國立臺灣大學理學院海洋研究所

博士論文

Institute of Oceanography
College of Science
National Taiwan University
Doctoral Dissertation

北太平洋長鰭鮪生活史特徵及單位加入生產量分析

Life-history traits and yield-per-recruit analysis of North Pacific albacore (*Thunnus alalunga*)

陳國書

Kuo-Shu Chen

指導教授：許建宗 博士

Advisor: Chien-Chung Hsu, Ph.D.

中華民國 100 年 1 月

January, 2011

謝辭

本論文承蒙許多人之熱心協助才順利完成，在此致謝。首先，感謝恩師指導教授 許建宗博士多年來有耐心地指導我的學業及研究，時時督促我學習新知及創新研究方法，並對我日常生活上的關心及照顧。誠摯感謝本所名譽教授 劉錫江博士、本校動物學研究所 丘臺生博士、數學系 陳宏博士、漁業科學研究所 李英周博士、海洋大學海洋事務與資源管理研究所所長 劉光明博士與高雄海洋科技大學海洋環境工程系 陳志遠博士，對本論文詳細審閱，並提供許多寶貴的修改建議，使本論文能更完善，謝謝各位老師。

本論文承蒙國科會計畫(NSC90-2313-B-002-314; NSC91-2313-B-002-290; NSC92-2313-B-002-060)之經費補助。誠摯感謝本所 葉顯椏老師、戴昌鳳老師、本校分子與細胞生物學研究所 楊西苑老師及高雄海洋科技大學海洋環境工程系陳志遠老師熱心支援儀器設備，使本論文的實驗工作能順利進行，謝謝各位老師的幫忙。由於採集長鰭鮪樣本時，遇到很多瓶頸，使得本論文的完成耗時費日。在此，感謝高雄銘達漁業公司 陳柱龍先生及豐國水產關係企業 蔡添富先生，熱心協助採集遠洋漁業所捕撈的長鰭鮪漁獲。也由衷感謝東港和小琉球的漁民們，以及許多在東港魚市場工作的魚販和人員，有你們熱心的幫忙，本論文的樣本才勉強蒐集齊備，進而有成果發表。在此，也感謝日本遠洋水產研究所人員 Toshiyuki Tanabe、Tamaki Shimose 及 Hiroshi Ashida 協助採集長鰭鮪未成熟魚的樣本。在處理樣本魚時，經由許多實驗室同仁的合力協助，讓採樣的工作更省時省力地完成，在此一併致謝。此外，也要感謝那些樣本魚的付出。

感謝許多已畢業的學長姊、同學及學弟妹們(人數實在太多，不一一列舉)，還有尚在為學業打拼的同學及學弟妹們，以及很多的山友們，有你們的相伴及勉勵，在我求學的日子裡增添了許多樂趣及歡笑，感恩啦。在此，也要謝謝在我求學過程中，許多老師們的傳道、授業與解惑，讓我的學業及人格能持續地成長進步。最後，感謝家人在我求學過程中始終如一的支持與鼓勵，你們的支持與鼓勵是我心中的活力泉源，讓我能坦然面對並順利克服求學過程中所遇到的種種困難，謝謝我親愛的家人們。謹在此對曾幫助及關心我的人，獻上我最誠摯的謝意。

國書　2011年1月

摘要

本論文主要內容為研究北太平洋長鰭鮪(*Thunnus alalunga*)的生物學(包括年齡、成長及生殖生物學)，並對此系群進行雌雄別單位加入生產量分析，以提供此系群生活史參數及生物參考點。在 2001 至 2008 年期間，總共採集到 293 尾北太平洋長鰭鮪(其中，133 尾雌魚，尾叉長 46 cm 至 101 cm；160 尾雄魚，尾叉長 45 cm 至 118 cm)，做為生物學研究樣本。耳石邊緣分析的結果驗證扁平石切片上所判讀的年輪是一年形成一輪，年輪形成盛期為 9 月至翌年 2 月。以耳石微細構造分析第一年輪形成時的魚齡，結果發現第一年輪形成時，並非魚齡皆已達 1 歲。本論文的結果建議第一年輪所代表的魚齡約為 0.75 歲。成長研究的結果指出，雌魚和雄魚具有不同的成長方程式。本論文所估計的 von Bertalanffy 成長參數如下：雌魚為 $L_\infty = 103.5$ cm、$K = 0.340$ year^{-1} 及 $t_0 = -0.53$ years；雄魚為 $L_\infty = 114.0$ cm、$K = 0.253$ year^{-1} 及 $t_0 = -1.01$ years。再者，此系群體長與體重關係式(指數函數)的參數估計值為：$a = 2.964\times10^{-5}$ 及 $b = 2.928$。此系群達 50%性成熟的尾叉長約為 85 cm。成熟雄魚比雌魚成長到較大的體型及年齡，而雄魚和雌魚在達到性成熟後，成長速率才有較大的差異。由 von Bertalanffy 參數所估計的自然死亡率(M, in year^{-1})值顯示，雌魚的 M 值比雄魚高。單位加入生產量分析所估計最佳的初捕年齡為 2 歲(2.5 歲魚平均尾叉長約為 67 cm)。以雌魚為例，在 $M = 0.3$ 時，模式一(使用一組漁具選擇率)所估計的參考點 $F_{0.1}$ (year^{-1})及 $F_{25\%}$ (year^{-1})分別為 0.32 及 0.30，而模式二(使用另一組漁具選擇率)所估計的值分別為 0.36 及 0.35。再者，在 $M = 0.5$ 時，模式一所估計的 $F_{0.1}$ 及 $F_{25\%}$分別為 0.55 及 0.36，而模式二所估計的值分別為 0.62 及 0.43。若此系群的 M 值大於 0.3 時，則以 $F_{25\%}$做為漁業管理的參考點會比使用 $F_{0.1}$ 為佳。

關鍵詞：年齡驗證，長鰭鮪，生物參考點，漁業管理，成長參數，耳石微細構造。

Abstract

This dissertation presents the results of biological investigations (including information on age, growth, and reproductive biology) and sex-specific yield-per-recruit analyses of North Pacific albacore (*Thunnus alalunga*) to provide life-history parameters and biological reference points for this stock. North Pacific albacore specimens (133 females, 46 to 101 cm in fork length, L_F; 160 males, 45 to 118 cm L_F) were collected for biological investigations from 2001 to 2008. The results of otolith edge analysis indicate that the sagittal otolith growth zones composed of relatively compact micro-increments represent annual growth marks that are primarily formed during the months of September and February. The age estimates of first annulus formation obtained by examining otolith microstructure suggest that the first annulus represents an age of less than 1 year. This dissertation estimates 0.75 years to be the age represented by the first annulus. The results of fish growth modeling indicate that this stock exhibits sex-specific growth patterns. The estimated von Bertalanffy growth parameters for females were $L_\infty = 103.5$ cm, $K = 0.340$ year^{-1}, and $t_0 = -0.53$ years; the parameters for males were $L_\infty = 114.0$ cm, $K = 0.253$ year^{-1}, and $t_0 = -1.01$ years. The length-weight parameters (for a power function) estimated for this stock were $a = 2.964\times10^{-5}$ and $b = 2.928$. The estimated length at 50% maturity of this stock was 85 cm L_F. The results of the biological investigations suggest that males attain to a greater size and age than females and that sexual size dimorphism increases after sexual maturity is reached. The natural mortality (M, in year^{-1}) estimates obtained with von Bertalanffy growth parameters indicate that females tend to have a higher M value than males. The simulated yield-per-recruit values suggest that the optimal age at first capture is approximately 2 years (with an average L_F of 67 cm for 2.5-year-old fish). For females, the reference points $F_{0.1}$ (year^{-1}) and $F_{25\%}$ (year^{-1}) estimated at $M = 0.3$ under Model Scenario 1 (a set of gear selectivity for all age classes) are 0.32 and 0.30, respectively; the values obtained with Model Scenario 2 (another set of gear selectivity) are 0.36 and 0.35, respectively. At $M = 0.5$, the reference points obtained with Model Scenario 1 are $F_{0.1} = 0.55$ and $F_{25\%} = 0.36$, and those obtained with Model Scenario 2 are $F_{0.1} = 0.62$ and $F_{25\%} = 0.43$. The reference point $F_{25\%}$ is preferable to $F_{0.1}$ for the fisheries management of this stock if $M > 0.3$.

Key words: age validation, albacore, biological reference point, fisheries management, growth parameter, otolith microstructure.

Table of Contents

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

List of Tables

Chapter 2

Chapter 3

Chapter 4

Chapter 1—Introduction

1.1 Albacore morphology

The albacore tuna (Fig. 1.1), *Thunnus alalunga* (Bonnaterre, 1788), is a cosmopolitan species in the family Scombridae. Its common size in commercial catches is less than 110 cm in fork length (L_{F}) (Suda, 1956; Otsu & Sumida, 1968; Yoshida, 1975) and less than 30 kg in body weight (W) (Lu et al., 1998). The albacore tuna has a streamlined shape with dark blue color on the dorsal side and silvery white color on the ventral side. The first dorsal fin is noticeably longer than the second (Collette & Nauen, 1983). This species possesses 7 to 9 dorsal finlets and 7 or 8 anal finlets (Collette, 2001). In large albacore, the pectoral fins are noticeably long and usually extend beyond the second dorsal fin (Collette, 2001). In addition, the posterior margin of the caudal fin is white, which is a useful morphological characteristic for distinguishing albacore from other *Thunnus* species (Collette & Nauen, 1983).

Albacore are unisexual fish (i.e., gonochorists), and both sexes have similar external appearances. In albacore, the gill rakers of the first arch range in number from 25 to 31 (Collette & Nauen, 1983). The number of vertebrae is 39 (Collette & Nauen, 1983). Inside the albacore abdomen, the ventral surface of the liver is striated, and the swim bladder is less developed in albacore of less than 50 cm L_{F} (Collette & Nauen, 1983). Albacore exhibit gonad weight asymmetry (Ueyanagi, 1955; Ratty et al., 1990; Ramon & Bailey, 1996; Chen et al., 2010); the right lobe of the gonad is generally larger and heavier than the left lobe.

1.2 The geographical distribution and stock structure of North Pacific albacore

Albacore are an oceanic and highly migratory species. They inhabit in the tropical, subtropical, and temperate waters of the world's oceans (Fig. 1.2). Two albacore stocks are customarily assumed to exist in the Pacific Ocean (Otsu & Hansen, 1962; Nakamura, 1969; Foreman, 1980; Murray, 1993); one stock inhabits in the North Pacific Ocean, and the other lives in the South Pacific Ocean. However, gene flow of albacore has been suggested to occur between the North Pacific and South Pacific stocks (Chow & Ushiama, 1995). Because limited information is available on the interaction of albacore between the North and South Pacific, this dissertation assumes that two distinct albacore stocks live in the Pacific Ocean. Moreover, a single albacore stock is commonly assumed to exist in the North Pacific Ocean (Clemens, 1961; Foreman, 1980; Uosaki & Bayliff, 1999). Mitochondrial DNA sequence analysis of albacore in the western North Pacific Ocean indicates that albacore from this general area constitute a single stock (Wu et al., 2009). In contrast, two subgroups of albacore have been proposed to exist in the eastern North Pacific Ocean (Laurs & Wetherall, 1981; Laurs & Lynn, 1991; Barr, 2009). Because of limited information on the stock structure of albacore throughout the North Pacific Ocean, this dissertation assumes that a single albacore stock inhabits in the North Pacific Ocean.

Here, the albacore in the North Pacific Ocean are referred to as the North Pacific albacore. The distribution of the North Pacific albacore (Fig. 1.2) ranges from the equator to 45°N in the west and from the waters off Mexico to the Gulf of Alaska in the east (Yoshida & Otsu, 1962; Foreman, 1980). North Pacific albacore seasonally migrate across the exclusive economic zones of the nations along the North Pacific Ocean (Foreman, 1980; Bartoo & Foreman, 1993). Migrations of young albacore show movement patterns associated with the waters of the North Pacific Transition Zone (Laurs & Lynn, 1991) and a capability for transoceanic migration (Ganssle & Clemens, 1953; Blunt, 1954; Kikawa et al., 1977; Sharp & Dotson, 1977). In addition, young albacore tend to exhibit frequent westward movements and infrequent eastward movements (Ichinokawa et al., 2008). In general, mature albacore are distributed throughout the ocean more widely than younger albacore and may seasonally migrate to subtropical waters of the central and western North Pacific Ocean to spawn (Otsu & Uchida, 1963). Furthermore, mature albacore may have a wider migration range during El Niño years (Kimura et al., 1997).

1.3 The ecology and environmental physiology of North Pacific albacore

North Pacific albacore live in epipelagic and mesopelagic zones (Collette & Nauen, 1983) and are mostly found at depths of 0 to 300 m (Yoneta & Saito, 1973). These tuna prefer to live in ocean waters at temperatures typically higher than 15 °C (Laurs et al., 1977; Foreman, 1980) and with a deep and oxygen-rich oceanic realm (Clemens, 1961). They also prefer to congregate along thermal discontinuities, that is, oceanic fronts (Pearcy, 1973; Laurs & Lynn, 1977; Squire, 1981; Laurs et al., 1984). High catch rates of albacore are associated with hydrographic features, frontal zones, and eddy fields (Uda, 1973; Zainuddin et al., 2006). The catch rate of albacore tends to be negatively correlated with surface water temperature (Dai et al., 2006). Large albacore tend to live below the thermocline (Collette, 2001) and in waters with temperatures ranging from 13.5 to 25.2 °C (Saito, 1973). Young albacore typically form large schools and may also form mixed schools with other tunas (Collette & Nauen, 1983); older albacore tend to form more compact schools (Collette & Nauen, 1983). The mean swimming speed of tagged albacore is at least 4 nm per day in offshore areas and at least 15 nm per day during transoceanic migration (Clemens, 1961). Tagged albacore swim slightly faster during the day than at night (Laurs et al., 1977).

Albacore are carnivorous fish in the marine ecosystem. Both young and mature albacore primarily feed on various kinds of fishes, cephalopods, and crustaceans (Iversen, 1962; Iverson, 1971; Bernard et al., 1985, Glaser, 2009). Food abundance is an important factor affecting albacore migration (Sund et al., 1981; Fiedler & Bernard, 1987). Water clarity may affect the predatory behavior (Murphy, 1959) and result in the aggregation of albacore in the vicinity of oceanic fronts (Laurs, 1983). Albacore are preyed upon by top predators (e.g., billfishes, sharks, and mammals) in the marine ecosystem (Foreman, 1980).

Like other tunas, albacore have high metabolic rates and the ability to keep their core muscles warm through thermoregulation (Stevens & Neill, 1978; Graham & Dickson, 1981; Cech et al., 1984). Albacore can maintain an internal body temperature 15 °C warmer than the ambient seawater (Thompson, 2005). The reported internal temperature of landed albacore is approximately 31 °C (Thompson, 2005). The total mercury concentration in the muscle tissue of young albacore from the eastern North Pacific Ocean is approximately 0.14 mg/kg (Morrissey et al., 2004); in albacore from the central and western North Pacific Ocean, the average concentration is approximately 0.44 mg/kg (Lai, 2009). The total mercury concentration in the muscle tissue of North Pacific albacore is relatively lower than the concentrations reported for other *Thunnus* species, including yellowfin tuna (*T. albacares* Bonnaterre), reported by Kojadinovic et al. (2006); bigeye tuna (*T. obesus* Lowe), reported by Lai (2009) and Chen et al. (2011); and Atlantic bluefin tuna (*T. thynnus* Linnaeus), reported by Srebocan et al. (2007).

