and that counts of daily rings provided an underestimation of annual age relative to counts of annual rings. The authors hypothesised that differences in age estimations between fin rays and otoliths likely results from loss of increments due to vascularisation and bone remodelling with age within fin rays, consistent with observations in other billfish species (Kopf et al., 2010). On this basis, Farley et al. (2016) concluded that otolith-based estimates of age be used in future stock assessments. However, given the difficulties associated with the collection and preparation of otoliths, the authors conceded that fin rays were likely the most practical structure for ageing fish up to 170 cm eye orbit-fork length (EFL) for females and 120 cm EFL for males, with otoliths likely providing the most accurate estimation of age for fish above these lengths.

To date, there have been no successful direct ageing validation experiments for swordfish in the Pacific Ocean or elsewhere. This is due in part to the solitary and mobile nature of swordfish, relatively high post-release mortality, and low recapture rates of tagged fish (Young and Drake, 2004). Bomb radiocarbon approaches for validating swordfish age from vertebrate have also been trialled, however studies to date have been limited due to the resorption and reworking of vertebral material (Kalish and DeMartini, 2001). Accordingly, validation of daily and annual growth increments in fin rays and otoliths has largely focused on indirect approaches, in particular marginal increment ratio (MIR) analysis, whereby monthly or seasonal changes in the width of opaque vs. translucent material on the otolith margin are compared to that of the previous band. Results from these studies indicate that increments are laid down on an annual basis, with the deposition of opaque material typically commencing in late summer (Sun et al., 2002; DeMartini et al., 2007; Cerna, 2009; Farley et al., 2016).

Growth of swordfish in the Pacific Ocean has been predominantly described by the standard von Bertalanffy growth function (VBGF) (von Bertalanffy, 1938) on either raw or back-calculated lengthat-age (Table 1), due to its simplicity and generality. However, several authors have found that the standard VBGF may not adequately describe swordfish growth and so have modelled growth using the generalised, four-parameter VBGF (Table 1). There have been no published attempts to fit other forms of growth models to adult and sub-adult Pacific swordfish length-at-age data. Table 1:Summary of studies into the age and growth of swordfish, Xiphias gladius, in the Pacific Ocean.Standard errors (SE) are provided where supplied by the
authors. CNPO = Central North Pacific Ocean, NPO = North Pacific Ocean, NWPO = Northwest Pacific Ocean, SEPO = Southeast Pacific Ocean, SWPO = Southwest Pacific
Ocean. F = females, M = males, C = sexes combined, U = unknown.

Pagian Pafaranca		Ageing	Madel method	Sox	VBGF			Maximum	
Region	Reference	method	wodel method	Sex	L∞	К	t _o	т	age (yrs)
SWPO (Coral and Tasman Seas)	Farley et al. (2016)	Fin rays	Standard VBGF on raw length-at-age	F	279.6 ± 16.0	0.123 ± 0.017	-2.55 ±0.34		14
,				М	213.8 ± 10.5	0.197 ± 0.031	-2.28 ± 0.36		10
		Otoliths		F	249.6 ± 7.6	0.157 ± 0.016	-2.13 ± 0.30		21
				М	191.9 ± 6.0	0.235 ± 0.022	-2.10 ± 0.35		17
SEPO (Chile)	Cerna (2009) ²	Fin rays	Standard VBGF on back- calculated length-at-age ¹	F	321 ± 8.30	0.133 ± 0.008	-2.46 ± 0.10		12
				М	279 ± 9.11	0.158 ± 0.013	-2.65 ± 0.153		9
SEPO (Chile)	Chong and Aguayo (2009)	Fin rays	Standardised VBGF on back-calculated length-at- age ¹	F	304.7	0.153	-2.06		15
			~~~	М	275.1	0.177	-2.11		11
			Generalised VBGF on back- calculated length-at-age	F	344 ± 39.69	0.077 ± 0.055	-1.81 ± 0.68	-0.307 ± 0.389	12
				М	365 ± 158.47	0.027 ± 0.051	-1.14 ± 0.75	-1.023 ± 0.081	9
NPO	Valeiras et al. Fin ray	ras et al. Fin rays Standardised	Standardised VBGF on raw	F	376	0.070	-2.162		13
	()			М	271.4	0.121	-1.543		13
CNPO (Hawaii)	DeMartini et al. (2007)	Fin rays	Fin rays Standardised VBGF on back-calculated length-at-	F	230.5 ± 3.94	0.246 ± 0.019	-1.24 ± 0.17		12
			0 <u>5</u> 0	Μ	208.9 ± 5.60	0.271 ± 0.034	-1.37 ± 0.259		11

Desien	Deferre	Ageing	Mandal works at	6			VBGF		Maximum
Region	Reference	method	Model method	Sex	L∞	К	<i>t</i> 0	m	age (yrs)
			Generalised VBGF on back- calculated length-at-age	F	227.2 ± 6.180	0.524 ± 0.871	-2.41 ± 2.968	0.448 ± 0.771	12
				Μ	221.0 ± 20.1	0.070 ±080	-0.15 ± 0.576	-1.27 ± 1.122	11
SWPO (New Zealand)	Griggs et al. (2005)	Fin rays	Standardised VBGF on raw length-at-age	F	434.7 ± 105.8	0.053 ± 0.023	-3.46 ± 1.18		15
	()			M ³	394.4 ± 248.5	$0.044 \pm 0.047$	-5.86 ± 2.72		12
SWPO (Coral and Tasman Seas)	Young and Drake (2004)	Fin rays	Standardised VBGF on raw length-at-age	F	296.0	0.08	-3.70		18
				Μ	224.2	0.13	-3.00		15
NWPO (Taiwan)	Sun et al. (2002) ²	Fin rays	Standardised VBGF on back-calculated length-at- age ⁴	F	281.809 ± 6.805	0.101 ± 0.006	-3.204 ± 0.171		10
				Μ	224.170 ± 12.802	0.140 ± 0.025	-3.089 ± 0.523		12
			Generalised VBGF on back- calculated length-at-age ^{1,4}	F	300.656 ± 38.869	$0.040 \pm 0.116$	-0.750 ± 2.272	-0.785 ± 1.324	10
				Μ	213.052 ± 19.153	0.086 ± 0.035	-0.626 ± 1.196	-0.768 ± 1.730	12
CNPO (Hawaii)	Uchiyama et al. (1998)	Fin rays	Standardised VBGF on raw length-at-age	С	321.0	-0.14	1.3		8 (F) <i>,</i> 7 (M)
EPO	Boggs (1989)	U	U	U	309	124	-1.169		U

¹ Denotes best fitting model of those tested.

² Models fitted using lower jaw-fork length (LJFL) measurements (other models are fitted using eye orbit-fork length (EFL)).

³ Excludes two fish that were likely outliers.

⁴ Parameters are presented for the best-fitting model within each model fit type (i.e., standardised VBGF vs. generalised VBGF) only.

### 3.5 Length-length and length-weight relationships

Swordfish landed commercially are typically processed at sea in a variety of forms, including whole, bill removed at a point level with the tip of the lower jaw), and gilled, gutted and headed (i.e., trunked). Accordingly, the development of length-length and length-weight conversion factors is critical for standardising catch weights and in biomass estimations.

Few studies have derived length-weight relationships for Pacific swordfish, due to their large size and associated difficulties in weighing fresh individuals, particularly at sea (Davies et al., 2005). Sun et al. (2002) found no significant difference in the length-weight relationships of male and female swordfish (n = 227) caught off the coast of Taiwan, and estimated the best fitting length-weight relationship for the species to be:

$$RW = 1.3528 \times 10^{-6} L J F L^{3.4297}$$

where *RW* = round weight and *LJFL* = lower jaw-fork length. Campbell and Dowling (2003) estimated the LJFL--whole weight (*WW*) relationship to be:

$$WW = 2.1355 \times 10^{-5} LJFL^{2.902}$$

for both sexes combined for individuals caught by Japanese longliners off the east coast of Australia. Davies et al. (2005) observed variation in length-weight relationships between female (n = 1,817) and male (n = 562) swordfish sampled within New Zealand's Exclusive Economic Zone (EEZ), as well as variation between fish sampled in the north and south of the EEZ. The authors attributed this latter result to the high ratio of females in the southern areas combined with the period of sample collection, which coincided with high gonad condition, although cautioned that due to the difficulties associated with measuring large individuals at sea, the samples measured from the southern area may not be representative of the length range of the catch. From these results, Davies et al. (2005) recommended that sex-specific length-weight parameters that capture spatial and temporal variability be estimated. Slight, non-significant, variation in length-weight relationships between sexes were similarly identified by Cerna (2009) in the SEPO between ~20–40°S, with females becoming heavier than male at length > 200 cm LJFL.

#### 3.6 Natural mortality

The instantaneous rate of natural mortality (*M*) is not known for any swordfish population. Due to the large size attained by swordfish, it has frequently been assumed that *M* might be as low as 0.2 (Hinton et al. 2005). Stock assessments of swordfish in the Pacific have used both constant and ageand sex-specific values for *M*, typically ranging from ~0.2–0.4, with *M* typically slightly higher for juveniles than adults (Figure 2;Table 2). A meta-analysis of natural mortality estimates for central North Pacific swordfish revealed a high degree of consistency across approaches, with estimates ranging from ~0.35 to 0.41 year⁻¹ (Brodziak, 2011). With refinement of techniques for ageing it has been found that swordfish in at least some regions of the Pacific are capable of living for at least 21 years for females and 17 years for males (e.g., Farley et al., 2016), suggesting that *M* may be lower than values previously considered, and likely differs between sexes.

#### 3.7 Stock-recruitment relationships

As is typical in assessments of wide-ranging pelagic fishes, limited understanding of the steepness (*h*) of the relationship between spawning stock biomass (SSB) and recruitment is a key area of uncertainty in swordfish assessments (Takeuchi et al., 2017). Where stock-recruitment relationships have been included, steepness values used in Pacific Ocean swordfish assessments have typically

been in the order of 0.8–0.9 for base-case models (Table 2) (Takeuchi et al., 2017, ISC Billfish Working Group, 2018), implying a weak relationship between recruitment and spawning stock biomass, with varying degrees of steepness included as sensitivity analyses in the WCNPO and EPO assessments, and in the uncertainty grid used for the SWPO assessment (Table 2) (see 'Stock assessments and status' section. These values are consistent with those used for assessments of swordfish elsewhere (e.g., ICCAT, 2017, Fu, 2020). In the most recent assessment of swordfish in the SEPO, recruitment was considered independent of spawning biomass (i.e., h = 1) for the base case model, with h = 0.75 considered as a sensitivity analysis (Table 2) (Hinton and Maunder, 2011).



**Figure 2:** Biological parameters used in the most recent stock assessments for swordfish, *Xiphias gladius*, in the Pacific Ocean. (a) von Bertalanffy growth curves, (b) length-weight relationships, and (c) natural mortality rates. EPO = Eastern Pacific Ocean, SEPO = southeast Pacific Ocean, SWPO = southwest Pacific Ocean, WCNPO = western and central North Pacific Ocean. Note growth and length-weight curves for the SEPO have been converted from lower jaw-fork length (LJFL) to eye orbit-fork length (EFL) for consistency with other assessment regions.

### 3.8 Reproductive biology

Maturity in Pacific Ocean populations of swordfish has been predominantly assessed via histological examination of gonad tissue. Studies have reported variation in the length at which 50% of the population reaches maturity ( $L_{50}$ ) among regions. For females,  $L_{50}$  is estimated to be 168.2 cm LJFL (=157.2 cm EFL) in the waters off Taiwan (Wang et al., 2003), 161.5 cm EFL off the east coast of Australia (Farley et al., 2016), and 143.7 cm EFL around Hawaii (DeMartini et al., 2000). These estimates appear comparable for swordfish caught in the Atlantic and Indian Oceans. Taylor and Murphy (1992) estimated  $L_{50}$  to be 182 cm LJFL (= ~161 EFL) for females in the Straits of Florida. Arocha and Lee (1996) estimated  $L_{50}$  to be 179 cm LJFL (= ~158 cm EFL) for female swordfish was estimated to be 170 cm LJFL (Poisson and Fauvel, 2009a). It is unclear whether the differences observed amongst studies in the Pacific reflect spatial variability in environmental influences (including water temperature, food availability, and competition), spatial aggregation by maturation stage, fishing pressure, genetics, methodological differences between studies or, most probably, a combination of factors.