1.4 The age, growth, and reproductive biology of North Pacific albacore

Many researchers have studied the age, growth, and reproductive biology of North Pacific albacore (see reviews by Shomura, 1966; Foreman, 1980; Wetherall et al., 1987; Bartoo & Foreman, 1993; Maxwell, 2002). In previous studies, various hard parts (including scales, fin rays, vertebrae, and otoliths), tagging data (Otsu, 1960; Clemens, 1961; Laurs & Wetherall, 1981), and length-frequency data (Brock, 1943; Suda, 1954b) have been used to investigate the age and growth of this stock. Most previous studies of this stock, however, were conducted before the 1970s.

This stock is found to exhibit sexual size dimorphism such that males predominate in the catches of large fish (Suda, 1954a; Suda, 1956; Otsu & Uchida, 1959b; Saito, 1973). Otsu & Uchida (1959b) suggested that mature males grow faster than mature females, but they did not provide sex-specific growth functions for this stock. Shomura (1966) and Foreman (1980) summarized several growth parameters reported for this stock, and all of the parameters were obtained with sex-pooled data. Although many growth parameters have been reported, there is little information available on the sex-specific growth functions of this stock.

Albacore are multiple-spawning fish with indeterminate annual fecundity (Otsu & Uchida, 1959a; Wu & Kuo, 1993; Chen et al., 2010). They have asynchronous gonadal development and can spawn several times during a spawning season (Chen et al., 2010). North Pacific albacore are found to reach sexual maturity within the size range of 78 to 94 cm L_F (Chen et al., 2010). The spawning of North Pacific albacore occurs mainly in spring and summer (Foreman, 1980; Chen et al., 2010), and the larvae of this stock are found to be associated with water temperatures above 24 °C (Ueyanagi, 1969). North Pacific albacore may engage in spawning activity year-round, but their spawning tends to be limited to waters below 20°N in colder months (Ueyanagi, 1969). Their spawning distribution ranges mainly from 10°N to 30°N in oceanic waters and from the Philippines to the Hawaiian Islands (Ueyanagi, 1969; Otsu & Sumida, 1970; Nishikawa et al., 1978). Specifically, the spawning distribution is centered on 20°N (Ueyanagi, 1969). In the waters off the Hawaiian Islands, albacore spawning may occur mainly from March to July (Otsu & Uchida, 1959a; Yoshida, 1968). In the western Philippine Sea, albacore spawning activity peaks in March and April (Chen et al., 2010). Chen et al. (2010) reported that the spawning frequency of albacore is approximately every 1.7 days in April in the western Philippine Sea. In previous fecundity research, researchers reported that one batch of spawn (in millions of eggs) ranged from 0.8 to 2.6 in the north-western Pacific Ocean (Ueyanagi, 1957), from 0.9 to 1.8 in Hawaiian waters (Otsu & Uchida, 1959a), and from 0.17 to 1.66 in the western Philippine Sea (Chen et al., 2010). Chen et al. (2010) reported that relative batch fecundity estimates (the number of eggs per gram of body weight) for albacore within the size range of 89 to 99 cm L_F ranged from 9.2 to 92.4, with a mean (standard deviation) of 50.5 (22.8). To date, histology-based maturity ogives (maturity schedules) have rarely been studied for this stock.

1.5 Fisheries and stock assessments of North Pacific albacore

Albacore are an important exploited resource in the North Pacific Ocean. Catches of albacore are commonly used for canned food. The International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean (ISC) reported that the annual fisheries production of North Pacific albacore from 1952 to 2008 ranged roughly from 37 000 to 127 000 mt (Fig. 1.3; ISC, 2010). The annual production of this stock peaked in 1976 and 1999 and declined to its lowest level in 1991 (Fig. 1.3). In recent years (2000 to 2008), the production of albacore ranged roughly from 63 000 to 105 000 mt (Fig. 1.3). This stock was primarily used by Japan, the United States, Canada, Taiwan, Mexico, and the Republic of Korea (ISC, 2010). The main types of fishing gear used to catch this stock included troll, pole-and-line, and longline gear (Fig. 1.3). In general, surface fishing gear (troll and pole-and-line) catches smaller albacore, and subsurface fishing gear (longline) catches larger albacore. Using tagging data, Bertignac et al. (1999) reported that the annual exploitation rate of this stock was approximately 40% in the mid-1970s and declined to less than 10% after the early 1980s. More recent information about this stock can be found on the ISC website.

According to the recent stock assessment of North Pacific albacore from the ISC (ISC, 2006), the current level of overall fishing mortality for this stock is relatively high. Scientists of the ISC suggested that fishing efforts should be limited to the most recent levels (ISC, 2006). In addition, the biological parameters used in stock assessment models should be updated to provide more recent information on the life-history traits of this stock (ISC, 2006).

Stock assessment and fisheries management strategies of an exploited fish stock are substantially based on the knowledge of the stock's life-history traits (e.g., age, growth, and reproduction). Although many researchers have investigated the age, growth, and reproductive biology of North Pacific albacore, there is little scientifically useful information available on the life-history traits of this stock (Parrish et al. 1989). To date, numerous life-history parameters of this stock remain poorly understood or need to be updated (Schaefer, 2001; Maxwell, 2002).

1.6 Objectives

The objectives of this dissertation are to investigate the life-history traits (including age, growth, reproductive biology, and mortality rates) of North Pacific albacore and to conduct sex-specific yield-per-recruit analyses for this stock based on the life-history parameters obtained. This dissertation will discuss the strategies for the stock assessment and fisheries management of this stock. An outline of this dissertation is as follows.

(a) Chapter 1: This chapter briefly reviews the biology, fisheries, and stock assessments of North Pacific albacore and describes the objectives of this dissertation.

(b) Chapter 2: This chapter presents the results of an age-and-growth study of this stock. The age-and-growth study was conducted with sectioned sagittal otoliths and aimed to determine sex-specific growth functions for this stock.

(c) Chapter 3: This chapter describes the results of a study on the reproductive biology of this stock; the goal of this study was to determine a maturity ogive for this stock.

(d) Chapter 4: This chapter presents sex-specific per recruit analyses of this stock based on the life-history parameters reported in Chapters 2 and 3.

(e) Chapter 5: Conclusions and recommendations for the stock assessment and fisheries management of this stock are presented in this chapter.

Chapter 2— The Age and Growth of North Pacific Albacore

2.1 Introduction

The age and growth of a fish stock are important biological information for modeling the population dynamics of the stock. In conducting the stock assessment of a particular fish stock, growth parameters are frequently used to determine the length-at-age, age composition, and mortality rates of the stock (Ricker, 1975; Punt et al., 2001; King, 2007). Using less precise biological parameters as inputs of stock assessment models can increase the uncertainty of model outputs (Vetter, 1988; Hilborn & Walters, 1992). Although many sex-pooled growth parameters have been reported for North Pacific albacore (see reviews by Shomura, 1966; Foreman, 1980), the parameters used for this stock vary greatly. To improve the stock assessment of this stock, biological parameters must be updated to provide recent information on its life-history traits (ISC, 2006).

In previous studies, various hard parts (e.g., scales, fin rays, vertebrae, and otoliths) as well as tag-and-recapture methods have been used to investigate the age and growth of North Pacific albacore. To date, however, the sex-specific growth functions of this stock remain poorly studied. Because albacore exhibit sexual size dimorphism, in which mature males attain a larger size than mature females (Otsu & Uchida, 1959b; Otsu & Sumida, 1968; Beardsley, 1971; Saito, 1973; Yoshida, 1975), knowing whether male and female North Pacific albacore have different growth functions is important for the accurate modeling of the population dynamics of this stock.

Sagittal otoliths are frequently used in age-determination studies of tunas and many other teleosts (Campana & Neilson, 1982; Tzeng, 1990; Neilson & Campana, 2008). Transversely sectioned otolith slices are commonly used to assess age in tunas. However, the otolith slices produced by oblique sections are longer and wider in appearance than the transversely sectioned slices. Longer and wider otolith slices are helpful for clarifying annual growth marks. In tunas, obliquely sectioned otoliths have been used in age-and-growth studies (e.g., Stéquert et al., 1996; Clear et al., 2000; Schaefer et al., 2006). In this study, obliquely sectioned otolith slices were produced and used to determine the age of North Pacific albacore.

This study aimed to investigate the sex-specific growth functions of North Pacific albacore based on the determined ages of fish specimens collected. In addition, the parameters for expressing the length-weight relationship of this stock were estimated with these fish specimens. Three growth models (ordinary von Bertalanffy, Gompertz, and Richards) were used to model fish growth. In modeling fish growth, the goodness of fit of each growth model was evaluated both by the coefficient of determination (R^2) and by an F-test for lack of fit. Sex-specific growth and length-weight functions were compared using likelihood ratio tests. Moreover, an extra randomization test was conducted to further assure the results of each likelihood ratio test. Bootstrapping was used to assess the uncertainty of the biological parameters estimated.

2.2 Materials and methods

2.2.1 Sample collection

Albacore specimens (112 females, 59 to 101 cm L_F; 132 males, 58 to 118 cm L_F) were sampled from the catches of Taiwanese longline vessels operated in the central and western North Pacific Ocean from October 2001 to April 2006 (A1 and A3 to A6 in Fig. 2.1). These specimens were landed at the fishing ports of Tungkang and Kaohsiung in Taiwan. In addition, the specimens of smaller albacore (21 females, 46 to 73 cm L_F; 28 males, 45 to 74 cm L_F) were collected by the National Research Institute of Far Sea Fisheries, Japan, from the catches of pole-and-line vessels during June 2006 and

January 2008 (A2 in Fig. 2.1). These specimens were landed at the fishing port of Kesennuma in Japan. For each fish specimen, the L_F (cm) and W (kg) were measured and recorded. Size information of the fish specimens (n = 293) collected are presented by year in Table 2.1 and by fishing-operation area in Table 2.2. Among large fish specimens (> 100 cm L_F), males clearly predominated over females (Fig. 2.2). In the laboratory, sagittal otoliths (Fig. 2.3) were collected from 288 fish (157 males, 45 to 118 cm L_F, 2.0 to 33.1 kg W; 131 females, 46 to 101 cm L_F, 2.2 to 23.0 kg W). The otoliths collected were dried at room temperature, weighed with an electronic balance (METTLER AE-200) to the nearest 0.1 mg, and stored in labeled plastic capsules.

2.2.2 Preparation of sagittal otolith slices

For each fish, an obliquely sectioned slice of the right or left sagittal otolith was obtained with a low-speed diamond saw (ISOMET, BUEHLER®). First, each otolith was embedded with slow-drying resin (Mark V Laboratory Inc., resin RR32 and hardener RH-4 in a weight ratio of 10:1) at room temperature and then cut off at the dorsal side close to the dashed line shown in Fig. 2.4. The surface of the sectioned side of the remnant resin block was ground close to the primordium (core) using sandpaper (800, 1 200, and 2 000 grit). The ground surface was then polished using aluminum oxide polishing powder (1 and 0.05 μm). After polishing, the resin block was cut off again to obtain a thin slice (approximately 1 to 2 mm in thickness) that included the primordium. The polished side of the thin slice was adhered to a glass slide using clear superglue (the surfaces of the slice and slide were kept dry and clean for better adhesion). The rough side of the slice was then ground and polished to obtain a slice of approximately 0.2 to 0.6 mm in thickness. Last, the annual growth marks in each prepared slice were examined by a single reader using a light microscope (magnification:

8X to 400X) with transmitted or reflected light. Images of the otolith slices were obtained using a digital camera attached to the microscope. For each slice, the length (L_P) of the postrostral axis was defined to be the length from the primordium to the posterior-ventral edge (Fig. 2.4). The L_P was calculated as

$$L_P = L_1 + L_2. \tag{2.1}$$

The lengths L_1 and L_2 were measured with a micrometer mounted on one ocular of the microscope.

2.2.3 Age determination

The annual growth marks (annuli) in each otolith slice were first presumed to be the zones composed of relatively compact (higher density) micro-increments (Fig. 2.5). The zones were assumed to represent slow-growth phases of the fish. Here, opaque and translucent zones were not used to represent annual growth marks because the visual characteristics of opaque and translucent zones in otolith slices can be confused under the different light sources used.

For each otolith slice, the condition of the posterior-ventral edge [Fig. 2.4(b)] was evaluated and classified based on whether annulus formation was occurring on the edge. To conduct edge analyses (Gambell & Messtorff, 1964; Campana, 2001; Shimose et al., 2009), the proportion of fish specimens possessing an annulus on the posterior-ventral edge was calculated for each month to verify the period of annulus formation. The presumed annual growth marks in the sagittal otoliths of North Pacific albacore were formed mostly during fall and winter, that is, from September to February (Fig. 2.6). High proportions of fish with an annulus on the posterior-ventral edge occurred in December (74%) and January (64%) (Fig. 2.6). In addition, during July and August, no fish had annuli formed on the posterior-ventral edge (Fig. 2.6). All of these findings indicated that the annulus identified in the sagittal otolith of North Pacific albacore is a fall-to-winter growth mark and is formed once a year. Moreover, the annulus found in the prepared otolith slice was frequently accompanied by a crenulation (Gambell, 1964; Anonymous, 2002), which occurred on the outer margin of the otolith slice (Fig. 2.5).

Because the spawning activity of North Pacific albacore peaks in April in the western Philippine Sea (Chen et al., 2010) and the annulus identified in this study was a fall-to-winter growth mark, the first annulus in the sagittal otolith might not represent the growth of a complete year. To confirm this point, the age of first annulus formation was assessed using 55 fish (71 to 105 cm L_F; Fig. 2.7) that had clearer micro-increments (presumed to be daily growth increments). For each fish, the micro-increments from the primordium to the end of the first annulus were counted two times at least one week apart (Fig. 2.8).

For the age estimation, the annuli in each otolith slice were assessed with light microscopes. When an annulus had formed on the posterior-ventral otolith edge, it was included in the count of annuli for the otolith. The age estimate of the fish was assigned to be the number of annuli counted. When no annulus was formed on the posterior-ventral edge, the age estimate of the fish was assigned to be the number of annuli plus 0.5. Thus, the precision of the age assessments based on the otolith edge condition was approximately 0.5 years.

Five age readings were conducted for each otolith slice to determine the fish age. To reduce the bias of age estimates caused by the reader’s recall of previous age estimates, a time interval of at least one week elapsed between the two age readings. To obtain a more precise age estimate based on the five readings, each fish that had at least three identical age estimates among the five readings was first selected for further growth investigations. The fish’s age was then determined to be the major age estimate among the fish's five age estimates. In addition, to include more samples in the growth investigations, an extra age reading was conducted for those fish that had only two identical estimates among the five readings. Subsequently, fish that had three identical age estimates among their six readings were also included in growth investigations. Subsequently, the age of each fish was determined to be the major age estimate among the fish's six age estimates. The index of the average percent error (I_A) was used to assess the precision of the age estimates of males and females with the following equation (Beamish & Fournier, 1981):

$$I_A = (100/N) \times \sum_{j=1}^{N} \left[(1/R) \times \sum_{i=1}^{R_A} \left| X_{ij} - X_j \right| / X_j \right], \tag{2.2}$$

where N is the number of age-determined fish,

R_A is the number of age readings,

X_{ij} is the ith age estimate of the jth fish, and

X_j is the mean age estimate calculated for the jth fish.

2.2.4 Modeling fish growth

Three growth models were used to model the growth of North Pacific albacore. The first model is the ordinary von Bertalanffy growth model (VBGM) (Bertalanffy, 1938), which can be expressed as

$$L_t = L_\infty \times \left(1 - \exp(-K \times (t - t_0))\right) + \varepsilon_t, \tag{2.3}$$

where L_t is the fish length at age t,

L_∞ is the theoretical asymptotic fish length,

K is a growth coefficient,

t is the fish age (in years), and

t_0 is the hypothetical age at a fish length of zero.

The epsilon (ε_t) in the model is assumed to be independent and normally distributed random errors with a mean of zero and unknown finite variance ($\sigma^2 > 0$). The second model used to model the growth of North Pacific albacore is the Gompertz model (Gompertz, 1825; Campana & Jones, 1992); one form of the Gompertz model can be written as

$$L_t = L_{\mathrm{G}} \times \exp\{-\exp[-K_2 \times (t - t_2)]\} + \varepsilon_t, \tag{2.4}$$

where L_{G} is the theoretical asymptote length,

K_2 is the instantaneous rate of growth at age t_2, and

t_2 is the inflection point of the curve (the age at which the absolute growth rate begins to decline).

The third model used is the Richards model (Richards, 1959) that can be expressed as

$$L_t = L_{\mathrm{R}} \times \{1 + r\exp[-K_3 \times (t - t_3)]\}^{-1/r} + \varepsilon_t. \tag{2.5}$$

Equation 2.5 equals Equation 2.3 (where $L_{\mathrm{R}} = L_\infty$, $K_3 = K$, and $t_3 = t_0$) if $r = -1$; Equation 2.5 equals Equation 2.4 (where $L_{\mathrm{R}} = L_{\mathrm{G}}$, $K_3 = K_2$, and $t_3 = t_2$) if r is close to zero; Equation 2.5 is identical to a logistic function if $r = 1$.

The above three models were each fitted to male and female age-length data to obtain sex-specific growth parameters with nonlinear least-squares estimation. In the fitting, individual age-length data were used to incorporate individual variability into the growth analyses.

2.2.5 The goodness of fit of each growth model

The goodness of fit of each growth model was evaluated by R^2 (Motulsky & Christopoulos, 2004) and an F-test for lack of fit (Neill, 1988). Separate R^2 values for males and females can be calculated as

$$R^2 = 1 - (SS_{\mathrm{err}} / SS_{\mathrm{tot}}), \tag{2.6}$$

where SS_{err} is the residual sum of squares and SS_{tot} is the total sum of squares. To conduct the F-test for lack of fit, the sum of squares caused by pure error (SS_{pur}) is calculated as

$$SS_{\text{pur}} = \sum_{i=1}^{m} \sum_{j=1}^{n_i} (L_{ij} - \overline{L_i})^2, \tag{2.7}$$

where m is the number of age classes,

n_i is the number of samples in each age class,

L_{ij} is the individual length (L_F) in each age class, and

$\overline{L_i}$ is the mean length in age class i.

The sum of squares caused by lack of fit (SS_{lof}) can be calculated as

$$SS_{\text{lof}} = SS_{\text{err}} - SS_{\text{pur}}, \tag{2.8}$$

where the degrees of freedom (df) of SS_{err} is the total data points (N) minus the number of parameters (p_1) fitted by regression,

the df of SS_{pur} is N minus m, and

the df of SS_{lof} is m minus p_1.

Finally, the test statistic of the F-test for lack of fit can be calculated as

$$F = \frac{SS_{\text{lof}} / (m - p_1)}{SS_{\text{pur}} / (N - m)}. \tag{2.9}$$

2.2.6 Model selection

The small-sample bias-corrected form of the Akaike information criterion (AIC) (Akaike, 1992), known as AICc (Hurvichand & Tsai, 1989; Katsanevakis, 2006), can be used to estimate the performance of different models by minimizing the AICc values of the candidate models. The AICc can be calculated as

$$\text{AICc} = \text{AIC} + \big(2k \times (k+1)\big)/(N-k-1), \qquad (2.10)$$

where

$$\text{AIC} = N \times \ln(\hat{\sigma}^2) + 2k, \qquad (2.11)$$

N is the number of samples, $\hat{\sigma}^2 = SS_{\text{err}}/N$, and k is the number of parameters (including $\hat{\sigma}^2$) in the model. Moreover, the AICc differences (Katsanevakis, 2006) for all candidate models were calculated as

$$\Delta_i = \text{AICc}_i - \text{AICc}_{\min}, \qquad (2.12)$$

where $\text{AICc}_{\min}$ is the minimum value of AICc values within each sex.

2.2.7 Bootstrapping procedure

Bootstrapping (Efron & Tibshirani, 1993) can be used to estimate the standard error (*SE*) of each parameter in each growth model and to construct bias-corrected and accelerated (BCa) confidence intervals (CIs) of the parameter (Appendix A). In the bootstrapping procedure, for each sex, individual age-length data were sampled with replacement with the same sample size of the original data. The sex-specific bootstrap age-length data were then fitted to each growth model to obtain a set of bootstrap growth parameters for each growth model. For each sex and model, a total of 5 000 sets of bootstrap growth parameters were obtained (i.e., bootstrap replicates = 5 000), and the parameters obtained using the original data were included as one set among the 5 000 sets.

2.2.8 Comparing sex-specific growth functions

Likelihood ratio tests (Kimura, 1980; Cerrato, 1990; Haddon, 2001) can be used to compare sex-specific growth curves obtained by the VBGM. In this study, the three parameters (L_∞, K, and t_0) of the VBGM were compared simultaneously using a likelihood ratio test instead of comparing one or two parameters. The test statistic of a likelihood ratio test is empirically a chi-square distribution (Haddon, 2001) and can be simplified as

$$\chi_{\lambda}^{2} = -N \times \ln(SS_{\mathrm{sep}} / SS_{\mathrm{con}}), \tag{2.13}$$

where N is the total number of samples,

λ is the degrees of freedom of the assumed chi-square distribution,

SS_{sep} is the total sum of squares derived from fitting the model by setting all parameters different between sexes, and

SS_{con} is the total sum of squares obtained by fitting the model using the hypothesized constraints of parameters (i.e., equal values of L_{∞}, K, and t_0 between sexes).

To avoid comparing the size distributions of male and female age-length data, as suggested by Haddon (2001), restricted age-length data (i.e., age classes of 1.25 to 10.25 years for both sexes) were used in the likelihood ratio test.

For hypothesis testing, the parameters of the VBGM for males (θ_{M}) and females (θ_{F}) are expressed as

$$\theta_{\mathrm{M}} = \begin{pmatrix} L_{\infty\mathrm{M}} \\ K_{\mathrm{M}} \\ t_{0\mathrm{M}} \end{pmatrix} \text{ and } \theta_{\mathrm{F}} = \begin{pmatrix} L_{\infty\mathrm{F}} \\ K_{\mathrm{F}} \\ t_{0\mathrm{F}} \end{pmatrix}. \tag{2.14}$$

The null hypothesis (H_0) of the likelihood ratio test (Kimura, 1980) is

$$\mathrm{H}_0 : \theta_{\mathrm{M}} = \theta_{\mathrm{F}}, \tag{2.15}$$

that is , $L_{\infty\mathrm{M}} = L_{\infty\mathrm{F}}, K_{\mathrm{M}} = K_{\mathrm{F}}, t_{0\mathrm{M}} = t_{0\mathrm{F}}$. The alternative hypothesis (H_1) is

$$\mathrm{H}_1 : \theta_{\mathrm{M}} \neq \theta_{\mathrm{F}}. \tag{2.16}$$

To check whether the test statistic of the likelihood ratio test adheres to the assumed chi-square distribution, the randomization test can be used to generate an empirical distribution of the test statistic of the likelihood ratio test from age-length data.

The results of the randomization procedure can be then compared with the assumed chi-square distribution. In each randomization procedure, the age-length data of males and females were randomized within each age class but between sexes, and the randomized likelihood ratio was then computed (i.e., a χ^2 value from the randomized age-length data of males and females was computed). In this study, a total of 5 000 randomized likelihood ratios were computed for the randomization test.

2.2.9 Length-weight relationship

The allometric equation used for length-weight relationship can be expressed as a power function:

$$W = a \times {L_{\mathrm{F}}}^{b}, \qquad (2.17)$$

where *a* and *b* are the parameters to be estimated (Hsu, 1999). In this study, these parameters were estimated with nonlinear least-squares estimation. Using a similar approach to that used in comparing sex-specific growth functions (see Section 2.2.8), the likelihood ratio test and randomization test were also used to compare sex-specific length-weight functions. Bootstrapping (5 000 replicates) was also used to estimate the *SE* of each parameter of the length-weight function. The statistical analyses (including curve fitting, bootstrapping, likelihood ratio test, and randomization test) used in this study were conducted using MATLAB (version 7.2, MathWorks Inc.; www.mathworks.com).

2.3 Results

2.3.1 Age validation of first annulus formation

In the age assessments of first annulus formation for the 55 fish examined, no statistical differences [paired *t*-test, $t(54) = 1.18$, $p = .24$] were found between the two counts of micro-increments (Fig. 2.9). Descriptive statistics for the mean values of the two counts were as follows: the mean was 257 (*SE* = 6), the median was 266, the minimum was 136, and the maximum was 337. These findings indicated that the median value of the age estimates of first annulus formation in North Pacific albacore is close to 0.75 years. Thus, for each fish, the age estimate for the first annulus was adjusted. In this adjustment, 0.25 years was subtracted from all age estimates, which is an estimate of the time interval between birth and annulus formation (i.e., the birth date was assumed to be 30 April, and the first annulus was assumed to form on 31 January).

2.3.2 Age estimation

Most examined otolith slices had observable annuli (Fig. 2.10), and only 4 fish (1.4% of 288 fish) had no visual annuli in their otolith slices. In summary, 257 fish (89.2%) had at least three identical readings among their five age readings (Fig. 2.11). Seventeen fish (5.9%) had three identical readings among their six age readings (Fig. 2.11). Ten fish (3.5%) that had inconsistent age estimates (fewer than three identical readings) were excluded from the growth modeling of this stock. The I_A values of the age-determined fish were 7.4% for 126 females and 8.6% for 148 males. Determining the ages of older fish appeared to be more difficult than determining the ages of younger fish (Fig. 2.11). The size distribution of the age-determined fish is shown in Fig. 2.12. The age estimates of females ranged from 1^+ to 10^+ years, and those of males ranged from 1^+ to 14^+ years (Table 2.3).

2.3.3 Growth functions

All three growth models were well fitted to male and female age-length data, as indicated by both R^2 and the *F*-test for lack of fit (Table 2.4). For both sexes, the residual plots (Fig. 2.13 and 2.14) indicated that the model fitting seemed to be adequate for all growth models. According to the AICc values obtained, male age-length data were best fitted to the VBGM, and female age-length data were best fitted to the Richards model (Table 2.4). Nevertheless, the computed Δ_i values of the candidate models were not high (< 5), indicating that there is support for each model. The sex-specific age-length data and fitted curves of the VBGM are plotted in Fig. 2.15. The sex-specific growth curves of the VBGM differed significantly [likelihood ratio test, $\chi^2(3) = 20.78$, $p < .001$]. The estimated parameters of the three growth models and their bootstrap estimates of the *SE* and CIs are presented in Table 2.5. As shown in the bootstrap estimates of growth parameters (Fig. 2.16 and 2.17), all distributions (indicated by histograms) seemed to be normal for the von Bertalanffy and Gompertz models, but not for the Richards model (Fig. 2.18 and 2.19). Correlations between growth parameters (indicated by scatter plots) existed at the fitting of the growth models.

2.3.4 Otolith weight and length as functions of fish age

Among 245 fish (114 females and 131 males; 45 to 118 cm L_F) examined (Fig. 2.20), the left and right otoliths showed no statistical differences in weight as tested by paired *t*-test [$t(244) = 1.24$, $p = .21$]. For each sex, the relationship between the weight of the left otolith (W_O, in milligrams) and L_F was expressed as an exponential growth function ($W_O = a_2 \times e^{b_2 \times L_F}$, where a_2 and b_2 are the parameters to be estimated). Subsequently, the likelihood ratio test [$\chi^2(2) = 0.32$, $p = .85$] indicated that males and females had no statistical differences in the parameters of the exponential functions. Therefore, the exponential growth function obtained using sex-pooled data was as follows:

$$W_O = 3.677 \times \exp(0.0260 \times L_F), \quad (2.18)$$

where the *SE* of a_2 obtained by bootstrapping (5 000 replicates) was 0.234, the *SE* of b_2 obtained by bootstrapping (5 000 replicates) was 7×10^{-4}, $R^2 = .86$, and $n = 260$ (Fig. 2.21). This equation can be rewritten as

$$W_{\mathrm{O}} = 3.677 \times 2^{L_{\mathrm{F}}/26.7}, \tag{2.19}$$

where 3.677 was the weight at $L_{\mathrm{F}} = 0$ and 26.7 was the increment of L_{F} at which W_{O} doubles. For each sex, the relationship between the log-transformed data of the fish age (A_{F}) and W_{O} was expressed by a simple linear function (Fig. 2.22). Males and females had different linear functions (i.e., two parallel lines), as tested by *t* tests (Zar, 1999) for difference between male and female regression coefficients [$t(247) = 0.03$, $p = .98$] and elevations [$t(248) = 3.91$, $p < .001$]. Simple linear regression was used to express the relationship between the log-transformed fish age and L_{P} for both sexes (Fig. 2.23). In the regression, males and females had different regression functions (i.e., two parallel lines), as indicated by *t* tests for difference between male and female regression coefficients [$t(270) = 0.35$, $p = .73$] and elevations [$t(271) = -2.61$, $p < .001$].

2.3.5 Length-weight relationship

Sex-specific length-weight curves did not differ significantly, as indicated by the likelihood ratio test [$\chi^2(2) = 2.81$, $p = .25$]. A power function [$a = 2.964\times10^{-5}$ ($SE = 4.86\times10^{-6}$), $b = 2.928$ ($SE = 0.036$), $n = 293$, and $R^2 = .98$] was then obtained using sex-pooled data (Fig. 2.24). The parameter *a* was found to closely correlate with *b* at fitting the length-weight function (Fig. 2.25). According to the growth and length-weight parameters estimated, the predicted mean L_{F} and *W* for 5-year-old females were 88 cm and 14.5 kg, respectively, and the values for 5-year-old males were 89 cm and 15.2 kg, respectively (Table 2.6).