Swordfish are batch spawners with indeterminate annual fecundity and asynchronous oocyte development throughout an extended spawning period (Young et al., 2003, Poisson and Fauvel, 2009a). Large females are more fecund than smaller fish (Young et al., 2003), indicating relationships between egg production and fish length/age should be accounted for in stock assessments. In the SWPO, relative batch frequency was found to be 11.4 oocytes per gram of body weight, equating to ~1.8 million eggs spawned per batch for an average 150 kg female (Young et al., 2003). Mean spawning interval for females in the SWPO was estimated to be 3.02 days, and was slightly shorter during the peak of spawning at 1.78 days, suggesting that either individual swordfish spawn more frequently during peak spawning, or that a greater proportion of individuals spawn at this time (Young et al., 2003). These estimates are similar to those for swordfish in other regions. For example, spawning frequency was estimated at 2.8 days for individuals in the southwest Indian Ocean (Poisson and Fauvel, 2009b), and 2.6 days for individuals in the North Atlantic Ocean (Arocha, 2007). Assuming females spawn continuously throughout the spawning period, Young et al. (2003) estimated a 200 cm EFL female off the east coast of Australia would release approximately 21–42 million oocytes between December and February.

Young et al. (2003) report a positive relationship between maximum oocyte size and EFL, as well as between the mean diameter of hydrated oocytes and EFL. The production of bigger eggs by larger individuals has been demonstrated to result in increased larval survival in several fish species (Barneche et al., 2018), and a similar result might therefore be expected for swordfish.

Inferences on the timing and location of spawning of Pacific swordfish populations have been primarily based on histological examination of gonad condition and trends in relative gonado-somatic index (GSI) values (Young et al., 2003; Claramunt et al., 2009), as well as patterns of larval distribution (Nishikawa and Ueyanagi, 1975; Grall et al., 1983; Nishikawa et al., 1985). Observations of swordfish larvae in waters > 24°C (Nishikawa et al., 1985, Govoni et al., 2000) suggests spawning may be restricted to these temperatures. From patterns in gonad histology and GSIs, spawning in Pacific swordfish is considered to take place in tropical and subtropical waters, typically peaking in summer, although the extent of spawning period varies geographically and likely relates to ambient sea surface temperature (Young et al., 2003). Off the east coast of Australia at around 20–35°S, spawning occurs between September and March, with a peak from December to February (Young et al., 2003), while larval surveys conducted between 10°S and 20°S indicates peak spawning occurs from July to September at these lower latitudes (Nishikawa et al., 1985). The earlier onset of

spawning observed in lower latitudes suggests spawning may be restricted by both a lower and an upper thermal limit. It is unclear whether individuals in equatorial waters stop spawning and remain in these waters during the austral summer or move southwards and continue spawning over the summer period. Swordfish in the southern EPO similarly spawn during the austral summer, principally during January and February (Claramunt et al. 2009). Off Hawaii, swordfish are considered to spawn from March-July, with a likely peak in May-June (DeMartini et al., 2000).

Finer-scale spawning dynamics of Pacific swordfish are largely unknown. DeMartini et al. (2000) found the relative numbers of reproductively active females and imminent spawners to be independent of moon phase, indicating no lunar spawning periodicity. In the western Atlantic Ocean, swordfish are considered to spawn during selected moon phases near boundary currents and front zones (Govoni et al., 2000) that transport their larvae to areas of suitable habitat (Suca et al., 2018). The degree of fidelity to spawning regions is unknown.

Table 2:Key biological input parameters used in recent assessments of Pacific swordfish stocks.WCNPO = Western and Central North Pacific Ocean, EPO = EasternPacific Ocean, SEPO = southeast Pacific Ocean, SWPO = southwest Pacific Ocean.SS = Stock Synthesis; MFCL = MULTIFAN-CL. ¹Based on models fitted to lower jaw-forklength (LJFL) measurements (otherwise models were fitted to eye orbit-fork length (EFL) measurements . na = not applicable.

Devenetor		St	ock	
Parameter	WCNPO	EPO	SEPO	SWPO
Reference	ISC Billfish Working Group (2018)	ISC Billfish Working Group (2014)	Hinton and Maunder (2011)	Takeuchi et al. (2017)
Model implementing software	SS	na	SS	MFCL
Regional structure	None; fleets-as-areas	None; fleets-as-areas	None; fleets-as-areas	2 sub-regions delineated at 165°E
Sex-specific	Yes	Yes		No
Length-weight relationship	Both sexes combined: <i>a</i> = 1.299 x 10 ⁻⁵ , <i>b</i> = 3.0738	Females: <i>a</i> = 1.37 x 10 ⁻⁵ , <i>b</i> = 3.04 Males: <i>a</i> = 6.60 x 10 ⁻⁶ , <i>b</i> = 3.19	Females ¹ : $a = 3.7 \times 10^{-6}$ , b = 3.26 Males ¹ : $a = 4.5 \times 10^{-6}$ , b = 3.21	Both sexes combined: <i>a</i> = 3.879 x 10 ⁻⁶ , <i>b</i> = 3.24
Growth rate ( <i>k</i> )	0.246 (females), 0.271 (males); 0.130 (females) and 0.198 (males) used in sensitivity analyses	0.116 (females), 0.077 (males)	0.133 (females ¹ ), 0.158 (males ¹ )	0.196 (both sexes combined)
Length at minimum age (L1)	97.7 cm EFL (females), 99.0 cm EFL (males)	116.91 cm EFL (females), 75.49 cm EFL (males)	89.57 cm LJFL (females), 95.45 cm LJFL (males)	85.75 cm EFL (both sexes combined)
Natural mortality ( <i>M</i> )	Age- and sex-specific: females: $M_0 = 0.42$ , $M_1 = 0.37$ , $M_2 = 0.32$ , $M_3 = 0.27$ , $M_{4+} = 0.22$ ; males: $M_0 = 0.40$ , $M_{1-2} = 0.38$ , $M_{3-5} = 0.37$ , $M_{6+} = 0.36$ ; ±10% than base case values used in sensitivity analyses	Age- and sex-specific: females: $M_0 = 0.39$ , $M_{1-2} = 0.38$ , $M_{3-6} = 0.37$ , $M_{7+} = 0.36$ , males: $M_0 = 0.48$ , $M_1 = 0.47$ , $M_2 = 0.46$ , $M_{3-4} = 0.45$ , $M_{5-8} = 0.44$ , $M_{9+} = 0.43$	Fixed at 0.4 across ages and sexes	Age-specific: $M_1 = 0.28$ , $M_2 = 0.25$ , $M_{3-4} = 0.23$ , $M_5 = 0.26$ , $M_6 = 0.31$ , $M_7 = 0.34$ , $M_{8-10} = 0.35$ , $M_{11-20} = 0.34$ ; sensitivity analyses conducted at varying scenarios for temperature and the ratio of adult $M$ : juvenile $M$
Age at 50% female maturity (A ₅₀ ) (years)	-	-	2; all individuals considered mature by 4 years	5.4; all individuals mature by ~9 years
Length at 50% maturity ( $L_{50}$ )	143.6 cm EFL (females), 102.0 cm EFL (males)	150.0 cm EFL (females), 120.0 cm EFL (males)	165–175 cm LJFL (females), 115–120 cm LJFL (males)	
Steepness	0.9; 0.70, 0.81 and 0.99 used in sensitivity analyses	na	1; 0.75 used in sensitivity analyses	0.8; 0.65 and 0.95 used in sensitivity analyses
Maximum age	15+	15+	15+	20+

#### 3.9 Vertical movements

Several studies have used electronic tagging technologies to investigate the vertical movements and depth distribution of swordfish in the Pacific Ocean. Results from these studies demonstrate that swordfish exhibit a pattern of vertical migration in response to diel and lunar cycles, with individuals occurring at significantly greater depths during the day than at night (Carey and Robison, 1981; Takahashi et al., 2003; Abascal et al., 2010; Dewar et al., 2011; Evans et al., 2014; Sepulveda et al., 2018). Broadly, swordfish show a mix of behaviours during the daytime, including: i) basking in surface waters, ii) a mixed-layer distribution between sub-surface waters and the thermocline, and iii) prolonged dives below the thermocline, often to depths of > 600 m (Sepulveda et al., 2010; Evans et al., 2014; Sepulveda et al., 2018). Considerable spatio-temporal variability in the frequency and extent of these movements is evident, likely resulting from differing environmental conditions, in particular the oxygen minimum layer, and associated prey distribution over space and time (Evans et al., 2014; Dewar et al., 2011). At night, swordfish tend to remain in surface waters < 50 m in depth (Sepulveda et al., 2010; Evans et al., 2014; Dewar et al., 2010; Evans et al., 2014).

#### 3.10 Horizontal movements and stock structure

#### 3.10.1 Tagging

Electronic tagging technologies are being increasingly applied to investigate the horizontal movements of individual swordfish in the Pacific Ocean. Results from these studies suggest a degree of regional fidelity, seasonal latitudinal migrations between higher latitude foraging areas and low latitude spawning areas, particularly in larger individuals, and limited longitudinal movements (Holdsworth et al., 2007; Abascal et al., 2010; Dewar et al., 2011; Evans et al., 2014).

Takahashi et al. (2003) tracked a single swordfish (estimated weight = 120 kg) carrying an archival tag for more than 11 months off the east coast of Japan. The authors describe a cyclic seasonal migration between northern areas (40–45° N) associated with the food-rich Oyashio current in summer and subtropical areas (10–20° N) in autumn and winter.

Sepulveda et al. (2020) used a range of electronic tag types to examine the horizontal movements, migration patterns and stock affiliation of swordfish tagged off the coast of California, within the western and central North Pacific Ocean (WCNPO) stock assessment boundary. Although results were limited by the number of swordfish tagged (n = 71) and relatively short deployments durations (typically between ~1 to 6 months), a range of movement behaviours were observed, including regional residency, broadscale latitudinal migration (with one individual moving 3,877 km towards the equator), and occasional longitudinal displacement (with one individual moving ~3,700 km westwards, to the east of Hawaii). Notably, of the fish that moved outside of the Southern California Bight (SCB) tagging area, 76% (38 individuals) moved into the EPO stock assessment area to the south, while 10 moved west within the WCNPO area. These findings are similar to those of Dewar et al. (2011), and Abecassis et al. (2012), who showed that the majority of fish (~70% and 56%, respectively) tagged within the SCB entered the EPO management area. Sepulveda et al. (2020) also observed a high degree of seasonal site fidelity, with several individuals returning to the SCB tagging area in the following year. Similar observations of fidelity to particular areas have been observed for swordfish in other oceans. For example, most of the recaptures of large females tagged in the Canadian Large Pelagic Fish Tagging Program have occurred within a few kilometres of the original release site, some after being at sea for many years (Burnett et al., 1987).

Evans et al. (2014) analysed movement data from swordfish tagged with pop-up satellite tags (PSATs) in the waters off eastern Australia, Cook Islands, and northeast of New Zealand between Fiji and

French Polynesia, as well as northern New Zealand (Holdsworth et al., 2007), and northern Chile (Abascal et al., 2010). Observed movements suggest a lack of connectivity between the southern and northern regions of the WCPO, and between the WCPO and far eastern EPO. Evans et al. (2014) also identified cyclical latitudinal movements of fish tagged at multiple locations, and limited connectivity between the eastern and western areas of the Tasman and Corals Seas, delineated at approximately 165°E. Fish tagged north and east of New Zealand were found to display greater eastward movement than those tagged off the east coast of Australia. The authors noted that the limited eastwards movements displayed by fish tagged of the east coast of Australia may reflect their relatively small size (estimated mean weight = 111 kg), and recommended further deployments be undertaken to determine the extent of connectivity between these areas.

Similar cyclical movements between presumed southern feeding and northern spawning areas were observed for swordfish tagged with PSATs off the east coast of Tasmania, Australia, in the study of Tracey and Pepperell (2018). Times at which individuals were at liberty (TAL) were largely similar (mean TAL = 159.0 ± 32.5 days) to that those tagged of the east coast off Australia in Evans et al. (2014) (mean TAL = 153.5 ± 17.0 days). In contrast to Evans et al. (2014), however, and despite small sample sizes, two of the seven tagged individuals were estimated to have travelled east beyond 165°E – one individual was estimated to have travelled south and east of New Caledonia and Vanuatu to the Solomon Islands, before returning to the north coast of New South Wales, Australia, and a second was estimated to have moved north to southern and central Queensland (~20–25°S, 155–160°E) between April and August and then travelled directly east offshore of southern Queensland to ~174°E (Tracey and Pepperell, 2018). It is unclear whether the discrepancy between these movement patterns and those described by Evans et al. (2014) reflects the larger size (estimated weights of 280 kg (= ~266 cm LJFL) and 140 kg (= ~217 cm LJFL), respectively) of these individuals relative to those tagged in the study of Evans et al. (2014), or other factors. Tracey and Pepperell (2018) also report a high degree of fidelity to particular areas, with one tagged individual observed to return to within 100 km of its initial tagging location following a journey of approximately 5,400 km.