2.3.6 Robust likelihood ratio tests based on randomization tests

In comparing sex-specific growth curves, the randomized likelihood ratios seemed to deviate slightly from the assumed chi-square distribution ($df = 3$) at χ^2 values of less than 8, but they adhered to the assumed distribution at large χ^2 values [Fig. 2.26(a)]. The findings indicated that the likelihood ratio test [$\chi^2(3) = 20.78$, $p < .001$] conducted to compare the sex-specific von Bertalanffy curves is appropriate because of the large value of χ^2 (> 8) obtained. Furthermore, in comparing sex-specific length-weight curves, the randomized likelihood ratios closely adhered to the assumed chi-square distribution with $df = 2$ [Fig. 2.26(b)].

2.4 Discussion

The results of this study provide sex-specific growth parameters for North Pacific albacore. An updated allometric function for this stock is also presented. Obliquely sectioned otoliths can be useful material for determining the age of North Pacific albacore. The I_{A} values of males (8.6%) and females (7.4%) were not high, indicating that the precision of the age estimates is acceptable. The annuli found in North Pacific albacore sagittae were fall-to-winter growth marks, and the first annulus indicated growth of less than 1 year.

In this study, a single reader estimated the ages of all fish because of the unequal experience among different readers in estimating fish age. Because the I_{A} and coefficient of variation (Chang, 1982) are functionally equivalent, as reported by Campana (2001), only the I_{A} was used to measure the precision of the age estimates. Although this study aimed to obtain more accurate and precise age estimates with the methodologies used, the age estimates may be biased because of individual variability in the times of birth and annulus formation, misidentification of annuli, or a combination of these factors. Also, the growth modeling may be biased because of fish sampling, but this is difficult to verify. Albacore are highly migratory fish, and they have a wide distribution in the North Pacific Ocean. Collecting more representative samples from the entire stock distribution for biological investigations is difficult and time consuming.

Although the micro-increments in North Pacific albacore sagittae have been shown to be daily growth marks (Laurs et al., 1985), the micro-increments found in the otolith slices prepared in the present study were compact, except for those micro-increments close to the primordium. In older annual growth marks, the daily growth increments could not be precisely counted. To conveniently compare sex-specific growth functions by a randomization test, the precision of the age estimate based on otolith edge condition was set to 0.5 years. In addition, it is difficult to precisely define the margins of all annuli in older fish. Thus, marginal increment widths were not analyzed in this study. In the edge analysis conducted in the present study, the micro-increments formed on the postrostral-ventral edge in spring and summer were broader than those found in fall and winter, indicating that North Pacific albacore tend to grow faster in spring and summer than they do in fall and winter. Moreover, as indicated by L_∞, mature males are expected to attain a larger size than mature females. Quinn & Deriso (1999) reported that several factors (e.g., depth, sex, habitat, weather, locality, interannual variation, genetics, year-class, and density) may affect fish growth. The disparity between the sex-specific growth curves of North Pacific albacore seems to occur in the size range of approximately 85 to 90 cm L_F (Fig. 2.15 and Table 2.3), which coincides with the size at 50% maturity of this stock (see Chapter 3). Thus, reproduction seems to be an important factor affecting the growth of mature North Pacific albacore.

For both sexes, all three growth models seem to be fitted well to age-length data as indicated by both R^2 and F-test values (Table 2.4). In addition, the AICc differences (Δ_i) among candidate models were smaller than 5, indicating that all candidate models have support (Burnham & Anderson, 2002). Because the parameters of the VBGM are commonly used in fisheries research and are easier to compare with results of previous studies, more results from the VBGM are presented in this study despite uncertainty about whether the VBGM is the best-fitted model among several growth models (e.g., Schnute & Richards, 1990) for male or female age-length data. The Gompertz model is usually used to express a sigmoid growth curve, such as for the growth modeling of young fish (Campana & Jones, 1992). In this study, there were only small differences in the predicted mean lengths of age classes 1 through 10 between the Gompertz model and VBGM (Table 2.6). An additive error term was used for each growth model rather than a multiplicative error term because older age classes did not exhibit larger residuals at the fitting of the three growth models (Fig. 2.13 and 2.14). The negative values of t_0 indicate that juvenile fish are likely to grow (in length) faster than older fish (King, 2007). For both the VBGM and the Gompertz model, the normality of each parameter was obvious for both sexes, and all scatter plots for the correlation between parameters appeared to have linear mean functions (Fig. 2.16 and 2.17). These findings suggest that large sample inference is adequate for the bootstrappings of the von Bertalanffy and Gompertz models (Weisberg, 2005). Also, the bootstrapping of sex-pooled length-weight data seems to be adequate (Fig. 2.25). The bootstrapping of the Richards model is likely to be less adequate for male data because of the large *SE* obtained for t_3 (Fig. 2.19 and Table 2.5). The Richards model has four parameters, resulting in a less steady condition at the fitting of this model by bootstrapping male age-length data under some circumstances than a three-parameter model (e.g., VBGM or Gompertz model) would have.

Because correlations between the parameters of the VBGM were obvious, in the likelihood ratio test of this study, all parameters were compared simultaneously instead of comparing one or two parameters. A disadvantage of the likelihood ratio test is that the size ranges of males and females should be identical to avoid comparing the size distributions of the two datasets (Haddon, 2001). To clarify the reliability of the likelihood ratio test in comparing sex-specific growth or allometric functions, an extra randomization test was conducted in this study. The randomization test can be also used for hypothesis testing, and the randomized likelihood ratios are the test statistic. Bootstrapping can be also used for hypothesis testing, but this method may be less accurate (Efron & Tibshirani, 1993). In this study, the 95% bootstrap CIs of the parameters L_∞ and K did not overlap between males and females (Table 2.5). Other methods can also be used to compare sex-specific growth curves, for example, the analysis of the residual sum of squares (Chen et al., 1992) and Hotelling's T^2-test (Bernard, 1981; Cerrato, 1990).

Many papers have reported the parameter estimates (L_∞, K, and t_0) of the VBGM not only for North Pacific albacore (Fig. 2.27 and Table 2.7) but for other albacore stocks as well (Table 2.8). More growth parameters for albacore stocks can be found in Santiago's dissertation (Santiago, 2004). Among the growth curves reported for North Pacific albacore, most curves seem to be parallel to each other (Fig. 2.27), which probably results from the greater number of age classes of fish smaller than 60 cm L_F used for growth modeling (e.g., Otsu, 1960; Yabuta & Yukinawa, 1963). Aside from those reported by Megalofonou (2000) and Ortiz de Zárate & C-Parrack (1996), the present study reported lower L_∞ values and larger K values than those of the albacore stocks presented in Table 2.8. According to the parameters of the VBGM obtained in the present study, the mean predicted L_F values of 1-year-old fish (at the beginning of

May) were 42 cm L_F for females and 45 L_F cm for males (Table 2.6). These two estimates are close to the estimate (a standard length of 38 cm) reported by Yoshida (1968). Yoshida (1968) reported that juvenile albacore grow in body length at a rate of approximately 3.12 cm per month. All length-weight curves reported for North Pacific albacore are similar for fish smaller than 110 cm L_F (Fig. 2.28 and Table 2.9).

Many researchers have used the parameters of the VBGF to estimate fish longevity (Taylor, 1958; Fabens, 1965; Cailliet et al., 2006). When applying the growth parameters obtained in this study to estimate the longevity of North Pacific albacore, I recommend that a large proportion of L_∞ be used in such analysis (e.g., using $L_\infty \times .99$). If a small proportion of L_∞ (e.g., $L_\infty \times .95$) is used to estimate the longevity of North Pacific albacore, the longevity may be underestimated because the mean L_F values of older age classes are similar for both sexes, as predicted by growth parameters (Table 2.6). In this case, the longevity estimate may be better interpreted as the age at which the mean fish length tends to increase slowly towards L_∞ with increasing age. The longevity of a fish species may be better estimated by ageing a large sample of mature fish than by growth parameters. The maximum age estimated in this study was 14.25 years for a male (106 cm L_F). Age estimates for both males and females included individuals older than 10 years. In comparing the maximum fish age estimate obtained in this study with those reported for other *Thunnus* species (Table 2.10), it becomes clear that North Pacific albacore are relatively short lived. Albacore are a small *Thunnus* species, and their common size in commercial catches is less than 110 cm L_F (Suda, 1954b; Koto & Hisada, 1966; Yoshida, 1975; Griggs & Murray, 2000). Fish size is an important factor affecting the longevity of a pelagic fish species; because of predation, small pelagic fish species are believed to have higher natural mortality rates compared to large ones.

Because North Pacific albacore exhibit sex-specific growth, the use of an identical growth function for both sexes in stock assessment research may cause great uncertainty in stock assessment results. Modeling population dynamics using sex-specific growth parameters, however, is difficult because little information exists on sex-specific age compositions. Because older fish have similar mean lengths, it is difficult to precisely divide mature fish into several age classes using growth parameters and sex-specific length-frequency data. More important, sex-specific age compositions cannot be precisely constructed using growth parameters and sex-pooled size data. I recommend that more simplified groups be used to represent this stock in stock assessment models, for example, immature fish (recruited to fisheries or not recruited) and mature fish (the spawning stock, all recruited).

To assess this stock's current status, sex-specific age compositions must be constructed. Precise sex-specific age compositions need to be constructed by ageing a large sample of fish rather than by analyzing size composition data. Several topics relevant to the age and growth of this stock need to be thoroughly investigated: (a) the validation of annual growth marks by tagging, (b) the growth of juvenile fish, (c) the seasonal or geographical variation in fish growth, (d) the factors affecting fish growth, and (e) the interaction of this stock with the South Pacific stock.

Chapter 3—The Reproductive Biology of North Pacific Albacore

3.1 Introduction

Knowing the reproductive biology of a particular fish stock is important for modeling the population dynamics of that stock. Although the reproductive biology of North Pacific albacore has been studied, little information is currently available on the histology-based maturity ogives of this stock. The maturity parameters used in previous assessments of this stock have been based on studies (e.g., Ueyanagi, 1957; Otsu & Uchida, 1959a) conducted more than five decades ago. In previous reproductive biology studies, however, histology-based maturity ogives have rarely been studied. Analyzing gonad samples by histological techniques (a more precise method) can provide detailed information on the gonadal development of each fish specimen (Schaefer, 2001; Agarwal, 2009). In this way, the sexual maturity of each fish can be more precisely determined for the estimation of a maturity ogive.

The length at sexual maturity of North Pacific albacore is believed to be within the size range of 85 to 90 cm L_F (Ueyanagi, 1957; Suda, 1958; Otsu & Uchida, 1959a). Partlo (1955b) performed a histological examination of gonads of albacore collected from the eastern Pacific Ocean and concluded that no fully mature gonads were found. Chen et al. (2010) investigated the gonadal development of North Pacific albacore and presented results on the sex ratio, sexual maturity, spawning season, spawning frequency, and batch fecundity of this stock. Aside from these studies, little information is available on the maturity ogives of this stock. Maturity ogives can provide important information for determining the spawning stock biomass in stock assessment models.

This study aimed to investigate the reproductive biology of North Pacific albacore based on the histological examination of collected gonad samples. This study focused on the estimation of maturity ogives, which can provide important maturity parameters for determining the spawning stock size of this stock. Detailed information on the histological criteria for determining sexual maturity and statistical estimation procedures are presented in this study.

3.2 Materials and methods

3.2.1 Specimen collection

As presented in Section 2.2.1 (Sample collection), albacore specimens (133 females, 46 to 101 cm L_F; 160 males, 45 to 118 cm L_F) were collected from the catches of Taiwanese longline vessels and Japanese pole-and-line vessels operated in the central and western North Pacific Ocean from 2001 to 2008 (Fig. 2.1 and 2.2). In the laboratory, gonads were removed from the fish specimens, weighed using an electronic balance to the nearest 0.1 g, and preserved with 10% neutral-buffered formalin in labeled plastic containers for further histological investigations. Using the normal approximation to the binomial test, the 1:1 sex ratio examination was analyzed for each length class (in 5-cm intervals) of the fish specimens.

3.2.2 Preparing histological slices of gonad samples

In preparing histological slices for each fish, gonad subsamples were taken from the middle section of the right or left lobe of the gonad, dehydrated with a graded series of ethyl alcohol solutions, cleared with xylene, infiltrated by Paraplast Plus, and embedded in Paraplast. The embedded subsamples were then sectioned (6 μm) using a microtome and stained with Mayer's hematoxylin and eosin. The serial sections were then mounted on a microscope slide using balsam. All prepared sections were examined with light microscopes, and images of histological sections were taken with a digital camera attached to the light microscope. Germ cells were measured using a light microscope with a micrometer mounted on one ocular.

3.2.3 Histological classification of sexual maturity

The cellular stages of spermatogenesis (e.g., spermatogonia, spermatocytes, spermatids, and spermatozoa) were classified by histological evaluations. The sexual maturity and gonad stage of each male specimen were determined based on the histological examination of its gonad samples. The classification scheme of Chen et al. (2010) was used to determine the sexual maturity of each male specimen. In their classification scheme, immature males possess small testes that are characterized by the small size occupied by the lobule lumen. Immature males may possess no spermatozoa in their testes or only a few spermatozoa that accompanied by only a few nests of spermatids in the lobules. Mature males are often characterized by large testes. They possess abundant spermatozoa in developed lobules, and the size of the lobule lumen in their testes is larger than that in immature testes. They also possess abundant nests of spermatids in their developing lobules.

The oocytes of oogenesis in albacore ovaries can be grouped into five stages: unyolked, early yolked, advanced yolked, migratory nucleus, and hydrated (Schaefer, 1998). Postovulatory follicles and atretic oocytes were also observed during histological examination. The sexual maturity of each female specimen was determined according to the histological examination of its gonad samples using a classification scheme similar to that used by Schaefer (1998) for yellowfin tuna. In this classification scheme, immature females possess only unyolked oocytes, early yolked oocytes, or both of these kinds of oocytes in their ovaries. Their ovaries contain neither atresia of yolked oocytes nor advanced yolked oocytes. In addition, more advanced oocytes (i.e., migratory nucleus and hydrated oocytes) and postovulatory follicles are not found in their ovaries. In contrast, mature females have atresia of yolked oocytes, advanced yolked oocytes, or both of these kinds of oocytes in their ovaries. Other advanced oocytes (migratory nucleus and hydrated oocytes) and postovulatory follicles may also be found in their ovaries. Furthermore, females possess running-ripe or spawned ovaries containing postovulatory follicles (Chen et al., 2010).

3.2.4 Estimating maturity ogives by logistic regression

The sexual maturity (immature or mature) of each fish was determined according to the histological examination of its gonad samples. To construct the maturity ogive of each sex using length-maturity data, the binomially distributed maturity data can take the form of

$$Y_i \sim B(1, P_i), \quad \text{for } i = 1, \ldots, n, \tag{3.1}$$

where $Y_i = 0$ represents an immature individual,

$Y_i = 1$ represents a mature individual,

P_i is the probability of being mature, and

n is the number of individuals.