#### 3.10.2 Genetics

Studies of the genetic structure of swordfish have indicated significant inter-oceanic differentiation between Atlantic, Indo-Pacific, and Mediterranean populations (Alvarado Bremer et al., 1995; 1996; 2005; Rosel and Block, 1996; Chow et al., 1997; Chow and Takeyama, 2000). Recently, Grewe et al. (2020) found significant population differentiation at single nucleotide polymorphic (SNP) loci between samples collected from Coral Sea in the SWPO and off the coast of Western Australia in the Indian Ocean, confirming the separation of Pacific and Indian Ocean populations.

A number of genetic studies have been conducted on Pacific swordfish, often yielding conflicting results (Table 3). Using restriction fragment length polymorphism (RFLP) analysis on mitochondrial DNA (mtDNA), Grijalva-Chon et al. (1994) found no evidence for differentiation among samples from the North Pacific Ocean, suggesting that there was likely sufficient gene flow to result in a single genetic stock. Later, Grijalva-Chon et al. (1996) reported significant differences between fish from Hawaii and Mexico at three allozyme loci. Using RFLP analysis on mtDNA, Chow et al. (1997) similarly found little genetic differentiation amongst swordfish samples from the northwest (Japan), northeast (Mexico), eastern (Ecuador), the southeast Pacific (Peru) and southwest Pacific, while Chow and Takeyama (2000) found no evidence of differentiation between individuals from the northwest (Japan) and southeast (Peru) Pacific from nuclear DNA.

From patterns in mtDNA, Reeb et al. (2000) proposed a broad '>-shaped' pattern of connectivity of swordfish in the Pacific, such that individuals in the southwest and northwest Pacific are the most distinct from each other, with individuals in the central and eastern Pacific intermediate between the two. As noted by Lu et al. (2016) however, several authors have questioned whether mtDNA adequately reflects the genetic signature of swordfish populations, given its matrilineal mode of inheritance, combined with the geographic separation of large female swordfish to higher latitude feeding grounds (Alvarado Bremer et al., 1998; Muths et al., 2013). A similar, albeit weaker, pattern was evident from microsatellite DNA markers (Kasapidis et al., 2008), but only after pooling their two southwest Pacific samples collected northeast and northwest of New Zealand. Greater sampling coverage and larger sample sizes are required to support this finding. Based on differences in allele frequency of the lactate dehydrogenase-A (Idh-A) gene, Alvarado Bremer et al. (2006) concluded that individuals from the southeast Pacific (Chile) were genetically distinct from those in the central north, northeast and southwest Pacific. In addition, individuals sampled from the northeast Pacific (encompassing Ecuador to Mexico) were different from those sampled from the central north Pacific (Hawaii), which were in turn different from individuals sampled off eastern and western Australia. The authors concluded that such spatial structuring resulted from philopatric behaviour to separate breeding grounds, and recommended that larger sample sizes and additional sampling locations be used to explore finer-scale structuring of swordfish in the Pacific Ocean.

Lu et al. (2016) examined the population structure of swordfish collected from 16 localities spanning tropical, subtropical and temperate areas across the Pacific Ocean using high resolution multilocus SNPs. The authors describe a complex structure, with differences observed between temperate and most tropical areas, as well as among several tropical areas. Of note, however, Lu et al. (2016) identified no significant difference between samples from temperate regions despite large distance separating them (up to 18,000 km), a result largely at odds with observations from tagging data.

Reference	Data type	Region compared	Interpretation
Grijalva-Chon et al. (1994)	mtDNA (RFLP)	CNPO (Hawaii), ENPO (Mexico), WNPO (Japan and China Sea)	No differences
Rosel and Block (1996)	mtDNA CR (Seq)	EPO (Mexico, Chile), CNPO (Hawaii), WNPO (Japan, Taiwan)	No differences
Grijalva-Chon et al. (1996)	Allozymes	CNPO (Hawaii), ENPO (Mexico)	Significant difference between these two locations
Chow et al. (1997)	mtDNA CR (PCR-RFLP)	WNPO (Japan), CNPO (Hawaii), ENPO (Mexico, Ecuador and Peru), SWPO (NZ)	No differences
Chow and Takeyama (2000)	mt DNA CR (PCR-RFLP)	WNPO (Japan), EPO (Peru)	No differences
Reeb et al. (2000)	mt DNA CR (Seq)	WNPO (Japan), CNPO (Hawaii), central equatorial PO, ENPO (California, Mexico), SWPO (Australia)	Isolation-by-distance (IBD), $\supset$ -shaped corridor
Lu et al. (2006)	mt DNA CR (Seq)	WNPO (Taiwan) and CSPO (north of French Polynesia)	No differences
Alvarado Bremer et al. (2006)	nDNA <i>ldh-A</i> (Seq)	CNPO (Hawaii), SEPO (Chile), ENPO (Mexico), SWPO (Eastern and Western Australia)	SEPO different to all regions ENPO and SWPO different from CNPO
Kasapidis et al. (2008)	Microsatellites	WNPO, SWPO, South Pacific, SEPO, central eastern Pacific, Central Pacific	No differences between locations. Slight support for IBD and $\supset$ -shaped corridor when locations pooled
Lu et al. (2016)	SNPs	16 locations spanning NWPO, CNPO, SWPO, central equatorial Pacific, ENPO, SEPO	Differences between tropical and temperate samples, potentially among tropical samples No differences between temperate samples

#### Table 3: Summary of previous genetic research into the population structure of swordfish, Xiphias gladius, in the Pacific Ocean.

#### 3.10.3 Otolith and muscle chemistry

Humphreys et al. (2005) examined the otolith chemistry of young of the year (YOY) swordfish among four sites situated between 165–160°W and 0–31°N in the central north Pacific. Elemental fingerprints differed between sampling sites, with the magnitude of differentiation increasing with latitudinal separation. The authors recommended more comprehensive sampling of putative nursery grounds be conducted, and suggested that given the clear differences in elemental profiles among nursery areas it should be possible to track movement patterns of adult swordfish by applying laser ablation inductively-coupled plasma mass spectrometry (LA-ICP-MS) techniques to sectioned adult otoliths.

Examination of the stable isotopes of muscle and fin ray tissues also suggests some spatial structuring of swordfish. Acosta-Pachón et al. (2020) examined carbon ( $\delta^{13}$ C) and nitrogen ( $\delta^{15}$ N) stable isotope ratios in fin ray and muscle tissue of swordfish caught off Baja California Sur (Mexico), California (USA), and in the North Pacific Subtropical Gyre (NPSG) near Hawaii to assess the species' finer-scale movements in the NEPO. Significant differences in isotopic ratios of both fin ray and muscle tissue between fish from Baja California Sur and California lead Acosta-Pachón et al. (2020) to hypothesise that swordfish may exhibit a high degree of site fidelity. Similarities between fish from California and the NPSG near Hawaii were observed, suggesting possible movement between these areas. However, the authors noted that more advanced analytical methods providing better temporal resolution and an improved understanding of tissue-specific isotope turnover rates are required to investigate these patterns.

#### 3.10.4 Parasites

In a preliminary study, Smith et al. (2007) examined the parasite fauna of swordfish from Australia, New Caledonia, and New Zealand, to assess their utility as stock markers. Most of the observed parasites were considered to have a short residence time in or on the fish, making them unsuitable for use a biological tags. However, three species were considered appropriate as biological tags, including the digenean *Hirudinella* sp., encysted larval stages of the cestode *Hepatoxylon* sp., and a pennellid copepod, although larger sample sizes were required to assess any area-specific differences in parasite abundance or prevalence (Smith et al., 2007).

#### 3.10.5 Insights from fishery data

Several authors have explored fishery data as a means of delineating stock boundaries of swordfish in the Pacific Ocean. From patterns in annual nominal catch-per-unit-effort (CPUE) data, Sakagawa and Bell (1980) and Bartoo and Coan (1989) proposed the occurrence of three stocks in the Pacific Ocean, broadly centred around the NWPO, SWPO and EPO. From monthly-resolved patterns in CPUE, Sosa-Nishizaki (1990) and Sosa-Nishizaki and Shimizu (1991) proposed a four-stock hypothesis, with separate stock units in the NWPO, SWPO, NEPO and SEPO. On the basis of spatio-temporal patterns in standardised catch rates, size frequency distributions and gonad index values, Hinton and Deriso (1994) proposed the occurrence of separate north-eastern and south-eastern stocks of swordfish in the EPO, separated at ~5°S. From spatial patterns in Japanese longline CPUE data, Ichinokawa and Brodziak (2008) proposed a two-stock hypothesis for swordfish in the North Pacific Ocean, with a boundary following a step-wise pattern from Baja California to the equator delineating the WCNPO stock from the EPO stock. This structure has since been used in recent stock assessments for the North Pacific Ocean (see 'Stock assessment and status' section). On the basis of CPUE and mean body weight data from the Japanese longline fishery, Ijima and Kanaiwa (2018) suggested that the WCNPO

### 4 Fisheries

#### 4.1 Commercial fisheries

Archaeological evidence has shown that fishing for swordfish has occurred for millennia, with harvests of swordfish from the Mediterranean dating back to the Aegean Bronze Age (3rd and 2nd millennium BC) (Rose, 1994). Since industrial times, swordfish have been harvested in all oceans and major seas, with catches historically made by artisanal fleets using harpoon and gillnet gears. Commercial harvests of swordfish increased significantly in the early 1950s due to the sharp increase in demand for canned tuna which drove major changes in global tuna fisheries, with swordfish caught as bycatch. As noted in the 'Diet and trophic ecology' section, an abrupt drop in global catches was observed between 1970–1971 (Figure 1) due to the implementation of strict regulations of mercury content in swordfish (Sonu, 1997). These regulations were relaxed in the late-1970s and catches increased in all global oceans and major seas thereafter. In recent years, global catches have exceeded 110,000 mt, peaking at ~118,600 mt in 2104–2015 (Figure 1) (FAO, 2020). The bulk of this catch has come from targeted fisheries, with swordfish caught at night by surface longlines that include gear modifications to increase catches such as changes in line material and the inclusion of light sticks (Bigelow et al., 1999; Hsu et al., 2015).

In the Pacific, swordfish are predominantly taken by longline, with smaller catches by other gears, including gillnets and harpoon, and occasionally pole-and-line and purse seine (Williams and Ruaia, 2020). The bulk of landings come from waters between 45°N and 40°S in the WCPO, and between 10°N and 40°S in the EPO (Figure 3). Pacific-wide, catches have increased steadily since the early 1950s, consistent with global trends, with annual landings in recent years exceeding 50,000 mt, just under 50% of the global commercial catch (Figure 1). Below, a breakdown of historical trends in catches of swordfish is presented, with catches grouped into the four broad geographic areas for which previous stock assessments have been conducted (see 'Stock Assessments and Status' section below), namely the WCNPO, the SWPO, the central EPO and the SEPO.

Historically, the majority of the Pacific commercial catch of swordfish has come from the waters of the WCNPO (Figure 4). Swordfish have been harvested in the far west WCNPO for centuries, predominantly by Japanese fishers in coastal waters using surface gear, including harpoons, handlines, and set nets (Sonu, 1997). Commercial fishing for swordfish in the WCNPO commenced in the early 1900s with the Californian harpoon fishery (PFMC, 2020). This fishery peaked in the late 1970s, with approximately 1,650 mt landed in 1978. Today, only a small number of vessels participate in this fishery (14 in 2018), landing a few hundred individuals per year (PFMC, 2020). A domestic drift gillnet fishery commenced on the west coast of the U.S in the late 1970s, primarily targeting common thresher shark (*Alopias vulpinus*), with swordfish taken as bycatch. In the mid-1980s, swordfish replaced common thresher shark as the primary target species, owing to its greater public demand and higher price, and the implementation of management measures to protect the thresher shark resource (PFMC, 2020). Drift gillnet catches of swordfish peaked in 1992 at ~1,400 mt. Since 2010, catches of swordfish by this fishery have been less than 200 mt per annum (PFMC, 2020).