Subsequently, logistic regression (Hosmer & Lemeshow, 2000; Kutner et al., 2004) can be used to analyze length-maturity data and to construct a length-maturity curve for each sex using the following equation:

$$P_i = \{1 + \exp[-(\beta_0 + \beta_1 X_i)]\}^{(-1)}, \tag{3.2}$$

where β_0 and β_1 are the parameters to be estimated, X_i is the fish length, and $P_i = E(Y_i \mid X_i)$. Moreover, the unknown binomial probabilities can be modeled using the logit function (the natural logarithm of the odds) as a linear function of X_i, which can be expressed as

$$\mathrm{logit}(P_i) = \ln[P_i/(1-P_i)] = \beta_0 + \beta_1 X_i. \tag{3.3}$$

The parameters (β_0 and β_1) can be estimated by the maximum likelihood method (Appendix B) using PROC LOGISTIC in SAS (SAS version 9.1, SAS Institute Inc.; www.sas.com).

In logistic regression analyses, the goodness of fit of a logistic model can be evaluated by the coefficient of determination and by the Hosmer and Lemeshow goodness-of-fit test (H-L test). In the PROC LOGISTIC of SAS, two kinds of R^2 (Maddala, 1983; Cox & Snell, 1989; Nagelkerke, 1991) can be calculated, respectively, as

$$R_{\mathrm{S}}^{2} = 1 - \exp\{2 \times [\log L(\mathrm{M}) - \log L(0)]/n\} \tag{3.4}$$

and

$$R_{\mathrm{sas}}^{2} = R_{\mathrm{S}}^{2}/[1 - \exp(2 \times \log L(0)/n)], \tag{3.5}$$

where

$\log L(\mathrm{M})$	is the maximized log likelihood of the fitted model,
$\log L(0)$	is the null model with only an intercept term, and
n	is the sample size.

According to the predicted probabilities obtained, the H-L test partitions subjects into 10 groups. For each group, a chi-square value is calculated based on the observed and expected frequencies (Hosmer & Lemeshow, 2000). The null hypothesis for the test is that there are no differences between the observed and expected frequencies of the response variable. Thus, if the test is not significant (i.e., the null hypothesis cannot be rejected), the result suggests that the model fits the data well.

3.2.5 Comparing sex-specific maturity ogives

Sex-specific maturity ogives were compared by a randomization test (Edgington, 1995; Manly, 1997). In the randomization procedure, male (n = 122) and female (n = 133) length-maturity data from the same length range (i.e., 46 to 101 cm L_F) were randomized within each length class and between sexes. Thus, the randomized length-maturity data for males and females were obtained in the randomization procedure. For each sex, 5 000 sets (including the original data as one set) of randomized length-maturity data were obtained. The parameters β_0 and β_1 for males (termed β_{0M} and β_{1M}) and for females (termed β_{0F} and β_{1F}) were estimated using the randomized length-maturity data (5 000 sets for each sex). Thus, a total of 5 000 sets of the parameters β_0 and β_1 were obtained for each sex. The parameter differences between males and females were then calculated as

$$D_1 = \beta_{0F} - \beta_{0M} \tag{3.6}$$

and

$$D_2 = \beta_{1F} - \beta_{1M}. \tag{3.7}$$

In hypothesis testing, the parameter differences (D_1 and D_2) between males and females were calculated using their respective 5 000 sets of randomized parameter estimates. The parameter differences between males and females that were obtained from the original data could then be compared to the results obtained with the 5 000 randomization replicates. The null (H_0) and alternative (H_1) hypotheses of the randomization test were written as

$$\mathrm{H}_0 : D_1 = 0 \text{ and } D_2 = 0 \tag{3.8}$$

and

$$\mathrm{H}_1 : D_1 \neq 0 \text{ or } D_2 \neq 0 \text{ or both.} \tag{3.9}$$

The level of significance for the randomization test was set to 5%. The randomization test used in this study was conducted with MATLAB (version 7.2, MathWorks Inc.; www.mathworks.com).

3.3 Results

3.3.1 Histological classification

In albacore testes, spermatogonia [Fig. 3.1 (a), (b), and (d)] are characterized by their large size. Each spermatogonium usually has a round nucleus with a nucleolus and clear nuclear membrane. The cytoplasm of the cell has less affinity for hematoxylin-eosin staining. The primary spermatocytes [Fig. 3.1 (b) and (d)] are basophilic and have no visible nucleoli. The chromatin of a primary spermatocyte occupies most of the cell. Secondary spermatocytes [Fig. 3.1 (b), (c), and (d)] are produced by the reduction division of the first meiosis division from primary spermatocytes. Their size is generally smaller than that of primary spermatocytes, and they are spherical in shape and basophilic. In a secondary spermatocyte, the nuclear membrane and nucleolus are generally invisible. Spermatids [Fig. 3.1 (c) and (d)] are produced by the second meiosis division of secondary spermatocytes. They are basophilic, and their size is obviously smaller than that of secondary spermatocytes. The appearance of spermatids varies greatly during spermiogenesis. Each spermatid matures into a spermatozoon. The spermatozoon is characterized by a basophilic head and an acidophilic flagellum [Fig. 3.1(c)]. The flagella of spermatozoa were not frequently seen in the histological sections of this study [Fig. 3.1(d)]. As spermatozoa mature, they are detached from the nest and accumulate toward the center of the lobule lumen [Fig. 3.1 (c) and (d)]. Histological sections of an immature testis and a mature testis are shown in [Fig. 3.1 (e) and (f)].

In albacore ovaries, unyolked oocytes [Fig. 3.2(a)] are small (< 280 μm) and strongly basophilic. In the oocyte, no yolk granules exist. An early yolked oocyte [Fig. 3.2(b)] is characterized by a centrally placed nucleus and small and acidophilic yolk granules that peripherally occupy the ooplasm. Advanced yolked oocytes [Fig. 3.2(c)] possess larger yolk granules than early yolked oocytes, and their yolk granules are typically distributed throughout the ooplasm. In the oocyte, oil droplets are widely distributed in the ooplasm. Because of the large size of the oocyte, the nucleus of an advanced yolked oocyte is seen less frequently than in early yolked oocytes in histological slices. The atretic yolked oocyte [Fig. 3.2(d)] has an irregular shape caused by the degeneration and resorption of the oocyte. In the late stage of an atretic oocyte, normal organelles are rarely found in the oocyte remnant. The oocyte in the migratory nucleus stage [Fig. 3.2(e)] is characterized by a non-centrally placed nucleus (the migration of the nucleus toward the animal pole). The oocyte usually has a large oil droplet [Fig. 3.2(e)] that is close to the nucleus. The hydrated oocyte [Fig. 3.2(f)] has an irregular shape caused by the dehydration of the tissue sample in the histological procedure. In this oocyte, a homogeneous yolk mass is formed by the fusion of yolk granules and yolk plates. The initial stage of a postovulatory follicle is characterized by an outer layer of thecal cells and an inner layer of granulosa cells (Fig. 3.3). A postovulatory follicle is produced by the rupture of a hydrated oocyte, which is then expelled into the ovarian lumen. The external appearances of albacore oocytes are shown in Fig. 3.4.

The smallest mature specimens measured were 78 cm L_{F} for males and 83 cm L_F for females. The largest immature specimens were 93 cm L_F for males and 94 cm L_F for females. In addition, the youngest ages of mature specimens determined were 3.3 years for males and 4.3 years for females. The oldest ages of immature specimens were 5.8 years for males and 6.8 years for females.

3.3.2 Spawning ground, spawning season, and sex ratio

The females that possessed migratory nucleus oocytes or hydrated oocytes in their ovaries were all collected from the fishing operation area A1 (Fig. 2.1) in March ($n = 4$), April (n = 19), and August (n = 1). These females were deemed imminent-spawning fish. The females that possessed postovulatory follicles in their ovaries were all found in area A1 in March (n = 4), April (n = 20), June (n = 1), August (n = 1), and September (n = 1), indicating that the western Philippine Sea is a spawning ground for albacore (Fig. 3.5). These findings also indicated that the spawning of albacore in the western Philippine Sea occurred at least from March to September, with peak spawning activity in March and April. In the 1:1 sex-ratio examination, females predominated in the size range of 91 to 95 cm L_{F}, but males substantially outnumbered females at sizes larger than 100 cm L_{F} (Table 3.1).

3.3.3 Maturity ogive

In comparing sex-specific maturity ogives, the results of the randomization test (Fig. 3.6) indicated that no statistical differences existed between male and female maturity parameters ($p > .05$). Thus, the length-based maturity ogive (Fig. 3.7) was obtained by sex-pooled data with the following equation:

$$P = \frac{1}{1 + \exp\left(28.8136 - 0.3375 \times L_{\mathrm{F}}\right)}, \tag{3.10}$$

where $R_{\mathrm{S}}^2 = .61, R_{\mathrm{sas}}^2 = .82,$ and the H-L test parameters were $\chi^2(8) = 1.21$ and $p = .99$. Accordingly, the length at 50% maturity of this stock estimated by the above logistic function was approximately 85 cm L_{F} (i.e., 28.8136/0.3375).

3.4 Discussion

The results presented in this chapter provide a histology-based maturity ogive for North Pacific albacore. North Pacific albacore are found to reach 50% sexual maturity at a size of approximately 85 cm L_{F}, corresponding to 4.5 years of age for females and 4.4 years of age for males based on the von Bertalanffy growth curves presented in Chapter 2.

Males and females have similar maturity ogives; they reach sexual maturity at a similar size (or age) range. After reaching sexual maturity, males tend to grow faster than females (Fig. 2.15).

In this study, imminent-spawning and spawned females were all collected from the western Philippine Sea, indicating that this area seems to be an important spawning ground for North Pacific albacore. The spawning season of this stock in this area was at least from March to September with the peak spawning months of March and April. The western Philippine Sea is also an important spawning ground for Pacific bluefin tuna (*Thunnus orientalis* Temminck & Schlegel), and the spawning season of Pacific bluefin tuna in this area extends mainly from May to June (Chen et al., 2006). Although both albacore and Pacific bluefin tuna spawn in this area, their peak spawning months are likely to be different. North Pacific albacore have an extensive spawning distribution in the Pacific Ocean, and they probably spawn throughout the year in oceanic subtropical waters (Ueyanagi, 1969; Nishikawa et al., 1978, 1985). Moreover, there is little evidence that albacore spawn in the temperate waters of the North Pacific Ocean (Otsu & Uchida, 1959a; Otsu & Hansen, 1962; Ueyanagi et al., 1969).

The months of peak spawning activity for North Pacific albacore may differ by geographic area or by year. Yoshida (1968) investigated juvenile albacore found in the stomachs of billfishes in Hawaiian waters and concluded that albacore spawning extends from March to September, with peak spawning in May, in Hawaiian waters. In contrast, Ueyanagi (1957) and Otsu & Uchida (1959a) reported that albacore spawning in the central and western North Pacific peaks in June and July. According to the size composition data of commercial catches reported for North Pacific albacore (Suda, 1956; ISC, 2006), large albacore tend to live longer in tropical and subtropical waters than in temperate waters (Chen et al., 2005). In addition, mature North Pacific albacore may have several spawning aggregations, resulting in a wide spawning distribution and an extended spawning season of this stock. Furthermore, South Pacific albacore have been found to spawn at least throughout the austral summer months (Ishii & Inoue, 1956; Otsu & Hansen, 1962; Yoshida 1971; Ramon & Bailey, 1996), from December to February. Because large albacore can be found in the equatorial waters of the Pacific Ocean, more efforts are needed to clarify the spawning interaction between the North Pacific and South Pacific stocks.

With logistic regression analyses, individual length-maturity data can be directly used to fit a logistic function. Other methods can also be used to estimate the parameters of a logistic function, such as that used by King (2007). Using the length-maturity data from the present study, I demonstrate King's method here, which is analogous to logistic regression. To estimate the parameters β_0 and β_1, first, the proportion of mature fish to total fish in each length class is computed (as shown by the solid circles in Fig. 3.7; proportions of 0 and 1 are excluded). Each proportion obtained is then used to calculate the corresponding value of the logit function, $\ln[P/(1-P)]$. Using the proportion data obtained, the parameters β_0 and β_1 of a logistic function can be estimated by simple linear regression. Last, the length at 50% maturity can be estimated by calculating $\beta_0/(-\beta_1)$. Using King's method, I obtained an estimate of 85 cm L_F (i.e., $\beta_0 = 23.0363$ and $\beta_1 = -0.2708$) for the length at 50% maturity, and this estimate is the same as that obtained by logistic regression. With King's method, however, a wide length interval may be used for calculating the proportions of mature fish if the sample size is small for some length classes. Combining individual data within a large length interval changes the original data and may result in different parameter estimates.

The length at 50% maturity of North Pacific albacore reported in this study is close to that suggested in previous studies (Ueyanagi, 1957; Suda, 1958; Otsu & Uchida, 1959a). Nevertheless, the classification criteria used in previous studies to determine sexual maturity differ greatly. Otsu & Uchida (1959a) classified albacore ovaries into three categories according to oocyte size (in diameter) as follows: early developing (maximum oocyte size, 0.4 mm), late developing (the size range of the most advanced oocytes, 0.4 to 0.8 mm), and advanced (the size range of the most advanced oocytes, 0.7 to 1 mm). In their classification, females that possessed late developing and advanced ovaries were deemed mature fish. Using their classification criteria, non-spawning but mature females may be classified as immature fish. Ueyanagi (1957) used the criteria that fish with a pair of testes containing milt and weighing over 150 g were mature and postulated that males reached sexual maturity at a size of 97 cm L_F. Using Ueyanagi's criteria may overestimate the size at sexual maturity because mature albacore may possess testes weighing less than 150 g, as reported by Chen et al. (2010).

The results of the present study suggest that North Pacific albacore reach sexual maturity mostly within the size range of approximately 80 to 90 cm L_F (Fig. 3.7), corresponding to a limited age range of approximately 4 to 5 years (Table 2.6). According to the von Bertalanffy growth curves presented in Chapter 2 (Fig. 2.15), males tend to grow faster than females do after reaching sexual maturity. This finding coincides with that reported by Otsu & Uchida (1959b). Because of a lack of suitable albacore samples, the maturity ogive of this stock has hardly been investigated in previous reproductive-biology studies, for example, Partlo (1955b), Ueyanagi (1957), and Otsu & Uchida (1959a). In the present study, the maturity ogive of this stock was estimated with length-maturity data pooled by geographic areas and years regardless of geographic and temporal variations in the maturity-ogive estimation. Using less representative samples in maturity-ogive estimation might cause less bias than using inadequate criteria to determine the sexual maturity of fish. Because albacore are highly migratory fish and are widely distributed in the North Pacific Ocean, collecting more representative fish samples for maturity-ogive estimation is costly and time consuming. Moreover, North Pacific albacore reach sexual maturity within a limited size (or age) range, indicating that the bias of maturity-ogive estimation caused by the lack of more representative samples might be relatively weak.