As with other areas globally, the industrialisation of the tuna fishery in the 1950s resulted in increased catches of swordfish from the WCNPO. During the 1950s, Japanese distant water and offshore longline vessels targeting tuna accounted for more than 80% of the annual swordfish harvest in the WCNPO. Catches in the WCNPO peaked at 22,000 mt in 1961 but rapidly decreased in the 1960s, coincident with shifts in species targeting by longline fleets, reaching a historical low of 6,800 mt in 1972 (ISC Billfish Working Group, 2018). The rapid expansion of the Hawaii-based longline fishery, and to a lesser extent the Taiwanese distant-water longline fishery, resulted in an

increase in catches through the 1980s and 1990s, reaching ~19,000 mt in 1994. During the 2000s, the annual reported catches of swordfish in the WCNPO were between 10,000 and 14,000 mt. Since 2010, catches have declined to an average of ~10,000 mt per year (ISC Billfish Working Group, 2018).



**Figure 3:** Distribution and magnitude of longline catches (mt) of swordfish, *Xiphias gladius*, by decade and 5° square from the Pacific Ocean, a) 1979–1988, b) 1989–1998, c) 1999–2008, d) 2009–2018. Source: public domain data from WCPFC (available at: <a href="https://www.wcpfc.int/node/4648">https://www.wcpfc.int/node/4648</a>) and IATTC (available at: <a href="https://www.iattc.org/PublicDomainData/IATTC-Catch-by-species1.htm">https://www.iattc.org/PublicDomainData/IATTC-Catch-by-species1.htm</a>). Note catch data provided in numbers of fish have been converted to estimated weights on the basis of length composition by flag, period and area fished (where available), using information provided in Uchiyama et al. (1999), DeMartini et al. (2000), Sun et al. (2002), Hinton and Maunder (2011), ISC Billfish Working Group (2014), and ISC Billfish Working Group (2018) and references therein.

Fisheries for swordfish have operated in the SWPO since the early 1950s. As with the WCNPO, swordfish landings in the region were primarily made as bycatch by distant water longline vessels fishing for tuna. Catches increased steadily from the early 1970s up until around 2000, with the majority of catches made by Japanese fleets (Takeuchi et al., 2017). In the 1980s, a longline fishery developed off the east coast of Australia, with the species first fished by Japanese vessels, and later by Australian vessels operating in the East Coast Tuna and Billfish Fishery (ETBF). Catches from this fishery increased rapidly from less than 100 mt in 1995 to ~2,500 mt in the late 1990s to early 2000s (Ward and Elscot, 2000; Campbell and Hobday, 2003). Since the mid-2000s, catches in the ETBF have been relatively stable at around 1,100 mt, due to the implementation of much reduced total allowable catch (TAC) limits that aimed to avoid localised depletion and maintain economically viable catches rates in the fishery (Larcombe et al., 2020; Delegation of Australia, 2019). Similar rapid expansions of fishing effort and catch have been observed in the eastern region of the SWPO, with catches increasing from around 3,000 mt in the mid-1990s to over 9,000 by the mid-2000s, largely due to increases in catches by distant water fishing nations (DWFN) in tropical waters between 150° and 130°W and the equator and 20°S, particularly on the high seas by European Union vessels (Delegation of Australia, 2019) (Figure 3). Since the early 2000s, catches of swordfish in the SWPO

have stabilised at around 9,000 to 11,000 mt per year. In recent years, the majority of the catch of swordfish in the SWPO has been made in the south central Pacific Ocean region, primarily by the Spanish and Chinese longline fleets, off the east coast of Australia, and off the northeast of New Zealand (Figure 3) (Takeuchi et al., 2017).



**Figure 4:** Total annual catches of swordfish, *Xiphias gladius*, in the Pacific Ocean by geographic region, **1952–2015.** EPO = Eastern Pacific Ocean, SEPO = southern EPO, SWPO = southwest Pacific Ocean, WCNPO = western and central North Pacific Ocean. Based on data provided in Takeuchi et al. (2017), IATTC (2018), and ISC (2020). Note there are differences in catches reported from these sources and those reported in the respective stock assessments due to differences in geographical assignments of catches between documents.

Commercial longline fishing in the EPO assessment area began in the early 1950s by Peruvian vessels, with the Japanese longline fleet entering the fishery in the mid-1950s (ISC Billfish Working Group, 2014), followed by Korean and Mexican-flagged vessel. Catches by these fleets increased steadily until 1970, and fluctuated between 1,000 and 7,500 mt through to the 1990s, before declining sharply in the early-2000s. Since then, however, catches have risen abruptly, reaching a peak of 9,910 mt in 2012. In recent years, vessels flagged to Japan, Spain, China and Taiwan have jointly caught the majority of swordfish in the central EPO, landing around 85% for the total EPO harvest in 2012 (ISC Billfish Working Group, 2014).

Commercial fishing for swordfish in the southern EPO has occurred since at least the mid-1940s, with catches in early years made exclusively by the Chilean artisanal fleet, targeting large individuals using predominantly harpoon and gillnet gear (Hinton and Maunder, 2011). Peruvian coastal vessels and Japanese distant-water longline vessels joined the fishery in the mid-1950s, principally to target tuna, and by the mid-1970s the latter was responsible for the majority of the swordfish catch, landing an average of ~1,460 mt annually between 1975–1985 (Hinton and Maunder, 2011). Rapid expansion of the southern EPO fishery occurred in the late 1980s with the development of targeted fisheries for the species, and the subsequent inclusion of Spanish offshore longline vessels and Chilean industrial longline vessels, with estimated total landings increasing from 1,347 mt in 1985 to 12,514 mt in 1991. Increases in CPUE of the main fleets were observed over the same period (Hinton and Maunder, 2011), although it is unclear whether these increases reflect changes in swordfish abundance in abundance or technological advancements in swordfish fishing, in particular changes in

line material and inclusion of light sticks on longlines. In the early 2000s, the Spanish coastal longline fleet joined the fishery, and in recent years the combined Spanish offshore longline and coastal longline fleets have taken the majority of the catch, landing an estimated 8,011 mt of a total of 13,443 mt in 2009 (Hinton and Maunder, 2011). These fleets typically catch small fish, with fish fully selected at <90 cm LJFL (Hinton and Maunder, 2011). Since the early 2000s, catches in the SEPO have nearly doubled, often exceeding 24,000 mt per year in recent years, and reaching over 29,000 mt in 2016 (Figure 4) (IATTC, 2018). This rapid expansion has predominantly occurred in area previously subject to little fishing pressure, and thus has considerably reduced the spatial extent where swordfish are not exploited (Figure 3).

#### 4.2 Recreational and sport fisheries

Swordfish are highly prized by recreational and sports fishers due to their fighting ability and highquality flesh, and small quantities of swordfish are taken by these fishers throughout the range where the species occurs close to shore. Off the coast of California, swordfish have been targeted by recreational and sports fishers since the early 1900s (Bedford and Hagerman, 1983). From the late 1960s to the early 1980s, annual catches were in the order of ~30 fish, with a peak of 130 individuals taken in 1978 (Bedford and Hagerman, 1983). In recent years, however, catches have increased, largely due to the adoption of deep-drop techniques (NOAA, 2020). Swordfish have been caught recreationally off the east coast of Australia since at least the mid-1980s, albeit in low numbers. Similar to California, however, a growing seasonal recreational fishery has occurred off Victoria and Tasmania, in southeast Australia, in recent years, with fishers typically landing swordfish on the continental shelf break using deep-dropping techniques at depths of approximately 400-600 m from late summer to winter (Tracey and Pepperell, 2018). A total of 74 swordfish captures were reported by recreational fishers off eastern Tasmania between 2014–2016, and the success of this approach, combined with the large size of fish caught, has attracted greater attention from recreational fishers (Tracey and Pepperell, 2018). Post-capture survival of swordfish caught via this approach is considered to be low, with most fish suffering mild to severe forms of barotrauma (Tracey and Pepperell, 2018). Recreational landings of swordfish caught by deep-drop methods also occur off the northeast of New Zealand. A combined allowance of 20 tonnes is in place for the recreational and charter sectors under New Zealand's quota management system, although recent recreational catches are considered to be lower than this value (Fisheries New Zealand, 2019).

### 5 Stock assessment and status

Although there is considerable uncertainty regarding the stock structure of swordfish in the Pacific Ocean, formal stock assessments have been conducted for swordfish stocks spanning four broad regions of the Pacific Ocean: the WCNPO, EPO, SEPO, and SWPO (Figure 5). In lieu of formally agreed limit reference points, the status of these four stocks are currently assessed relative to spawning potential depletion (e.g., the ratio between current spawning stock biomass (SB_{CURR}) and the spawning stock biomass in the absence of fishing (SB_{F=0})), and/or maximum sustainable yield (MSY) based reference points (e.g., the ratio between current spawning stock biomass and the spawning stock biomass at MSY (SB/SB_{MSY})), and the ratio between fishing mortality and fishing mortality at MSY (F/F_{MSY}) (Hinton and Maunder, 2011; ISC Billfish Working Group, 2014; Takeuchi et al., 2017; ISC Billfish Working Group, 2018).

The most recent stock assessment for swordfish in the WCNPO was conducted in 2018, using data from 1975–2016 (ISC Billfish Working Group, 2018). The assessment built upon that conducted in 2014, and was based on fitting a sex-specific, age-structured model to standardised CPUE and size composition data. The base case model estimated female spawning biomass to be ~90% above SB_{MSY}, while fishing mortality (*F*) was estimated to be ~45% below  $F_{MSY}$ . Although there are no currently agreed reference points for the stock, the authors concluded that at the time of the assessment, swordfish in the WCNPO were not likely overfished and not likely experiencing overfishing relative to MSY-based or 20%SB_{F=0}-based reference points (ISC Billfish Working Group, 2018). The authors noted that the key areas of uncertainty in the assessment were the simplified treatment of spatial structure and the lack of sex-specific size composition data, and recommended the collection of sex-specific fishery data and management strategy evaluation work be undertaken to address these issues (ISC Billfish Working Group, 2018).



**Figure 5:** Boundaries of the spatial domains used in recent Pacific swordfish stock assessments. Dashed lines within stock assessment regions reflect model sub-regions (where present). References in parentheses indicate the most recent stock assessment for each region.

The status of swordfish in the EPO was last assessed in 2014, using data from 1951–2012 (ISC Billfish Working Group, 2014) in a surplus production model. Results indicated that overfishing had likely occurred in the past, and may be occurring in recent years, with recent average catches almost two times higher than the estimated MSY (5,490 mt) (ISC Billfish Working Group, 2014). In 2012, there was a 55% probability that overfishing was occurring, but less than a 1% probability that the stock was overfished. The authors concluded that maintaining the current (at the time of the assessment) EPO swordfish catch level through to 2016 would lead to a moderate risk of overfishing in the near future, but would lead to virtually no chance of the stock being overfished (ISC Billfish Working Group, 2014).

Swordfish in the SEPO were formally assessed in 2011, using data from 1945–2010 (Hinton and Maunder, 2011). Key results from the assessment were that swordfish in the SEPO were likely not experiencing overfishing and were not overfished, and that the spawning biomass ratio was estimated to be ~1.45, indicating that the spawning biomass is the level expected to produce catch at the MSY level (Hinton and Maunder, 2011). Current catch levels are estimated to be at about MSY (~25,000 mt) (IATTC, 2018). An updated assessment for this stock is planned for late 2021.

Assessments of swordfish in the SWPO have been conducted regularly since initial assessments were conducted in 2006 (Davies et al., 2006; Kolody et al., 2006), with additional assessments conducted in 2008 (Davies et al., 2008; Kolody et al., 2008) and 2013 (Davies et al., 2013). The last assessment for swordfish in the SWPO was conducted in 2017, using sex-aggregated data to 2015 (Takeuchi et al., 2017). The assessment assumed a single stock from 50°S to the equator between 140°E and 150°W, and from 50°S to 4°S between 150°W and 130°W, with a two-region structure, delineated at 165°E (Figure 5). The assessment was based on fitting an age-structured population dynamics model to catch, standardised CPUE and length frequency data in an uncertainty grid that included steepness, size data weighting, diffusion rate and M as the main uncertainties. Spawning stock biomass in both model regions was estimated to have progressively declined throughout the time series, with particularly steep declines occurring in the last 15 years, most notably in the eastern region. The rate of fishing mortality was estimated to have increased markedly from the mid-1990s onwards in both model regions. Despite these trends, spawning stock biomass was estimated to likely be above the default limit reference point of 20%SB_{F=0} (i.e., the stock was not overfished), while recent fishing mortality was likely below  $F_{MSY}$  (i.e., the stock was not experiencing overfishing) (Takeuchi et al., 2017).

### 6 International management

A harvest strategy has been in place for swordfish in the WCPFC Convention Area north of 20° N since 2019 (WCPFC, 2020). Under the harvest strategy, a limit reference point for the exploitation rate (F-limit) is set at  $F_{MSY}$ . At the time of writing, the harvest strategy requires further development and refinement; for example, there are currently no target reference points (TRPs) for either biomass (B-target) or exploitation rate (F-target).

Management of swordfish in the SWPO is enacted by Conservation and Management Measure (CMM) 2009–03 (WCPFC, 2009). This CMM outlines several strategies to ensure the long-term sustainability and economic viability of fisheries for South Pacific swordfish in the WCPFC Convention Area, including restraints on the number of vessels fishing for swordfish in the area south of 20°S, and the catch of those vessels; provisions to prevent a re-distribution of fishing effort to the area north of 20°S; and nomination of the maximum total annual catch by each CMM in the area south of 20°S between 2000–2006, from which to set future maximum total annual catches (WCPFC, 2009). In recent years, there has been growing concerns from some WCPFC members, co-operating nonmembers and participating territories (CCMs) that the measures contained in CMM 2009-03 are insufficient to ensure the ongoing sustainability or economic viability of swordfish fisheries in the region, or for future development opportunities for Small Island Developing States (SIDS) (Delegation of Australia, 2019). These concerns primarily relate to 1) a lack of restrictions on catch and effort for swordfish in the region between the equator and 20°S, where catches in high seas areas have increased markedly since the adoption of CMM 2009–03; 2) catch limits in the area south of 20°S being too high, noting that if the prescribed catch limits were fully utilised, the combination of those catches with recent catches north of 20°S would significantly increase the probability of overfishing; the species' vulnerability to sub-regional depletions, and 3) the expansion of fishing effort and catch of swordfish in the SEPO, noting the uncertainty around the stock structure and potential connectivity of swordfish among different regions of the South Pacific Ocean (Delegation of Australia, 2019).

There are no internationally adopted CMMs or harvest strategies in effect for swordfish in the EPO or the SEPO, although a range of management measures enacted to ensure the sustainability of tuna and shark stocks in the region may benefit swordfish.

### 7 Future research directions

Research conducted into swordfish since the industrialisation of tuna fisheries in the Pacific Ocean has greatly increased knowledge and understanding of the life history of this iconic apex predator. However, with fishing pressure in most regions of the Pacific Ocean increasing, and the extent of unfished areas diminishing, there is a pressing need to address several key knowledge gaps in order to strengthen future assessments, improve management, and ensure ongoing sustainability of the resource.

### 7.1 Life history

#### 7.1.1 Length-length and length-weight conversion factors

Swordfish landed commercially are typically processed at sea in a variety of forms, including whole; whole with bill removed at a point level with the tip of the lower jaw; gilled, gutted and headed; gilled, gutted, headed with all fins removed; or processed into loins. Accordingly, the development of length-length conversion factors across various processing forms is critical for standardising length data for use in stock assessments. Similarly, length-weight relationship coefficients are important parameters in stock assessments and are used for calculating estimates of weight from length measurements, calculating fish condition, and for estimating quantities of spawning biomass. For Pacific swordfish, length-length and length-weight conversions factors have been generated for samples covering a short temporal periods, limited geographical ranges relative to stock assessment areas, or limited length ranges. For example, the assessment of swordfish in the SWPO by Takeuchi et al. (2017) used the length-weight relationship of Davies et al. (2005). Samples used to develop this relationship were collected from a small part of the assessment model's spatial domain (i.e., within the EEZ of New Zealand), and thus are likely not to be representative of the entire stock. Increased sampling, covering the geographic extent of the stock boundaries, should be conducted to ensure length-length and length-weight relationships are representative of the stock(s) being assessed.

#### 7.1.2 Age and growth

The lack of direct validation of swordfish age estimation methods is a key limitation of age and growth studies, and a critical source of uncertainty when using resulting age-based information in stock assessments. To date, there have been no successful attempts at direct validation using chemical tagging approaches, although the viability of these approaches has been established for other billfishes (e.g., black marlin; Speare, 2003). Focusing chemical tagging studies in areas where swordfish congregate and exhibit relatively high site fidelity and seasonal predictability, such as around seamounts off the east coast of central Queensland, Australia (Campbell and Hobday, 2003), or in the vicinity of the continental shelf break off the east coast of Tasmania, Australia (Tracey and Pepperell, 2018), may provide the best opportunity to recapture chemically-tagged fish. Additionally, application of bomb radiocarbon or radiometric analyses to otolith material may also provide a means of validating swordfish age estimations, with these approaches having been used successfully on other species of billfish and tunas in recent years (Andrews et al., 2018; Ishihara et al., 2017). At the very least, this technique would allow age estimation scenarios to be eliminated.

Standardised approaches to ageing, including assessment of the most appropriate structure from which to base age estimates, and protocols for delineating otolith increments, should be developed for swordfish with high priority. Currently, fin rays are used to estimate ages and generated lengthat-age information for three of the four stock assessments for Pacific swordfish. Recent work on the age and growth of swordfish in the SWPO, however, indicates that relative to otolith ageing, determining age using fin rays could underestimate the age of individuals (Farley et al., 2016). In light of this, growth for swordfish across the Pacific should be revisited and alternative ageing methods including otolith ageing should be explored. Coordination across ageing laboratories through workshops, such as recently undertaken for bigeye and yellowfin tunas in the Pacific (IATTC, 2019), will be central to ensuring consistency in how age estimations are developed between assessment regions, and in stimulating future developments and improvements in swordfish ageing techniques. Once standardised criteria are established, a reference set of aged individuals should be created, to aid future interpretation and facilitate consistency in ageing estimated between laboratories and over time.

Increased spatial sampling for age and growth studies, including from areas where fishing pressure has increased in recent years such as the central equatorial Pacific, will be important for improving understanding of spatial variation in growth, and the resulting effect on stock status.

#### 7.1.3 Reproductive biology

Similar to the need for standardisation in ageing approaches, there is significant need for the standardisation of the collection, preservation, treatment and assignment of reproductive tissue, and approaches to assessing maturity status, between regions. Currently, there is considerable variation in how tissues are stored and processed, and reproductive assignments designated, between studies and regions. For swordfish, a particular challenge occurs when trying to differentiate immature (virgin) from mature–resting (post-spawning) females because after spawning, females absorb all their yolked eggs (oocytes) and appear histologically similar to immature females. Differentiation of these individuals can have a large effect on maturity ogives and subsequent estimates of stock status (Farley et al., 2016). Recent work conducted in the SWPO indicates that 'maturity markers' (e.g., muscle bundles, brown bodies) evident in frozen-fixed tissues may be highly suitable for differentiating these stages (Farley et al., 2016). As with age and growth, coordination across ageing laboratories through workshops will be central to ensuring consistency in the collection, preservation, preparation and designation of reproductive material. Once standardised criteria in reproductive assignments are established, a reference set of histological material should be developed to aid interpretation and facilitate consistency between laboratories and over time.

#### 7.1.4 Stock structure

While insights from tagging data, genetics, otolith chemistry and fishery data have greatly increased understanding of the movements and stock structure of swordfish in the Pacific Ocean, considerable uncertainty still remains, with a number of differing hypotheses proposed. This is because most studies have typically been constrained by effects of scale (both spatial and temporal), sampling design, limitations in resolution of the techniques, availability of samples or data. For example, although electronic tagging approaches have provided useful information where implemented, these studies have been restricted to relatively small numbers of fish tagged in widely separated areas. Furthermore, inferences of stock structure based on movement and mixing from tagging data have been limited by the time of individuals at liberty, limitations of the tags used, as well as uncertainties around the population representativeness of tagged individuals (Evans et al., 2014; Sepulveda et al. 2019).

While genetic studies have generally ruled out ocean-scale panmixia, research conducted to date has largely proven inconclusive in delineating stock boundaries of Pacific swordfish. This is because most genetic studies on Pacific swordfish conducted to date have used a small number of markers distributed in a limited portion of the genome, that are extremely sensitive to the movement of small numbers of individuals between populations (Slatkin, 1987), or that show low levels of genetic differentiation resulting from large population sizes and high fecundity (Palumbi, 2003). Studies have

also been limited by sampling design and logistical issues, including sample size limitations; opportunistic sampling of fish in foraging areas, which could potentially include a mix of several stocks, rather than targeted sampling of spawning fish; or by widely-separated sampling locations (Chow et al., 1997; Alvarado Bremer et al. 2006; Kasapidis et al. 2008).

Accordingly, dedicated and coordinated research into the stock structure of the species is required to improve understanding of swordfish stock structure in the Pacific. Ideally, this research should adopt a holistic approach that incorporates a range of complementary genomic and non-genomic approaches, such as recently proposed for addressing uncertainty regarding stock structure of skipjack, bigeye, yellowfin and South Pacific albacore tunas in the Pacific Ocean (Moore et al., 2020a; Moore et al., 2020b). In particular, use of more powerful and cost-effective genomic tools (e.g., next generation sequencing tools; NGS) would represent a clear way forward for resolving swordfish stock structure.

Extension of electronic tag releases, particularly in tropical areas and around current assessment boundaries, would be an important inclusion in a multidisciplinary study into swordfish stock structure, and, if implemented successfully, would help to fill important knowledge gaps and evaluate how well management areas agree with population structure (Evans et al., 2014). In particular, fin-mounted Smart Position or Temperature (SPOT) transmitting tags hold considerable promise for improving understanding of swordfish movements, identifying putative spawning areas and delineating spatial structure. These tags provide, are capable of providing movement information at near real-time positions over relatively long periods (i.e., multi-year), and are not subject to issues associated with estimating position from ambient light levels, which can be problematic for swordfish given their diving behaviour.

Resolving uncertainties around swordfish spawning behaviour, including fine-scale spatio-temporal patterns of spawning and any potential fidelity to particular spawning areas, is key to delineating the stock structure of swordfish in the Pacific Ocean. A comprehensive assessment of spawning activity, including both spatial patterns and associated timing of spawning (particularly identifying temporal overlaps or offsets between locations), examined in conjunction with known information on mesoscale oceanographic features such as eddies, currents and upwellings, would provide a key first-step in better understanding the spatio-temporal structuring of the spawning dynamics of swordfish. Examination of a range of data sources, including larval distributions from scientific surveys, the stomach contents of predators of larval swordfish, records of visibly spawning (i.e., running ripe) fish from fisheries observers, histological examination of previously collected gonad material, and multi-year movement data from tagged reproductively mature individuals, including depth data and diving behaviour, should help further resolve spatial and temporal dynamics in spawning.

#### 7.1.5 Dietary and whole-of-ecosystem studies

While not necessary for stock assessments, quantitative dietary information is important for ecosystem models (e.g., SEAPODYM; Lehodey et al., 2008) to allow simulation of fishing and climate change effects on pelagic species and ecosystems. To date, however, research into the diet and trophic ecology of swordfish has been conducted over relatively restricted temporal periods, and the vast majority of research to date has been conducted in the EPO. Future research into the diet and trophic ecology of swordfish should be conducted, particularly in the WCPO, to inform ecosystem models, understand to what extent changes in swordfish abundance indices are related to changes in prey or predator densities, and better understand the effects of global stressors such as climate change on Pacific swordfish populations.

#### 7.2 Data collection to inform stock assessments

Lack of sex-specific data has been raised as a key source of uncertainty in the most recent assessments of swordfish in the WCNPO (ISC Billfish Working Group, 2018) and SWPO (Takeuchi et al., 2017). In each instance, the authors recommended that collection of sex-specific fishery data be improved. However, the implementation of, or move towards, electronic monitoring (EM) within several Pacific fisheries will mean that the availability of sex-specific catch information may be further reduced in the future. Improving understanding of spatio-temporal patterns in sex ratios, in particular, intra-annual variability would help provide a basis for determining catch proportions by sex using probabilistic methods. Opportunities to maximise the collection of sex-specific data from commercial landings, including by observers, through port sampling programs, or via coordination of fishing crews where fish are gutted at sea, would help in this regard. Improved collection of gear characteristics used in fishing operations, such as the number of light sticks used on a line or other technological advancements in place that may increase the catchability of swordfish, would help better understand changes in abundance indices.