Small ovarian subsamples may fail to adequately capture the specifics of gonadal development. For example, a few females were first classified to be at the unyolked stage according to their histological results, yet some yolked oocytes were found in their formalin-preserved ovarian samples. One possible explanation for this discrepancy is that only small ovarian subsamples were taken from the fish ovaries for histological examination. To avoid this situation, more subsamples should be taken from the gonad of each fish for future histological examinations, if possible. To determine the sexual maturity of each fish, a gross anatomical examination of the whole gonad must be conducted as an auxiliary approach. In this study, several mature males with histological evidence of sexual maturity possessed small gonads (< 10 g). Possible explanations for this finding are that they underwent a reproductively inactive phase or that they had less spawning potential than those fish with larger gonads.

Although male and female North Pacific albacore have different growth functions, they tend to have similar maturity ogives. Thus, a sex-pooled maturity ogive can be used to define the potential spawning stock of this stock. More efforts are needed to study on the reproductive biology of this stock with more representative biological samples for clarifying the spawning distribution and seasons of this stock and the interaction of this stock with the South Pacific stock.

Chapter 4—Yield-per-Recruit Analysis of North Pacific Albacore

4.1 Introduction

Yield-per-recruit (YPR) analysis is a classical approach used to assess the optimal fishing mortality rates of a particular fish stock and to provide biological reference points (BRPs) for fisheries management of the stock (Beverton & Holt, 1957; King, 2007). In the YPR analysis of a fish stock, the growth and population size of the stock are frequently simulated based on the stock's life-history traits (e.g., growth, maturity, and mortality). The results of the YPR analysis can provide benchmarks regarding fishing mortality rates and size limits for this stock to theoretically prevent the stock from being overfished (Gulland, 1983; King, 2007).

Specifically, the BRP $F_{\max}$ obtained in the YPR analysis of a fish stock represents the probable maximum yield from a recruit, but applying the $F_{\max}$ value to the fisheries management of the stock may result in unsustainable harvests (King, 2007). Thus, another BRP, $F_{0.1}$, is commonly computed and used in YPR research. Spawning-stock-biomass-per-recruit (SSBPR) and spawning-potential-ratio (SPR) analyses of a fish stock can provide benchmarks regarding fish mortality rates that can theoretically prevent the stock from recruitment overfishing. Here, SSBPR and SPR analyses are considered as extensions of YPR analysis.

Although many stock assessment studies have been done on North Pacific albacore, the life-history parameters of this stock obtained in this dissertation (see Chapters 2 and 3) substantially differ from those used in previous stock assessment studies. In particular, North Pacific albacore exhibit sex-specific growth (see Chapter 2). Using an identical growth function for both sexes in stock assessment models would increase the uncertainty of stock assessment results. In this chapter, the results of sex-specific YPR analyses (including SSBPR and SPR analyses) are presented for this stock based on the life-history parameters obtained in Chapters 2 and 3.

The first goal of this chapter is to provide sex-specific BRPs for North Pacific albacore. The BRPs estimated in this chapter include $F_{\max}$, $F_{0.1}$, $F_{20\%}$, $F_{25\%}$, $F_{30\%}$, and $F_{40\%}$ (see Appendix C). In the sex-specific YPR analyses, bootstrap estimates of von Bertalanffy growth parameters and length-weight parameters are used to incorporate the uncertainties of growth and length-weight parameters into BRP estimates. The relationship between each BRP and natural mortality is also studied because reliable natural mortality estimates for this stock are not currently available.

4.2 Materials and methods

4.2.1 Data and model setting

Data used in this chapter include information on growth, gear selectivity, and maturity (Table 4.1). Specifically, von Bertalanffy growth parameters are used to compute the values of length-at-age, longevity, and natural mortality. The mean weight at each age is calculated using growth and length-weight parameters at the midyear of each age (Sun et al., 2005). Because reliable sex-specific size (or age) compositions for North Pacific albacore are not available, no catch-curve analyses are presented in this chapter. In addition, no estimates of current fishing mortality are presented.

4.2.2 Natural mortality estimation

For both sexes, Pauly’s and Hoenig’s equations (Pauly, 1980; Hoenig, 1983) are used to estimate the instantaneous rate of natural mortality (M). Using these two equations, the von Bertalanffy growth parameters (L_∞, K, and t_0) are the basic information required for estimating the M values. The Pauly equation is

$$\log_{10} M = -0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} T, \tag{4.1}$$

where L_∞ and K are the von Bertalanffy growth parameters and T is the seawater temperature used for this stock. Here, T is set to be 17.5 °C because Clemens (1961) reported that high catchability of albacore is associated with seawater temperatures ranging from 15.6 to 19.4 °C. To incorporate the parameter uncertainty of Pauly's equation, a modified Pauly equation is then constructed and used in this chapter based on the data reported in Pauly's paper (Pauly, 1980). The modified Pauly equation is expressed as

$$\log_{10}(M) = \beta_1 \log_{10}(L_\infty) + \beta_2 \log_{10}(K) + \beta_3 \log_{10}(T). \tag{4.2}$$

The parameters (β_1, β_2, and β_3) are obtained with least-squares estimation. Moreover, bootstrapping (1 000 replicates) is then conducted to obtain bootstrap parameters of the modified Pauly equation (Table 4.2). The R^2 value obtained by the modified Pauly equation is similar to that obtained by the Pauly equation (Table 4.2). Details of the bootstrap parameter estimates of the modified Pauly equation are shown in Fig. 4.1. The Hoenig equation (for fishes) is written as

$$\ln M = 1.46 - 1.01 \times \ln(t_\lambda), \tag{4.3}$$

where t_λ is the maximum fish age. For both sexes, the t_λ values are estimated using the formula of Taylor (1958), which can be written as

$$t_\lambda = t_0 - \frac{\ln(1 - P_\mathrm{L})}{K}, \tag{4.4}$$

where t_0 and K are the von Bertalanffy growth parameters and P_L is the proportion of L_∞ used (in this chapter, $P_\mathrm{L} = .99$). To incorporate the uncertainty of growth modeling into M estimates, the bootstrap von Bertalanffy growth parameters (5 000 sets for each sex) presented in Chapter 2 are used for the above equations (4.1, 4.2, 4.3, and 4.4).

4.2.3 The yield-per-recruit model

In the YPR analyses of this chapter, both natural and fishing mortalities are simulated within a reasonable range of values. That is, M ranges from 0.1 to 0.6 year^{-1}, with an increment of 0.01, and the instantaneous rate of fishing mortality (F) ranges from 0 to 4 year^{-1}, with an increment of 0.01. The M value is assumed to be identical for all age classes because of limited information on the M values of this stock. To incorporate gear selectivity into the YPR analyses, the F value for each age class is multiplied by a selectivity proportion (S_t):

$$F_t = F \times S_t, \tag{4.5}$$

where S_t is the selectivity proportion at age t and F_t is the instantaneous rate of fishing mortality at age t. For both sexes, two sets of gear selectivity schemes are presumed and used in this chapter (Table 4.1). The first set (denoted as Model Scenario 1 or MS1) is as follows: $S_1 = 0.2$ and $S_t = 1$ (where $t = 2, 3, \ldots, t_\lambda$). The second set (denoted as Model Scenario 2 or MS2) is as follows: $S_1 = 0.1$, $S_2 = 0.6$, and $S_t = 1$ (where $t = 3, 4, \ldots, t_\lambda$). The instantaneous rate of total mortality (Z, year^{-1}) is calculated as $Z = M + F$. Therefore, the instantaneous rate of total mortality at age t (Z_t) can be written as

$$Z_t = M + F_t. \tag{4.6}$$

Moreover, the rate of exploitation (E) (Quinn & Deriso, 1999) can be expressed as

$$E = \frac{F}{Z}, \tag{4.7}$$

where gear selectivity at age is ignored.

In the YPR analyses, the age at recruitment (t_r) is defined to be 1 year (i.e., $t_\mathrm{r} = 1$). According to the catch data reported by the ISC (ISC, 2006), the age at first capture (t_c) is set to equal t_r (i.e., $t_\mathrm{c} = t_\mathrm{r}$). The number of fish at recruitment is defined to be R. Thus, the number of fish surviving to age t ($t > t_\mathrm{r}$) can be expressed as

$$N_t = R \times e^{-\sum_{j=0}^{t-1} Z_j}, \tag{4.8}$$

where $Z_0 = 0$. The number of fish that die (caused by both M and F) at each age (D_t) is

$$D_t = N_t \times (1 - e^{-Z_t}). \tag{4.9}$$

The number of fish caught (caused by F) at each age (C_t) is

$$C_t = N_t \times (1 - e^{-Z_t}) \times \frac{F_t}{Z_t}. \tag{4.10}$$

Moreover, the yield (in kilograms) at age t (Y_t) is expressed as

$$Y_t = N_t \times (1 - e^{-Z_t}) \times \frac{F_t}{Z_t} \times W_t, \tag{4.11}$$

where W_t is the mean weight (in kilograms) at age t (Table 4.1).

According to the Thompson and Bell model (Thompson & Bell, 1934), the YPR (Chen & Gordon, 1997; Sun et al., 2002; Chiang et al., 2009) equation can be written as

$$Y/R = \sum_{t=t_r}^{t_\lambda} \left[W_t \frac{F_t}{Z_t} (e^{-\sum_{j=0}^{t-1} Z_j})(1 - e^{-z_t}) \right], \tag{4.12}$$

where the unit for Y/R (YPR) is kilograms per recruit and $Z_0 = 0$. In this equation, the yields from age classes older than t_λ are assumed to be close to zero and are excluded when calculating YPR values (Table 4.3). This equation is used to estimate the yields from a recruit of a stock, and thus, no spawner-recruitment relationship is incorporated into this equation. Moreover, bootstrap estimates of von Bertalanffy growth parameters (5 000 sets) and length-weight parameters (50 sets, randomly selected from 5 000 sets) are used in this model to incorporate the uncertainties of growth and length-weight parameters into the estimations of $F_{0.1}$ and $F_{\max}$. Because using different sets of bootstrap length-weight parameters produces similar $F_{0.1}$ estimates, only 50 sets of bootstrap length-weight parameters are used. By combining the bootstrap growth (5 000 sets) and length-weight (50 sets) parameters, a total of 250 000 sets of growth and length-weight parameters are used for the YPR equation for each sex.

4.2.4 Spawning potential ratios

The SSBPR equation (Gabriel et al., 1989) can be expressed as

$$SSB/R = \sum_{t=t_{\mathrm{m}}}^{t_\lambda} \left(P_t \times W_t \times e^{-\sum_{j=0}^{t-1} Z_j} \right), \tag{4.13}$$

where t_{m} is the age at sexual maturity,

P_t is the proportion of mature fish at age t, and

$Z_0 = 0$.

According to the results of the maturity-ogive estimation presented in Chapter 3, the parameters t_{m} and P_t (Table 4.1) are set as follows: $t_{\mathrm{m}} = 4$ years, $P_1 = 0$, $P_2 = 0$, $P_3 = 0$, $P_4 = .5$, and $P_t = 1$ (for $t = 5, 6, \ldots, t_\lambda$).

Furthermore, the SPR analysis can be used to measure the fishing impact on the potential productivity of a stock (Goodyear, 1990; Goodyear, 1993). The SPR can be calculated as

$$SPR = \frac{SSB/R \mid \text{fished}}{SSB/R \mid \text{unfished}} = \frac{SSB_{\text{fished}}}{SSB_{\text{unfished}}}, \tag{4.14}$$

where the denominator is the SSBPR without fishing and the numerator is the SSBPR affected by fishing. In this chapter, the BRPs estimated in the SPR analysis include $F_{20\%}$, $F_{25\%}$, $F_{30\%}$, and $F_{40\%}$ (see Appendix C). As in the method used in the YPR equation, bootstrap estimates of growth (5 000 sets) and length-weight parameters (50 sets) are used in the SPR analysis to incorporate the uncertainties of growth and length-weight parameters into the estimation of $F_{20\%}$, $F_{25\%}$, $F_{30\%}$, and $F_{40\%}$. The YPR analyses in this chapter were conducted with MATLAB (version 7.2, MathWorks Inc.; www.mathworks.com).

4.3 Results

4.3.1 Natural mortality estimates

As calculated with the three equations (Hoenig's, Pauly's, and modified Pauly equations), females have larger M (in year^{-1}) estimates than males (Fig. 4.2). For both the Pauly equation and the modified Pauly equation, the medians of the M estimates obtained with bootstrap growth parameters are 0.50 for females and 0.40 for males. Using Hoenig's equation, the medians of the M estimates are 0.32 for females and 0.24 for males. Higher M estimates are obtained by Pauly's equation than by Hoenig's equation. For females, the 25th and 75th percentiles of the M estimates obtained by the modified Pauly equation are 0.47 and 0.53, respectively, and those values for males are 0.38 and 0.42, respectively (Fig. 4.2).

4.3.2 Yield per recruit

At the same values of M and F, the results of the sex-specific YPR analyses indicate that males exhibit a slightly larger YPR value than females (Fig. 4.3). In addition, using MS2 produces a larger YPR value compared to using MS1 (Fig. 4.3). At a fixed F value, for both sexes, the smaller the M value is, the larger the YPR value becomes (Fig. 4.3). At a fixed M value ($M < 0.45$), the highest YPR value can be obtained if an appropriate F value (i.e., $F_{\max}$) is used (Fig. 4.3 and Table 4.4). Using MS1, the $F_{0.1}$ value estimated by $M = 0.3$ was 0.32 for females and 0.30 for males (Fig. 4.4 and Table 4.4). At a fixed M value, females have a larger $F_{0.1}$ value than males, both by MS1 and by MS2 (Fig. 4.5 and Table 4.4). At a larger M value, the YPR analyses using bootstrap growth and length-weight parameters tend to produce larger CIs of $F_{0.1}$ estimates (Fig. 4.5). A degree 3 polynomial can be used to express the relationship between the BRP ($F_{0.1}$ or $F_{\max}$) and M. The larger the M value used is, the larger the estimates of $F_{0.1}$ and $F_{\max}$

become (Fig. 4.6 and Table 4.5). According to the YPR values obtained, the optimal age at first capture appears to be 2 years for both sexes (Fig. 4.7 and 4.8).

4.3.3 Spawning potential ratios

At the same values of M and F, females have a larger SPR value than males (Fig. 4.9 and Table 4.6). In addition, using MS2 produces a larger SPR value (and a larger BRP value) compared to using MS1 (Fig. 4.9 and Table 4.6). At a larger M value ($M > 0.4$), males tend to have BRP ($F_{20\%}$, $F_{25\%}$, $F_{30\%}$, or $F_{40\%}$) estimates close to those of females (Fig. 4.10 to 4.13 and Table 4.6), indicating that the disparity in fish growth becomes a less important factor in the estimation of BRPs in the SPR analysis if the M value is large. Also, the SPR analyses using bootstrap growth and length-weight parameters tend to produce smaller CIs of BRP ($F_{20\%}$, $F_{25\%}$, $F_{30\%}$, or $F_{40\%}$) estimates (Fig. 4.10 to 4.13). A degree 3 polynomial can also be used to express the relationship between the BRP ($F_{20\%}$, $F_{25\%}$, $F_{30\%}$, or $F_{40\%}$) and M (Fig. 4.14 to 4.15 and Table 4.5); the larger the M value is, the larger the BRPs become.