#### 7.3 Stock assessments

There is a pressing need to increase the frequency of swordfish stock assessments, particularly for the EPO and SEPO. While both of these stocks will be assessed in 2021, previous assessments have been conducted somewhat sporadically, with the last assessments being conducted in 2014 and 2011, respectively (Hinton & Maunder, 2011; ISC Billfish Working Group, 2014). Accordingly, there will be 7- and 10-year gaps between assessments for the EPO and SEPO, respectively. Assuming current longevity estimations are accurate, a 10-year gap means that assessments are conducted over near non-overlapping generational timescales. Increasing the frequency at which these stock assessments are conducted (e.g., every 3–4 years) would better align assessments to biological processes, allow data provisioners and analysts critical foresight for planning towards assessments, and ultimately ensure stocks can be managed adaptively. An increase in the frequency of assessments is particularly important given the large increases in fishing mortality in recent years, and the largely unknown effects of increased climatic variability of Pacific swordfish.

#### 7.4 Reference points and harvest strategies

A critical priority for Pacific swordfish is the establishment of swordfish-specific harvest strategies for the SEPO, the refinement of the existing CMM 2009-03 for the SWPO, and the development of agreed reference points of stock status for each of the assessed stocks. Research to support these developments, tested the implications of proposed scenarios on catch, catches rates and stock status, should be conducted with high priority.

### 8 Acknowledgements

The author wishes to thank the large number of people who provided advice on Pacific swordfish life history, fisheries and management, or comments on the report, in particular Jennifer Devine, Steve Parker and Lynda Griggs (NIWA), Laura Tremblay-Boyer (Dragonfly Data Science), Nicholas Ducharme-Barth, Paul Hamer and Simon Nicol (SPC), John Annala, Heather Ward and Hilary Ayrton (Fisheries New Zealand), Chugey Sepulveda (Pfleger Institute of Environmental Research), Carolina Minte-Vera (Inter-American Tropical Tuna Commission), and Michelle Sculley (National Oceanic and Atmospheric Administration), as well as participants at the 1st Technical Workshop on Swordfish in the South EPO, December 2020. Development of this report was funded by NIWA and the Pacific Community (SPC).

#### 9 References

- Abascal, F.J., Mejuto, J., Quintans, M., Ramos-Cartelle, A. (2010) Horizontal and vertical movements of swordfish in the southeast Pacific. *ICES Journal of Marine Science*, 67: 466–474.
- Abecassis, M., Dewar, H., Hawn, D., Polovia, J. (2012) Modeling swordfish daytime vertical habitat in the North Pacific Ocean from pop-up archival tags. *Marine Ecology Progress Series*, 452: 219–236.
- Acosta-Pachón, T.A., Ortega-Garcia, S., Graham, B. (2020) Assessing residency and movement dynamics of swordfish *Xiphias gladius* in the Eastern North Pacific Ocean using stable isotope analysis. *Marine Ecology Progress Series*, 645: 171–185.
- Alvarado Bremer, J.R. (1994) Assessment of morphological and genetic variation of the swordfish (Xiphias gladius Linnaeus): evolutionary implications of allometric growth and of the patterns of nucleotide substitution in the mitochondrial genome. Ph.D thesis, University of Toronto.
- Alvarado Bremer, J.R., Baker, A.J., Mejuto, J. (1995) Mitochondrial DNA control region sequences indicate extensive mixing of swordfish (*Xiphias gladius*) populations in the Atlantic Ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, 52: 1720–1732.
- Alvarado Bremer, J.R., Hinton, M.G., Greig, T.W. (2006) Evidence of the spatial genetic heterogeneity in Pacific swordfish revealed by the analysis of LDH-A sequences. *Bulletin of Marine Science*, **79**, 493–503.
- Alvarado Bremer, J.R., LeClerc, G.M., Ely, B. (1998) Mitochondrial and nuclear DNA analyses in the study of swordfish, *Xiphias gladius*, population structure. *NOAA Technical Report*, *NMFS*, 142: 211–217.
- Alvarado Bremer, J.R., Mejuto, J., Gómez-Márquez, J., Boán, F., Carpintero, P., Rodríguez, J.
   M., Viñas, J., Greig, T.W., Ely, B. (2005) Hierarchical analyses of genetic variation of samples from breeding and feeding grounds confirm the genetic partitioning of northwest Atlantic and South Atlantic populations of swordfish (*Xiphias gladius* L.) *Journal of Experimental Marine Biology and Ecology*, 327: 167–182.
- Alvarado Bremer, J.R., Mejuto, J., Greig, T.W., Ely, B. (1996) Global population structure of the swordfish (*Xiphias gladius* L.) as revealed by analysis of the mitochondrial DNA control region. *Journal of Experimental Marine Biology and Ecology*, 197: 295–310.
- Andrews, A.H., Humphreys, R.L.J., Sampaga, J.D. (2018) Blue marlin (*Makaira nigricans*) longevity estimates confirmed with bomb radiocarbon dating. *Canadian Journal of Fisheries and Aquatic Sciences*, 75: 17–25.
- Arocha, F. (2007) Swordfish reproduction in the Atlantic Ocean: An overview. *Gulf and Caribbean Research*, 19: 21–36.
- Barneche, D.R., Robertson, D.R., White, C.R., Marshall, D.J. (2018) Fish reproductive-energy output increases disproportionately with body size. *Science*, 360: 642–645.
- Bartoo, N.W., Coan, A.L.J. (1989) An assessment of the Pacific swordfish resource. *In:* Stroud, R.H. (ed). *Planning the future of billfishes: Proceedings of the 2nd International*

*Billfish Symposium, 1989 Kailua-Kona, Hawaii*. National Coalition for Marine Conservation, Inc., Savannah, Georgia, p. 137–151.

- Bedford, D.W., Hagerman, F.B. (1983) The billfish fishery resource of the California current. *CalCOFI Report*, 24: 70–78.
- Bigelow, K.A., Boggs, C.H., He, X. (1999) Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. *Fisheries Oceanography*, 8, 178–198.
- Boggs, C.H. (1989) Vital rate statistics for billfish stock assessment. In: Stroud, R.H. (ed). Planning the future of billfishes: Proceedings of the 2nd International Billfish Symposium, 1989 Kailua-Kona, Hawaii. National Coalition for Marine Conservation, Inc., Savannah, Georgia, p. 225–233.
- Branco, V., Vale, C., Canário, J., Neves dos Santos, M. (2007) Mercury and selenium in blue shark (*Prionace glauca*, L. 1758) and swordfish (*Xiphias gladius*, L. 1758) from two areas of the Atlantic Ocean. *Environmental Pollution*, 150: 373–380.
- Braun, C.D., Gaube, P., Afonso, P., Fontes, J., Skomal, G.B., Thorrold, S.R. (2019) Assimilating electronic tagging, oceanographic modelling, and fisheries data to estimate movements and connectivity of swordfish in the North Atlantic. *ICES Journal of Marine Science*, 76: 2305–2317.
- Brodziak, J. (ed.) (2011) An investigation of potential natural mortality rates for North Pacific swordfish. U.S Department of Commerce, NOAA Technical Memorandum NMFS/SPO-119, Seattle, WA, USA.
- Burnett, C.D., Beckett, J.S., Dickson, C.A., Hurley, P.C.F., Iles, T.D. (1987) A summary of releases and recaptures in the Canadian large pelagic fish tagging program 1961–1986. *Canadian Data Report of Fisheries and Aquatic Sciences*, 673: 99 p.
- Campbell, R., Dowling, N. (2003) Development of an operating model and evaluation of harvest strategies for the Eastern Tuna and Billfish Fishery. *Final report for Project* 1999/107. Fisheries Research and Development Corporation, Canberra, Australia.
- Campbell, R.A., Hobday, A.J. (2003) Swordfish seamount environment fishery interactions off eastern Australia. *Working Paper BBRG-3, 16th Meeting of the Standing Committee on Tunas and Billfish.* July 9–17 2003, Mooloolaba, Australia.
- Carey, F.G., Robison, B.H. (1981) Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fishery Bulletin*, 79: 277–292.
- Cerna, J.F. (2009) Age and growth of the swordfish (*Xiphias gladius* Linnaeus, 1758) in the southeastern Pacific off Chile (2001). *Latin American Journal of Aquatic Research*, 37: 59–69.
- Chong, J., Aguayo, M. (2009) Age and growth of swordfish (*Xiphias gladius* Linnaeus, 1758) in the southeastern Pacific (December 1994-September 1996). *Latin American Journal of Aquatic Research*, 37: 1–15.
- Chow, S., Okamoto, H., Uozumi, Y., Takeuchi, Y., Takeyama, H. (1997) Genetic stock structure of the swordfish (*Xiphias gladius*) inferred by PCR-RFLP analysis of the mitochondrial DNA control region. *Marine Biology*, 127: 359–367.

- Chow, S., Takeyama, H. (2000) Nuclear and mitochondrial DNA analyses reveal four genetically separated breeding units of the swordfish. *Journal of Fish Biology*, 56: 1087– 1098.
- Claramunt, G., Herrara, G., Donoso, M. & Acuña, E. 2009. Spawning period and frequency of swordfish (*Xiphias gladius*) caught in the southeastern Pacific. *Latin American Journal of Aquatic Research*, 37: 29–41.
- Collette, B.B., McDowell, J.R., Graves, J.E. (2006) Phylogeny of recent billfishes (Xiphioidei). *Bulletin of Marine Science*, 79: 455–468.
- Davies, N., Bian, R., Kolody, D., Campbell, R. (2008) CASAL stock assessment for southwest-central Pacific broadbill swordfish 1952–2007. Working Paper WCPFC-SC4-2008/SA-WP-7, 4th Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission. 11–22 August 2008, Port Moresby, Papua New Guinea.
- Davies, N., Campbell, R., Kolody, D. (2006) CASAL stock assessment for south-west Pacific broadbill swordfish 1952–2004. Working Paper WCPFC-SC2-2006/ME WP-4, 2nd Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission. 7–18 August 2006, Manila, Philippines.
- Davies, N., Griggs, L., Unwin, M. (2005) Information available for developing a stock assessment for New Zealand swordfish (*Xiphias gladius*). *Final Research Report for Ministry of Fisheries Research Project SWO2003-01*. National Institute of Water and Atmospheric Research Ltd, Wellington, New Zealand.
- Davies, N., Pilling, G.M., Harley, S., Hampton, J. (2013) Stock assessment of swordfish (*Xiphias gladius*) in the southwest Pacific Ocean. Working Paper WCPFC-SC9-2013/SA-WP-05, 9th Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission. 6–14 August, Pohnpei, Federated States of Micronesia.
- Delegation of Australia (2019) Strengthening the management of South Pacific broadbill swordfish (*Xiphias gladius*). *Delegation Paper WCPFC16-2019-DP19, 16th Regular Session of the Western and Central Pacific Fisheries Commission.* 5–11 December 2019, Port Moresby, Papua New Guinea.
- DeMartini, E.E., Uchiyama, J.H., Humphreys, R.L.J., Sampaga, J.D., Williams, H.A. (2007) Age and growth of swordfish (*Xiphias gladius*) caught by the Hawaii-based pelagic longline fishery. *Fishery Bulletin*, 105: 356–367.
- DeMartini, E.E., Uchiyama, J.H., Williams, H.A. (2000) Sexual maturity, sex ratio, and size composition of swordfish, *Xiphias gladius*, caught by the Hawaii-based pelagic longline fishery. *Fishery Bulletin*, 98: 489–506.
- Dewar, H., Prince, E.D., Musyl, M.K., Brill, R.W., Sepulveda, C., Luo, J., Foley, D., Orbesen, E.
  S., Domeier, M.L., Nasby-Lucas, N., Snodgrass, D., Laurs, R.M., Hoolihan, J.P., Block, B.A., McNaughton, L.M. (2011) Movements and behaviours of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags. *Fisheries Oceanography*, 20: 219–241.
- Ehrhardt, N.M. (1992) Age and growth of swordfish, *Xiphias gladius*, in the northwestern Atlantic. *Bulletin of Marine Science*, 50: 292–301.

- Esposito, M., De Roma, A., La Nucara, R., Picazio, G., Gallo, P. (2018) Total mercury content in commercial swordfish (*Xiphias gladius*) from different FAO fishing areas. *Chemosphere*, 197: 14–19.
- Evans, K., Abascal, F., Kolody, D., Sippel, T., Holdsworth, J., Maru, P. (2014) The horizontal and vertical dynamics of swordfish in the South Pacific Ocean. *Journal of Experimental Marine Biology and Ecology*, 450: 55–67.
- FAO (2020) Fishery and Aquaculture Statistics. Global production by production source 1950–2018 (FishstatJ). FAO, Rome.
- Farley, J., Clear, N., Kolody, D., Krusic-Golub, K., Eveson, P., Young, J. (2016) Determination of swordfish growth and maturity relevant to the southwest Pacific stock. Working Paper WCPFC-SC12-2016/SA WP-11, 12th Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission. 3–11 August 2016. Bali, Indonesia.
- Fierstein, H.L. (2006) Fossil history of billfish (Xiphioidei). *Bulletin of Marine Science*, 79: 433–453.
- Fisheries New Zealand (2019) Fisheries Assessment Plenary, November 2019: Stock Assessments and Stock Status. Wellington, New Zealand: Compiled by the Fisheries Science and Information Group, Fisheries New Zealand.
- Fritsches, K.A., Brill, R.W., Warrant, E.J. (2005) Warm eyes provide superior vision in swordfishes. *Current Biology*, 15: 55–58.
- Fu, D. (2020) Preliminary Indian Ocean swordfish stock assessment 1950–2018 (Stock Synthesis). *IOTC-2020-WPB18-16*. Online meeting.
- Galli, G.L.J., Shiels, H.A., Brill, R.W. (2009) Temperature sensitivity of cardiac function in pelagic fishes with different vertical mobilities: yellowfin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*), mahi (*Coryphaena hippurus*), and swordfish (*Xiphias gladius*). *Physiological and Biochemical Zoology*, 82: 280–290.
- Gillett, R., Tautai, M.I. (2018) Fisheries of the Pacific Islands: Regional and National Information, Apia, Samoa, FAO.
- Govoni, J.J., Laban, E.H., Hare, J.A. (2003) The early life history of swordfish (*Xiphias gladius*) in the western North Atlantic. *Fishery Bulletin*, 101: 778–789.
- Govoni, J.J., Stender, B.W., Pashuk, O. (2000) Distribution of larval swordfish, *Xiphias gladius*, and probable spawning off the southeastern United States. *Fishery Bulletin*, 98: 64-74.
- Grall, C., De Silva, D.P., Houde, E.D. (1983) Distribution, relative abundance and seasonality of swordfish larvae. *Transactions of the American Fisheries Society*, 112: 235–246.
- Grewe, P., Feutry, P., Foster, S., Aulich, J., Lansdell, M., Cooper, S., Clear, N., Eveson, P., Fernando, D., Darnaude, A.M., Nikolic, N., Fahmi, Z., Marsac, F., Farley, J., Davies, C. (2020) Genetic population structure of sailfish, striped marlin, and swordfish in the Indian Ocean from the PSTBS-IO project. *IOTC-2020-WPB18-09, 18th Working Party on Billfish, Indian Ocean Tuna Commission.*

- Griggs, L., Francis, M., Ó Maolagáin, C. (2005) Growth rate, age at maturity, longevity and natural mortality rate of swordfish (*Xiphias gladius*). National Institute of Water and Atmospheric Research, Wellington, New Zealand.
- Grijalva-Chon, J.M., de la Rosa-Vélez, J., Sosa-Nishizaki, O. (1996) Allozyme variability in two samples of swordfish, *Xiphias gladius* L., in the North Pacific Ocean. *Fishery Bulletin*, 94: 589–594.
- Grijalva-Chon, J.M., Numachi, K., Sosa-Nishizaki, O., de la Rosa-Velez, J. (1994)
   Mitochondrial DNA analysis of North Pacific swordfish *Xiphias gladius* population structure. *Marine Ecology Progress Series*, 115: 15–19.
- Hinton, M.G., Deriso, R.B. (1994) Distribution and stock assessment of swordfish, *Xiphias gladius*, in the eastern Pacific Ocean from catch and effort data standardized on biological and environmental parameters. NOAA Technical Report NMFS, 142: 161–179.
- Hinton, M.G., Maunder, M.N. (2011) Status of swordfish in the eastern Pacific Ocean in 2010 and outlook for the future. *Document SAC-02-09, 2nd Scientific Advisory Committee Meeting, Inter-American Tropical Tuna Commission.* 9–12 May 2011, La Jolla, California, USA.
- Hinton, M.G., Bayliff, W.H., Suter, J. (2005) Assessment of swordfish in the eastern Pacific Ocean. *Inter-American Tropical Tuna Commission Stock Assessment Report*, 5: 291–326.
- Holdsworth, J.C., Sippel, T.J., Saul, P.J. (2007) An investigation into swordfish stock structure using satellite tag and release methods. *Working Paper WCPFC-SC3-BI SWG/WP-3, 3rd Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission.* 13–24 August 2007, Honolulu, Hawaii.
- Hsu, A.C., Boustany, A.M., Roberts, J.J., Chang, J.H., Halpin, P. (2015) Tuna and swordfish catch in the U.S. northwest Atlantic longline fishery in relation to mesoscale eddies. *Fisheries Oceanography*, 24: 508–520.
- Humphreys, R.L.J., Campana, S.E., DeMartini, E.E. (2005) Otolith elemental fingerprints of juvenile Pacific swordfish *Xiphias gladius*. *Journal of Fish Biology*, 66: 1660–1670.
- IATTC (2018) Tunas, billfishes and other pelagic species in the eastern Pacific Ocean in 2017.
   Working Paper WCPFC-SC14-2018/GN-WP-02, 14th Regular Session of the Scientific
   Committee of the Western and Central Pacific Fisheries Commission. 8–16 August 2018,
   Busan, Republic of Korea.
- IATTC (2019) Workshop on methodologies for estimating age of bigeye and yellowfin tunas from otoliths. Inter-American Tropical Tuna Commission, 25–26 June 2019, La Jolla, California, USA.
- ICCAT (2017) Report of the 2017 ICCAT Atlantic swordfish stock assessment session. International Commission for the Conservation of Atlantic Tunas, Madrid, Spain.
- Ichinokawa, M., Brodziak, J. (2008) Stock boundary between possible swordfish stocks in the northwest and southeast Pacific judged from fisheries data of Japanese longliners. *Special Session on Billfish Stock Structure, International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific, Billfish Working Group ISC/08/BILLWG-SS/04.*

- Ijima, H., Kanaiwa, M. (2018) Pattern recognition of population dynamics for North Pacific swordfish (*Xiphias gladius*): the operational data analysis of Japanese longline fishery using the finite mixture model. *Working Paper ISC/18/BILLWG-01/9, ISC Billfish Working Group.* 17–20 January 2018, Hawaii, USA.
- ISC (2020) Fisheries Statistics [Online]. Available: http://isc.fra.go.jp/fisheries_statistics/index.html [Accessed 16/11/2020 2020].
- ISC BILLFISH WORKING GROUP (2014) North Pacific swordfish (*Xiphias gladius*) stock assessment in 2014. *Report of the Billfish Working Group, International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean.* 16–22 July 2014, Taipei, Chinese-Taipei.
- ISC BILLFISH WORKING GROUP (2018) Stock assessment for swordfish (*Xiphias gladius*) in the western and central north Pacific Ocean through 2016. *Working Paper WCPFC-SC14-2018/SA-WP-07 Rev.1, 14th Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission.* 8-16 August 2018, Busan, Republic of Korea.
- Ishihara, T., Abe, O., Shimose, T., Takeuchi, Y., Aires-da-Silva, A.M. (2017) Use of post-bomb radiocarbon dating to validate estimated ages of Pacific bluefin tuna, *Thunnus orientalis*, of the North Pacific Ocean. *Fisheries Research*, 189: 35–41.
- Joyce, W.N., Campana, S.E., Natanson, L.J., Kohler, N.E., Pratt, H.L.J., Jensen, C.F. (2002) Analysis of stomach contents of the porbeagle shark (*Lamna nasus* Bonnaterre) in the northwest Atlantic. *ICES Journal of Marine Science*, 59: 1263–1269.
- Kalish, J., DeMartini, E. (2001) Determination of swordfish (*Xiphias gladius*) age based on analysis of radiocarbon in vertebral carbonate and collagen. *In:* Kalish, J. M. (ed.) *Use of bomb radiocarbon chronometer to validate fish age. Final Report for FRDC Project* 93/109. Fisheries Research and Development Corporation, Canberra, Australia.
- Kasapidis, P., Magoulas, A., García-Cortés, B., Mejuto, J. (2008) Stock structure of swordfish (Xiphias gladius) in the Pacific Ocean using microsatellite DNA markers. Working Paper WCPFC-SC4-2008/BI-WP-4, 4th Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission. 11–22 August 2008, Port Moresby, Papua New Guinea.
- Kolody, D., Campbell, R., Davies, N. (2006) A Multifan-CL stock assessment for south-west Pacific swordfish 1952–2004. Working Paper WCPFC-SC2-2006/ME WP-3, 2nd Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission. 7–18 August 2006, Manila, Philippines.
- Kolody, D., Campbell, R., Davies, N. (2008) A MULTIFAN-CL stock assessment of south-west Pacific swordfish 1952-2007. Working paper WCPFC-SC4-2008/SA-WP-6, 4th Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission. 11–22 August 2008, Port Moresby, Papua New Guinea.
- Kopf, R.K., Drew, K., Humphreys, R.L.J. (2010) Age estimation of billfishes (*Kajikia* sp.) using fin spine cross-sections: the need for an international code of practice. *Aquatic Living Resources*, 23: 13–23.

- Larcombe, J., Patterson, H., Mobsby, D. (2020) Eastern Tuna and Billfish Fishery. *In:* Patterson, H., Larcombe, J., Woodhams, J. & Curtotti, R. (eds.) *Fishery Status Reports 2020.* Australian Bureau of Agricultural and Resource Economics and Sciences, Canberra,
   Australia.
- Lehodey, P., Senina, I., Murtugudde, R. (2008) A spatial ecosystem and populations dynamics model (SEAPODYM) - Modelling of tuna and tuna-like populations. *Progress in Oceanography*, 78, 304–318.
- Lopez, S., Meléndez, R., Barria, P. (2010) Preliminary diet analysis of the blue shark *Prionace glauca* in the eastern South Pacific. *Revista de Biología Marina y Oceanografía*, 45: 745–749.
- Lu, C.-P., Smith, B.L., Hinton, M.G., Alvarado Bremer, J.R. (2016) Bayesian analyses of Pacific swordfish (*Xiphias gladius* L.) genetic differentiation using multilocus single nucleotide polymorphism (SNP) data. *Journal of Experimental Marine Biology and Ecology*, 482: 1– 17.
- Maia, A., Queiroz, N., Correia, J.P., Cabral, H. (2006) Food habits of the shortfin mako, *Isurus* oxyrinchus, off the southwest coast of Portugal. *Environmental Biology of Fishes*, 77: 157–167.
- Martinez-Ortiz, M., Aires-da-Silva, A.M., Lennart-Cody, C.E., Maunder, M.N. (2015) The Ecuadorian artisanal fishery for large pelagics: species composition and spatio-temporal dynamics. *PLoS ONE*, 10: e0135136.
- Moore, B.R., Bell, J.D., Evans, K., Farley, J., Grewe, P.M., Hampton, J., Marie, A.D., Minte-Vera, C., Nicol, S.J., Pilling, G.M., Scutt Phillips, J., Tremblay-Boyer, L., Williams, A. J., Smith, N. (2020a) Defining the stock structures of key commercial tunas in the Pacific Ocean I: Current knowledge and main uncertainties. *Fisheries Research*, 230: 105525.
- Moore, B.R., Adams, T., Allain, V., Bell, J.D., Bigler, M., Bromhead, D., Clark, S., Davies, C., Evans, K., Faasili, U.J., Farley, J., Fitchett, M., Grewe, P.M., Hampton, J., Hyde, J., Leroy, B., Lewis, A., Lorrain, A., Mcdonald, J.I., Marie, A.D., Minte-Vera, C., Natasha, J., Nicol, S., Obregon, P., Peatman, T., Pecoraro, C., Phillip, N.B.J., Pilling, G.M., Rico, C., Sanchez, C., Scott, R., Scutt Phillips, J., Stockwell, B., Tremblay-Boyer, L., Usu, T., Williams, A.J., Smith, N. (2020b) Defining the stock structures of key commercial tunas in the Pacific Ocean II: Sampling considerations and future directions. *Fisheries Research*, 230: 105524.
- Muths, D., Le Couls, S., Evano, H., Grewe, P., Bourjea, J. (2013) Multi-genetic marker approach and spatio-temporal analysis suggest there is a single panmictic population of swordfish *Xiphias gladius* in the Indian Ocean. *PLoS ONE*, 8: e63558.
- Nakamura, I. (1985) FAO Species Catalogue, vol. 5 Billfishes of the world.