4.3.4 Rate of exploitation

For females, the E values calculated by $F_{0.1}$ and $F_{25\%}$ estimates exhibit different trends as the M value is increased (Fig. 4.16). At a larger M value ($M > 0.3$), less variation is found in the E values calculated by $F_{0.1}$ estimates than those calculated by $F_{25\%}$ estimates (Fig. 4.16). For both MS1 and MS2, the E values calculated by $F_{25\%}$ estimates exhibit a clear decreasing trend as the M value is increased (Fig. 4.16). Therefore, if the M value of this stock is large, using the BRP $F_{0.1}$ for the fisheries management of this stock may result in recruitment overfishing (i.e., small spawning stock biomass).

4.4 Discussion

Using combinations of *M* and *F* values, this chapter presents simulations of sex-specific YPR analyses for North Pacific albacore based on the life-history parameters reported in Chapters 2 and 3. The results of natural mortality estimation suggest that females tend to have a larger *M* value than males. Because of the different growth parameters used, males and females exhibit different BRP estimates. The results of the YPR analyses suggest that the BRPs of $F_{20\%}$, $F_{25\%}$, $F_{30\%}$, and $F_{40\%}$ are preferable to the BRP of $F_{0.1}$ for the fisheries management of this stock if $M > 0.3$.

This chapter demonstrates that using different methods to estimate *M* can yield different results. For both sexes, the *M* estimates obtained by Pauly's equation differ from those obtained by Hoenig's equation, with differences of at least 1.5 year^{-1} (see Section 4.3.1). In addition, a change in *M* (by an increment of 0.1 year^{-1}) in the YPR analyses can produce significantly different BRP estimates (Fig. 4.5 and 4.10 to 4.13). These findings clearly demonstrate that the uncertainty of *M* predominates over the uncertainties of growth and length-weight parameters in the estimation of the BRPs. Thus, using precise *M* estimates in the YPR analyses is important for an accurate estimation of BRPs. In this chapter, an identical *M* value is used for all age classes in the YPR analyses regardless of the variation of *M* among age classes. In addition, the age of fish at recruitment is set to be 1 year rather than 0^+ years because the natural mortality rates of fry and juvenile fish are believed to be much higher than those of young and adult fish (Beverton & Holt, 1959). Empirical equations are widely used to estimate the *M* values of marine fishes as a more convenient way than tagging methods. On the use of empirical equations, however, Pascual & Iribarne (1993) reported that the original articles hardly explored the predictive power of empirical equations, and the prediction error in the *M* estimates obtained can be large. In this chapter, only the uncertainties of growth and length-weight parameters are incorporated into the three equations to obtain the *M* estimates of North Pacific albacore. In Pauly's paper, the three *M* values used for albacore are 0.22 (Tauti, 1940), 0.23 (Beardsley, 1971), and 0.20 (Bard, 1974), and the growth parameters used for linear regression are from Clemens (1961), Beardsley (1971), and Le Gall (1974). The growth parameters of albacore used in Pauly's paper substantially differ from the results of the growth modeling of North Pacific albacore presented in Chapter 2. Therefore, in this chapter, I use bootstrapping to assess the uncertainty of the parameters of the modified Pauly equation based on the data reported in Pauly's paper.

The YPR equation used in this chapter incorporates gear selectivity, and the results indicate that gear selectivity significantly affects both YPR values and BRP estimates (Fig. 4.5 and 4.10 to 4.13). The BRPs obtained by MS2 are significantly larger than those obtained by MS1. Moreover, gear selectivity has a more significant effect on the estimation of BRPs as the *M* value is increased (Fig. 4.6 and 4.14 to 4.15). Thus, using precise estimates of gear selectivity in the YPR analyses is also important for an accurate estimation of BRPs.

In the YPR analyses, the uncertainty of BRPs relating to growth and length-weight parameters is assessed with bootstrap estimates of growth and length-weight parameters. Because parameters are strongly correlated when fitting the growth (or length-weight) function (see Chapter 2), no growth (or length-weight) parameter can be used in isolation to determine which parameter has a more significant effect on the estimation of BRPs. Note that the bootstrap growth and length-weight parameters used in this chapter cannot include all uncertainty types of the growth modeling of North Pacific albacore. In this chapter, using bootstrap von Bertalanffy growth parameters is found to produce more variable BRP estimates compared to using bootstrap length-weight parameters. The possible explanations for this effect are that the sample size of the length-weight data is larger and that the measurement of length-weight data is more precise. Moreover, smaller CIs of BRP ($F_{20\%}$, $F_{25\%}$, $F_{30\%}$, or $F_{40\%}$) estimates are obtained as M increases above 0.4, suggesting that the uncertainties of growth and length-weight parameters become less important for the estimation of the BRPs if the M value is large. On the contrary, the CIs of $F_{0.1}$ estimates obtained by $M = 0.5$ tend to be slightly larger than those obtained with a smaller M value. No sensitivity analyses for the parameters of the maturity ogive are presented in this chapter because most North Pacific albacore reach sexual maturity within a limited age range, that is, from 4 to 5 years (Fig. 3.7 and Table 2.6). Thus, the bias of BRP estimates caused by the uncertainty of maturity parameters may be small.

At $M = 0.3$, the E values obtained by the $F_{0.1}$ estimates for females ($E = .52$ by MS1 and $E = .55$ by MS2) are slightly larger than 0.5 (Table 4.4). In addition, the E values obtained by the $F_{25\%}$ estimates for females ($E = .50$ by MS1 and $E = .54$ by MS2) are close to .5 at $M = 0.3$ (Table 4.6). In many papers (e.g., Alverson & Pereyra, 1969; Gulland, 1970; Francis, 1974; Deriso, 1987), fishing mortality at the point of the maximum sustainable yield has been assumed to equal natural mortality, which seems to be applicable to North Pacific albacore if this stock's M value is close to 0.3. At $M = 0.5$, however, the E values calculated with the $F_{25\%}$ estimates for females range from approximately .42 to .46. In addition, the $F_{25\%}$ estimates for females obtained at $M = 0.5$ are 0.36 by MS1 and 0.43 by MS2, which are clearly smaller than the M value (0.5) used (Table 4.6). Therefore, if the M value of this stock is higher than 0.3, the use of $F_{0.1}$ for the fisheries management of this stock may lead to a risk of recruitment overfishing; other BRPs, for example, $F_{25\%}$ and $F_{30\%}$, are preferable to $F_{0.1}$.

According to the YPR values obtained, the optimal t_c value for North Pacific albacore appears to be 2 years, despite the small individual value resulting from a small fish size (Fig. 4.7 and 4.8). Because only age 1 and age 2 fish are incorporated with a selectivity proportion of less than 1, using either MS1 or MS2, would be expected to yield similar results for the optimal t_c values. According to the catch data reported by the ISC (ISC, 2006), age 3 fish (Table 4.1) are likely to be fully recruited to fisheries. In the YPR equation, the optimal t_c estimate is substantially based on the growth rate of younger fish. The higher growth rate of younger fish would result in a smaller t_c value in the YPR equation. In this chapter, age 1 and age 2 North Pacific albacore are expected to have a larger size than that predicted by Yabuta and Yukinawa's growth parameters (see Shomura, 1966; Suda, 1966). Thus, the YPR values estimated in this chapter will be larger than those estimated using Yabuta and Yukinawa's parameters.

In conclusion, each estimated BRP ($F_{0.1}$, $F_{\max}$, $F_{20\%}$, $F_{25\%}$, $F_{30\%}$, or $F_{40\%}$) closely relates to the M value used, and the relationship between each BRP and M can be precisely expressed by a degree 3 polynomial. In general, the larger the M value used, the larger the BRPs obtained. For accurate estimation of BRPs, M values need to be estimated with precise methodologies. Using an arbitrary, assumed M value in YPR analyses can cause great uncertainty in BRP estimates. If the M value of North Pacific albacore is higher than 0.3, I recommend that the BRPs (e.g., $F_{25\%}$ and $F_{30\%}$) obtained by the SPR analysis be used for the fisheries management of this stock rather than the BRP of $F_{0.1}$.

Chapter 5—Conclusions and Recommendations

This dissertation presents biological investigations and sex-specific YPR analyses for North Pacific albacore to bolster efforts to assess and manage this stock. The results of Chapter 2 suggest that obliquely sectioned sagittal otoliths can be useful material for age determination in this stock. The annuli identified in sagittae are fall-to-winter growth marks. The first annulus found in sagittae generally forms when the fish is under 1 year old. Thus, the use of other hard parts (e.g., scales, spines, and vertebrae) for the age determination of this stock is recommended to assess the age of the first annulus identified. North Pacific albacore are found to have sex-specific growth functions. Mature males tend to attain greater size and age than females do; the sexual size dimorphism between males and females seems to develop after they have reached sexual maturity.

The results of Chapter 3 indicate that the western Philippine Sea is a spawning ground for this stock. Males and females are found to have similar maturity ogives; thus, a sex-pooled maturity ogive can be used for the determination of the spawning stock size. According to the present results, the potential spawning stock of this stock is made up of fish longer than 85 cm L_F.

The results of Chapter 4 suggest that females tend to have higher M estimates than males. Great uncertainty of M estimates can arise from using different methods to estimate M. According to YPR values, the optimal age at first capture for this stock tends to be 2 years. In the YPR analyses, the BRP estimates closely relate to the M value used. Moreover, the uncertainties of M estimates and gear selectivity affect the estimation of BRPs more significantly than the uncertainties of growth and length-weight parameters do. Therefore, using precise methodologies to estimate the M

and gear selectivity of this stock is exceedingly important for accurate BRP estimation. The BRPs of $F_{25\%}$ and $F_{30\%}$ are preferable to the BRP of $F_{0.1}$ for the fisheries management of North Pacific albacore if this stock's *M* value is higher than 0.3.

Because this stock exhibits sex-specific growth, sex-pooled size data provide only limited information on sex-specific catches and are probably useless for age-structured stock assessments. Collecting many sex-specific data for this stock, however, may be difficult because the sex of albacore can rarely be determined by external appearance, and albacore are commonly sold for canned food as nearly whole fish. Partitioning this stock into fewer groups (e.g., immature and mature fish) in stock assessment models is recommended rather than using many age classes. Furthermore, if the sex ratio of age 1 fish is close to 1:1, females are expected to be less abundant in the spawning stock than males because females tend to have a higher *M* value and a younger maximum age than males. I recommend that using females (or the entire spawning stock) as a target for the fisheries management of this stock. Because some albacore can be found in the equatorial waters of the Pacific Ocean, the interaction between the North Pacific and South Pacific albacore stocks is still not clear. Information on the interaction between these stocks is important for successful stock assessment and fisheries management efforts of these two stocks. Because of increasing concern regarding the sustainability of North Pacific albacore, more efforts are needed to construct the sex-specific age compositions of this stock for the accurate assessment of current stock status.

References

Agarwal, N. K. (2009). *Fish reproduction*. New Delhi: APH Publishing Corporation.

Akaike, H. (1992). Information theory and an extension of the maximum likelihood principle (Originally published in Proceeding of the Second International Symposium on Information Theory, B. N. Petrov and F. Caski, eds., Akademiai Kiado, Budapest, 1973, 267–281). In S. Kotz & N. L. Johnson (Eds.), *Breakthroughs in Statistics, Vol. I, Foundations and Basic Theory* (pp. 610–624). New York: Springer-Verlag.

Alverson, D. L., & Pereyra, W. T. (1969). Demersal fish explorations in the northeastern Pacific Ocean — an evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecasts. *Journal of the Fisheries Research Board of Canada, 26*, 1985–2001.

Anonymous. (2002). A manual for age determination of southern bluefin tuna *Thunnus maccoyii*: Otolith sampling, preparation and interpretation (Article prepared by the Direct Age Estimation Workshop of the CCSBT, June 11–14, 2002, Queenscliff, Australia). 1–36. Retrieved from http://www.ccsbt.org/docs/pdf/about_the_commission/age_determination_manual.pdf (last accessed 20 January 2011)

Bard, F. X. (1974). Etude sur le germon (*Thunnus alalunga*, Bonnaterre 1788) de l'Atlantique Nord. Elements de dynamique de population. *Collective Volume of Scientific Papers ICCAT, 2*(1), 198–224.

Bard, F. X., & Compean-Jimenez. (1980). Consequences pour l'evaluation du taux d'exploitation du germon (*Thunnus alalunga*) Nord Atlantique d'une courbe de croissance deduite de la lecture des sections de rayons epineus. *Collective Volume of Scientific Papers ICCAT, 9*(2), 365–375.

Barr, C. M. (2009). *Are there two subgroups of albacore, Thunnus alalunga, in the North Pacific? Evidence from variability in catch, seasonal migrations, and length composition for two subgroups in the coastal fishery of North America.* Master Thesis, Oregon State University, Corvallis.

Bartoo, N., & Foreman, T. J. (1993). A review of the biology and fisheries for North Pacific albacore (*Thunnus alalunga*). In R. S. Shomura, J. Majkowski & S. Langi (Eds.), *Interactions of Pacific tuna fisheries. Proceedings of the first FAO Expert Consultation on Interactions of Pacific Tuna Fisheries. 3–11 December 1991. Noumea, New Caledonia. Volume 2: papers on biology and fisheries. FAO Fisheries Technical Paper, No. 336, Vol. 2* (pp. 173–187). Rome: FAO.

Beamish, R. J., & Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences, 38*(8), 982–983. doi: 10.1139/f81-132

Beardsley, G. L. (1971). Contribution to population dynamics of Atlantic albacore with comments on potential yields. *Fishery Bulletin, 69*(4), 845–857.

Bell, R. R. (1962). Age determination of the Pacific albacore of the California coast. *California Fish and Game, 48*(1), 39–48.

Bernard, D. R. (1981). Multivariate analysis as a means of comparing growth in fish. *Canadian Journal of Fisheries and Aquatic Sciences, 38*(2), 233–236. doi: 10.1139/f81-030

Bernard, H. J., Hedgepeth, J. B., & Reilly, S. B. (1985). Stomach contents of albacore, skipjack, and bonito caught off southern California during summer 1983. *California Cooperative Oceanic Fisheries Investigations Reports, 26*, 175–182.

Bertalanffy, L. von (1938). A quantitative theory of organic growth (Inquiries on growth laws. II.). *Human Biology, 10*(2), 181–213.

Bertignac, M., Hampton, J., & Coan, A. L. (1999). Estimates of exploitation rates for north Pacific albacore, *Thunnus alalunga*, from tagging data. *Fishery Bulletin, 97*(3), 421–433.

Beverton, R. J. H., & Holt, S. J. (1957) On the dynamics of exploited fish populations. *Great Britain Fishery Investigations, Series II: Vol. 19* (pp. 1–533): Ministry of Agriculture, Fisheries and Food, United Kingdom.

Beverton, R. J. H., & Holt, S. J. (1959). A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In G. E. W. Wolstenholme & M. O'Connor (Eds.), *Ciba Foundation Colloquia on Ageing—The Lifespan of Animals* (Vol. 5, pp. 142–180). London: J. & A. Churchill.

Blunt, C. E. (1954). Two mid-Pacific recoveries of California-tagged albacore. *California Fish and Game, 40*(3), 339.