- Nishikawa, Y., Honma, M., Ueyangi, S., Kikawa, S. (1985) Average distribution of larvae of oceanic species of Scombrid fishes, 1956-1981. *Far Seas Fisheries Research Laboratory S Series*, 12: 1–99.
- Nishikawa, Y., Ueyangi, S. (eds.) (1975) *The distribution of the larvae of swordfish, Xiphias gladius, in the Indian and Pacific oceans. In*: Shomura, R.S., Williams, F. (eds) Proceedings

of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972, Part 2. Review and contributed papers, p 261–264.

- NOAA. (2020) Catch of swordfish takes off as Southern California anglers embrace new technique [Online]. Available: https://www.fisheries.noaa.gov/feature-story/catch-swordfish-takes-southern-california-anglers-embrace-new-technique [Accessed 9th November 2020].
- Olson, D.B., Hitchcock, G.L., Mariano, A.J., Ashijian, C.J., Peng, G., Nero, R.W., Podestá, G.P. (1994) Life on the edge: marine life and fronts. *Oceanography*, **7**, 52–60.
- Palko, B.J., Beardsley, G.L., Richards, W.J. (1981) Synopsis of the biology of the swordfish, *Xiphias gladius* Linnaeus. FAO Fisheries Synopsis No. 127.
- Palumbi, S.R. (2003) Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications*, 13: sS46–S158.
- PFMC (2020) Status of the U.S. west coast fisheries for highly migratory species through 2019. Pacific Fishery Management Council, Portland, Oregon, USA.
- Poisson, F., Fauvel, C. (2009a) Reproductive dynamics of swordfish (*Xiphias gladius*) in the southwestern Indian Ocean (Reunion Island), Part 1: oocytes development, sexual maturity and spawning. *Aquatic Living Resources*, 22: 45–58.
- Poisson, F., Fauvel, C. (2009b) Reproductive dynamics of swordfish (*Xiphias gladius*) in the southwestern Indian Ocean (Reunion Island), Part 2: fecundity and spawning pattern. *Aquatic Living Resources*, 22: 59–68.
- Reeb, C.A., Arcangeli, L., Block, B.A. (2000) Structure and migration corridors in Pacific populations of the swordfish *Xiphius gladius*, as inferred through analyses of mitochondrial DNA. *Marine Biology*, 136: 1123–1131.
- Righi, T., Splendiani, A., Fioravanti, T., Casoni, E., Gioacchini, G., Carnewali, O., Barucchi, V.
  C. (2020) Loss of mitochondrial genetic diversity in overexploited Mediterranean swordfish (*Xiphias gladius*, 1759) population. *Diversity*, 12.
- Romeo, T., Battaglia, P., Macaluso, D., Tagliavia, G. (2020) When prey becomes killer: does a double lethal attack on a blue shark reveal a precise defensive strategy in young swordfish? *Journal of the Marine Biological Association of the United Kingdom*, 100: 831–836.
- Romeo, T., Consoli, P., Castriota, L., Andaloro, F. (2009) An evaluation of resource partitioning between two billfishes, *Tetrapturus belone* and *Xiphias gladius*, in the central Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, 89: 849–857.
- Rosas-Luis, R., Loor-Andrade, P., Carrera-Fernández, M., Pincay-Espinoza, J.E., Vinces-Ortega, C., Chompoy-Salazar, L. (2016) Cephalopod species in the diet of large pelagic fish (sharks and billfishes) in Ecuadorian waters. *Fisheries Research*, 173: 159–168.
- Rosas-Luis, R., Vavarro, J., Loor-Andrade, P., Forero, M.G. (2017) Feeding ecology and trophic relationships of pelagic sharks and billfishes coexisting in the central eastern Pacific Ocean. *Marine Ecology Progress Series*, 573: 191–201.

- Rose, J.M. (1994) *With Line and Glittering Bronze Hook: Fishing in the Aegean Bronze Age.* Ph.D thesis, Indiana University.
- Rosel, P.E., Block, B.A. (1996) Mitochondrial control region variability and global population structure in the swordfish, *Xiphias gladius*. *Marine Biology*, 125: 11–22.
- Sakagawa, G.T., Bell, R.R. (1980) Swordfish, *Xiphias gladius*. *In:* Shomura, R.S., (ed.) Summary report of the billfish stock assessment workshop, Pacific resources. U.S. Department of Commerce, La Jolla, California: 40–50.
- Schaefer, K.M., Fuller, D. (2006) Estimates of age and growth of bigeye tuna (*Thunnus obesus*) in the eastern Pacific Ocean, based on otolith increments and tagging data. *Inter-American Tropical Tuna Commission Bulletin,* 23: 35–59.
- Seki, M., Polovina, J.J., Kobayashi, D.R., Bidigare, R.R., Mitchum, G.T. (2002) An oceanographic characterization of swordfish (*Xiphias gladius*) longline fishing grounds in the springtime subtropical North Pacific. *Fisheries Oceanography*, 11: 251–266.
- Sepulveda, C.A., Aalbers, S.A., Heberer, C., Kohin, S., Dewar, H. (2018) Movements and behaviors of swordfish *Xiphias gladius* in the United States Pacific Leatherback Conservation Area. *Fisheries Oceanography*, 27: 381–394.
- Sepulveda, C.A., Knight, A., Nasby-Lucas, N., Domeier, M.L. (2010) Fine-scale movements of the swordfish *Xiphias gladius* in the Southern California Bight. *Fisheries Oceanography*, 19: 279–289.
- Sepulveda, C.A., Wang, M., Aalbers, S.A., Alvarado Bremer, J.R. (2020) Insights into the horizontal movements, migration patterns, and stock affiliation of California swordfish. *Fisheries Oceanography*, 29: 152–168.
- Slatkin, M. (1987) Geneflow and the geographic structure of natural populations. *Science*, 236: 787–792.
- Smith, P.J., Diggles, B., Kim, S. (2007) Evaluation of parasite markers to assess swordfish stock structure. Information Paper WCPFC-SC3-BI SWG/IP-1, 3rd Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission. 13–24 August 2007, Honolulu, Hawaii.
- Sonu, S.C. (1997) The Japanese swordfish market. *NOOA Technical Memorandum.* U.S. Department of Commerce, National Oceanic and Atmospheric Administration.
- Sosa-Nishizaki, O. (1990) A study on the swordfish Xiphias gladius stocks in the Pacific Ocean. Ph. D. thesis, Department of Fisheries, Faculty of Agriculture, University of Tokyo.
- Sosa-Nishizaki, O., Shimizu, M. (1991) Spatial and temporal CPUE trends and stock unit inferred from them for the Pacific swordfish caught by the Japanese tuna longline fishery. *Bulletin of the National Research Institute of Far Seas Fisheries*, 28: 75–89.
- Speare, P. (2003) Age and growth of black marlin, *Makaira indica*, in east coast Australian waters. *Marine and Freshwater Research*, 54: 307–314.

- Suca, J.J., Rasmuson, L.K., Malca, E., Gerard, T., Lamkin, J.T. (2018) Characterizing larval swordfish habitat in the western tropical North Atlantic. *Fisheries Oceanography*, 27: 246–258.
- Sun, C.-L., Wang, S.-P., Yeh, S.-Z. (2002) Age and growth of the swordfish (*Xiphias gladius* L.) in the waters around Taiwan determined from anal-fin rays. *Fishery Bulletin*, 100: 822–835.
- Takahashi, M., Okamura, H., Yokawa, K., Okazaki, M. (2003) Swimming behaviour and migration of a swordfish recorded by an archival tag. *Marine and Freshwater Research*, 54: 527–534.
- Takeuchi, Y., Pilling, G. & Hampton, J. (2017) Stock assessment of swordfish (Xiphias gladius) in the southwest Pacific Ocean. Working Paper SC13-SA-WP-13, 13th Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission. 9–17 August 2017, Rarotonga, Cook Islands.
- Tracey, S., Pepperell, J. (2018) Understanding the movement, behaviour and post-capture survival of recreationally caught swordfish from southeast Australia - a pilot study. *FRDC Project No 2015–022.* Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania.
- Uchiyama, J.H., DeMartini, E.E., Williams, H.A. (1999) Length-weight interrelationships for swordfish, *Xiphias gladius* L., caught in the central North Pacific. *NOAA Technical Memorandum NMFS NOAA-TM-NMFS-SWFSC-284*. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Honolulu, Hawaii.
- Uchiyama, J.H., Skillman, R.A., Sampaga, J.D., DeMartini, E.E. (1998) A preliminary assessment of the use of hard parts to age central Pacific swordfish, *Xiphias gladius. In:* Barrett, I., Sosa-Nishizaki, O., Bartoo, N. (eds.) *Biology and fisheries of swordfish, Xiphias gladius.* Papers from the International Symposium on Pacific Swordfish, Ensenada, Mexico, 11–14 December 1994, U.S. Department of Commerce, NOAA Technical Report.
- Valeiras, X., Mejuto, J., Ruiz, M. (2008) Age and growth of swordfish (*Xiphias gladius*) in North Pacific. Working Paper WCPFC-SC4-2008/BI-WP-1, 4th Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission. 11–22 August 2008, Port Moresby, Papua New Guinea.
- Van den Burg, E.H., Peeters, R.R., Verhoye, M., Meek, J., Flik, G., Van der Linden, A. (2005) Brain response to ambient temperature fluctuations in fish: reduction of blood volume and initiation of a whole-body stress response. *Journal of Neurophysiology*, 93: 2849– 2855.
- Videler, J.J., Haydar, D., Snoek, R., Hoving, H.T., Szabo, B.G. (2016) Lubricating the swordfish head. *Journal of Experimental Biology*, 219: 1953–1956.
- von Bertalanffy, L. (1938) A quantitative theory of organic growth (Inquiries on growth laws II). *Human Biology*, 10: 181–213.
- Wang, S.-P., Sun, C.-L., Yeh, S.-Z. (2003) Sex ratios and sexual maturity of swordfish (*Xiphias gladius* L.) in the waters of Taiwan. *Zoological Studies*, 42: 529–539.

- Ward, P., Elscot, S. (2000) *Broadbill swordfish: Status of world fisheries*, Bureau of Rural Sciences, Canberra, Australia.
- WCPFC (2009) Conservation and Management for Swordfish. Conservation and Management Measure 2009-03, 6th Regular Session of the Western and Central Pacific Fisheries Commission. 7–11 December 2009, Papeete, Tahiti, French Polynesia.
- WCPFC (2020) Summary report of the Sixteenth Regular Session of the Commission for the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean. 5–11 December 2020, Port Moresby, Papua New Guinea,
- Wegner, N.C., Sepulveda, C.A., Bull, K.B., Graham, J. B. (2010) Gill morphometrics in relation to gas transfer and ram ventilation in high-energy demand teleosts: Scombrids and billfishes. *Journal of Morphology*, 271: 36–49.
- Williams, P., Ruaia, T. (2020) Overview of tuna fisheries in the western and central Pacific Ocean, including economic conditions 2019. *Information Paper WCPFC-SC16-2020/GN IP-1 rev 3, 16th Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission.* 11–20 August 2020, Online meeting.
- Young, J., Drake, A. (2004) Age and growth of broadbill swordfish (*Xiphias gladius*) from Australian waters. *Final report for FRDC project 2001/014*. CSIRO, Hobart, Tasmania.
- Young, J., Drake, A., Brickhill, M., Farley, J., Carter, T. (2003) Reproductive dynamics of broadbill swordfish, *Xiphias gladius*, in the domestic longline fishery off eastern Australia. *Marine and Freshwater Research*, 54: 1–18.
- Young, J., Humphreys, R., Uchiyama, J., Clear, N. (2008) Comparison of maturity and ageing of swordfish from Hawaiian and Australian waters. *Information Paper WCPFC-SC4-*2008/BI-IP-2, 4th Regular Session of the Scientific Committee Meeting of the Western and Central Pacific Fisheries Commission. 11–22 August 2008, Port Moresby, Papua New Guinea.
- Young, J., Lansdell, M., Riddoch, S., Revill, A. (2006) Feeding ecology of broadbill swordfish, *Xiphias gladius*, off eastern Australia in relation to physical and environmental variables. *Bulletin of Marine Science*, 79: 793–809.
- Zambrano-Zambrano, R.W., Mendoza-Moreira, P.E., Gómez-Zamora, W., Varela, J.L. (2019) Feeding ecology and consumption rate of broadbill swordfish (*Xiphias gladius*) in Ecuadorian waters. *Marine Biodiversity*, 49: 373–380.