Bonnaterre, P. J. (1788). *Tableau encyclopédique et méthodique des trois règnes de la nature ..., Ichthyologie*. Paris: Chez Panckoucke.

Brock, V. E. (1943). Contribution to the biology of the albacore *(Germo alalunga)* of the Oregon coast and other parts of the North Pacific. *Stanford Ichthyological Bulletin, 2*(7), 199–248.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York: Springer.

Cailliet, G. M., Smith, W. D., Mollet, H. F., & Goldman, K. J. (2006). Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. *Environmental Biology of Fishes, 77*(3–4), 211–228. doi: 10.1007/s10641-006-9105-5

Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology, 59*(2), 197–242. doi: 10.1006/jfbi.2001.1668

Campana, S. E., & Jones, C. M. (1992). Analysis of otolith microstructure data. In D. K. Stevenson & S. E. Campana (Eds.), *Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences* (Vol. 117, pp. 73–100).

Campana, S. E., & Neilson, J. D. (1982). Daily growth increments in otoliths of starry flounder (*Platichthys stellatus*) and the influence of some environmental variables in their production. *Canadian Journal of Fisheries and Aquatic Sciences, 39*(7), 937–942. doi: 10.1139/f82-127

Cech, J. J., Laurs, R. M., & Graham, J. B. (1984). Temperature-induced changes in blood gas equilibria in the albacore, *Thunnus alalunga*, a warm-bodied tuna. *Journal of Experimental Biology, 109*(1), 21–34.

Cerrato, R. M. (1990). Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Canadian Journal of Fisheries and Aquatic Sciences, 47*(7), 1416–1426. doi: 10.1139/f90-160

Chang, S. K., Liu, H. C., & Hsu, C. C. (1993). Estimation of vital parameters for Indian albacore through length frequency data. *Journal of the Fisheries Society of Taiwan, 20*(1), 1–13.

Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences, 39*(8), 1208–1210. doi: 10.1139/f82-158

Chen, I. C., Lee, P. F., & Tzeng, W. N. (2005). Distribution of albacore (*Thunnus alalunga*) in the Indian Ocean and its relation to environmental factors. *Fisheries Oceanography, 14*(1), 71–80. doi: 10.1111/j.1365-2419.2004.00322.x

Chen, K. S., Crone, P., & Hsu, C. C. (2006). Reproductive biology of female Pacific bluefin tuna *Thunnus orientalis* from south-western North Pacific Ocean. *Fisheries Science, 72*(5), 985–994. doi: 10.1111/j.1444-2906.2006.01247.x

Chen, K. S., Crone, P. R., & Hsu, C. C. (2010). Reproductive biology of albacore *Thunnus alalunga*. *Journal of Fish Biology, 77*(1), 119–136. doi: 10.1111/j.1095-8649.2010.02662.x

Chen, M. H., Teng, P. Y., Chen, C. Y., & Hsu, C. C. (2011). Organic and total mercury levels in bigeye tuna, *Thunnus obesus*, harvested by Taiwanese fishing vessels in the Atlantic and Indian Oceans. *Food Additives and Contaminants: Part B: Surveillance, 4*(1), 15–21. doi: 10.1080/19393210.2010.535908

Chen, Y., & Gordon, G. N. G. (1997). Assessing discarding at sea using a length-structured yield-per-recruit model. *Fisheries Research, 30*(1–2), 43–55. doi: 10.1016/S0165-7836(96)00559-0

Chen, Y., Jackson, D. A., & Harvey, H. H. (1992). A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. *Canadian Journal of Fisheries and Aquatic Sciences, 49*(6), 1228–1235. doi: 10.1139/f92-138

Chiang, W. C., Sun, C. L., Wang, S. P., Yeh, S. Z., Chen, Y., Su, W. C., . . . Chen, W. Y. (2009). Analysis of sex-specific spawning biomass per recruit of the sailfish (*Istiophorus platypterus*) in the waters off eastern Taiwan. *Fishery Bulletin, 107*(3), 265–277.

Chow, S., & Ushiama, H. (1995). Global Population structure of albacore (*Thunnus alalunga*) inferred by RFLP analysis of the mitochondrial ATPase gene. *Marine Biology, 123*(1), 39–45. doi: 10.1007/BF00350321

Clear, N. P., Gunn, J. S., & Rees, A. J. (2000). Direct validation of annual increments in the otoliths of juvenile southern bluefin tuna, *Thunnus maccoyii*, by means of a large-scale mark-recapture experiment with strontium chloride. *Fishery Bulletin, 98*(1), 25–40.

Clemens, H. B. (1961). The migration, age, and growth of Pacific albacore (*Thunnus germo*), 1951–1958. *California Department of Fish and Game, Fish Bulletin, 115*, 1–128.

Collette, B. B. (2001). Scombridae. Tunas (also, albacore, bonitos, mackerels, seerfishes, and wahoo). In K. E. Carpenter & V. Niem (Eds.), *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific* (Vol. 6. Bony fishes part 4 (Labridae to Latimeriidae), estuarine crocodiles, sea turtles, sea snakes and marine mammals., pp. 3721–3756). Rome: FAO.

Collette, B. B., & Nauen, C. E. (1983). FAO species catalogue. Vol. 2. Scombrids of the world. An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. *FAO Fisheries Synopsis No. 125* (Vol. 2, pp. 1–137). Rome: FAO.

Cox, D. R., & Snell, E. J. (1989). *Analysis of binary data* (2nd ed.). London: Chapman & Hall/CRC.

Dai, F.-Q., Li, X.-S., Wang, F.-C., Xu, Y.-C., & Li, Q. (2006). Study on loneline fishing of *Thunnus alalunga* in the Eastern and Central Pacific Ocean. *Marine Fisheries Research, 27*(6), 37–42.

Deriso, R. B. (1987). Optimal $F_{0.1}$ criteria and their relationship to maximum sustainable yield. *Canadian Journal of Fisheries and Aquatic Sciences, 44*(2), 339–348. doi: 10.1139/f87-335

Edgington, E. S. (1995). *Randomization tests* (3rd ed.). New York: Marcel Dekker.

Efron, B., & Tibshirani, R. J. (1993). *An introduction to the bootstrap*. New York: Chapman & Hall.

Fabens, A. J. (1965). Properties and fitting of the von Bertalanffy growth curve. *Growth, 29*(3), 265–289.

Farley, J. H., Clear, N. P., Leroy, B., Davis, T. L. O., & McPherson, G. (2006). Age, growth and preliminary estimates of maturity of bigeye tuna, *Thunnus obesus*, in the Australian region. *Marine and Freshwater Research, 57*(7), 713–724. doi: 10.1071/Mf05255

Fiedler, P. C., & Bernard, H. J. (1987). Tuna aggregation and feeding near fronts observed in satellite imagery. *Continental Shelf Research, 7*(8), 871–881. doi: 10.1016/0278-4343(87)90003-3

Foreman, T. J. (1980). Synopsis of biological data on the albacore tuna, *Thunnus alalunga* (Bonnaterre, 1788), in the Pacific Ocean. In W. H. Bayliff (Ed.), *Synopses of biological data on eight species of scombrids. Inter-American Tropical Tuna Commission, Special Report No. 2* (pp. 17–70). La Jolla, CA: Inter-American Tropical Tuna Commission.

Francis, R. C. (1974). Relationship of fishing mortality to natural mortality at the level of maximum sustainable yield under the logistic stock production model. *Journal of the Fisheries Research Board of Canada, 31*(9), 1539–1542. doi: 10.1139/f74-189

Gabriel, W. L., Sissenwine, M. P., & Overholtz, W. J. (1989). Analysis of spawning stock biomass per recruit: an example for Georges Bank Haddock. *North American Journal of Fisheries Management, 9*(4), 383–391. doi: 10.1577/1548-8675(1989)009<0383:AOSSBP>2.3.CO;2

Gambell, R., & Messtorff, J. (1964). Age determination in the Whiting *(Merlangius merlangus* L.*)* by means of the otoliths. *Journal du Conseil International pour l'Exploration de la Mer, 28*(3), 393–404. doi: 10.1093/icesjms/28.3.393

Ganssle, D., & Clemens, H. B. (1953). California-tagged albacore recovered off Japan. *California Fish and Game, 39*(4), 443.

Glaser, S. M. (2009). *Foraging ecology of North Pacific albacore in the California Current System.* Ph.D. Thesis, University of California, San Diego.

Gompertz, B. (1825). On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of Life Contingencies. *Philosophical Transactions of the Royal Society of London, 115*, 513–583. doi: 10.1098/rstl.1825.0026

Goodyear, C. P. (1990). Spawning stock biomass per recruit: the biological basis for a fisheries management tool. *Collective Volume of Scientific Papers ICCAT, 32*(2), 487–497.

Goodyear, C. P. (1993). Spawning stock biomass per recruit in fisheries management: foundation and current use. In S. J. Smith, J. J. Hunt & D. Rivard (Eds.), *Risk evaluation and biological reference points for fisheries management. Canadian Special Publication of Fisheries and Aquatic Sciences* (Vol. 120, pp. 67–81).

Graham, J. B., & Dickson, K. A. (1981). Physiological thermoregulation in the albacore *Thunnus alalunga*. *Physiological Zoology, 54*(4), 470–486.

Griffiths, S. P., Fry, G. C., Manson, F. J., & Lou, D. C. (2010). Age and growth of longtail tuna (*Thunnus tonggol*) in tropical and temperate waters of the central Indo-Pacific. *ICES Journal of Marine Science, 67*(1), 125–134. doi: 10.1093/icesjms/fsp223

Griggs, L., & Murray, T. (2000). Determination of size composition, sex ratio, and length:weight relationships of albacore tuna during the 1998–99 fishing year from samples collected in fish sheds. *National Institute of Water and Atmospheric Research Ltd (NIWA), Final Research Report for Ministry of Fisheries Research Project TUN9801* (pp. 1–16).

Gulland, J. A. (1970). The fish resources of the oceans. *FAO Fisheries technical paper, 97*, 1–425.

Gulland, J. A. (1983). *Fish stock assessment: A manual of basic methods*. Chichester: John Wiley & Sons.

Gunn, J. S., Clear, N. P., Carter, T. I., Rees, A. J., Stanley, C. A., Farley, J. H., & Kalish, J. M. (2008). Age and growth in southern bluefin tuna, *Thunnus maccoyii* (Castelnau): Direct estimation from otoliths, scales and vertebrae. *Fisheries Research, 92*(2–3), 207–220. doi: 10.1016/j.fishres.2008.01.018

Haddon, M. (2001). *Modelling and quantitative methods in fisheries*. New York: Chapman & Hall/CRC.

Hilborn, R., & Walters, C. J. (1992). *Quantitative fisheries stock assessment: Choice, dynamics and uncertainty*. New York: Chapman & Hall.

Hoenig, J. M. (1983). Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin, 81*(4), 898–903.

Hosmer, D. W., & Lemeshow, S. (2000). *Applied logistic regression* (2nd ed.). New York: John Wiley & Sons.

Hsu, C. C. (1999). The length-weight relationship of albacore, *Thunnus alalunga*, from the Indian Ocean. *Fisheries Research, 41*(1), 87–92. doi: 10.1016/S0165-7836(99)00002-8

Huang, C. S., Wu, C. L., Kuo, C. L., & Su, W. C. (1990). Age and growth of the Indian Ocean albacore, *Thunnus alalunga*, by scales. *FAO Indo-Pacific Tuna Development and Management Programme, Collective Volume Working Documents, 4*, 111–122.

Hurvich, C. M., & Tsai, C. L. (1989). Regression and time series model selection in small samples. *Biometrika, 76*(2), 297–307. doi: 10.1093/biomet/76.2.297

Ichinokawa, M., Coan, A. L., & Takeuchi, Y. (2008). Transoceanic migration rates of young North Pacific albacore, *Thunnus alalunga*, from conventional tagging data. *Canadian Journal of Fisheries and Aquatic Sciences, 65*(8), 1681–1691. doi: 10.1139/F08-095

ISC. (2006). Report of the albacore working group workshop, Annex 5. *Proceedings of the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean, November 28–December 5, 2006, National Research Institute of Far Seas Fisheries, Orido, Japan*. Retrieved from http://isc.ac.affrc.go.jp/pdf/ISC7pdf/Annex_5_ALBWG_Nov2Dec_06.pdf (last accessed 20 January 2011)

ISC. (2010). Report of the albacore working group workshop, Annex 8. *Proceedings of the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean, July 12–13, 2010, Victoria, BC, Canada*. Retrieved from http://isc.ac.affrc.go.jp/pdf/ISC10pdf/Annex_8_ISC10_BILLWG_Jul10.pdf (last accessed 20 January 2011)

Ishii, K., & Inoue, M. (1956). Some notes on the ovary of albacore, *Germo germo*, taken from the Coral Sea. *Bulletin of the Japanese Society of Scientific Fisheries, 22*(2), 89–93.

Iversen, R. T. B. (1962). Food of albacore tuna, *Thunnus germo* (Lacépède), in the central and northeastern Pacific. *Fishery Bulletin of the Fish and Wildlife Service, 62*(214), 455–481.

Iverson, I. L. K. (1971). Albacore food habits. In L. Pinkas, M. S. Oliphant & I. L. K. Iverson (Eds.), *Food habits of albacore, bluefin tuna, and bonito in California waters. California Department of Fish and Game, Fish Bulletin* (Vol. 152, pp. 11–46).

Katsanevakis, S. (2006). Modelling fish growth: Model selection, multi-model inference and model selection uncertainty. *Fisheries Research, 81*(2–3), 229–235. doi: 10.1016/j.fishres.2006.07.002

Kikawa, S., Shiohama, T., Morita, Y., & Kume, S. (1977). Preliminary study on the movement of the North Pacific albacore based on the tagging. *Bulletin of Far Seas Fisheries Research Laboratory, 15*, 101–113.

Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin, 77*(4), 765–776.

Kimura, S., Nakai, M., & Sugimoto, T. (1997). Migration of albacore, *Thunnus alalunga*, in the North Pacific Ocean in relation to large oceanic phenomena. *Fisheries Oceanography, 6*(2), 51–57. doi: 10.1046/j.1365-2419.1997.00029.x

King, M. (2007). *Fisheries biology, assessment and management* (2nd ed.). Oxford: Blackwell Publishing.

Kojadinovic, J., Potier, M., Le Corre, M., Cosson, R. P., & Bustamante, P. (2006). Mercury content in commercial pelagic fish and its risk assessment in the Western Indian Ocean. *Science of the Total Environment, 366*(2–3), 688–700. doi: 10.1016/j.scitotenv.2006.02.006

Koto, T., & Hisada, K. (1966). Studies on the albacore—XII. Length frequency distribution of albacore caught by Japanese longline and pole-and-line fisheries in the western North Pacific in 1960–64 seasons. *Report of Nankai Regional Fisheries Research Laboratory, 24*, 15–19.

Kutner, M. H., Nachtsheim, C. J., & Neter, J. (2004). *Applied linear regression models* (4th ed.). New York: McGraw-Hill/Irwin.

Labelle, M., Hampton, J., Bailey, K., Murray, T., Fournier, D. A., & Sibert, J. R. (1993). Determination of age and growth of South Pacific albacore (*Thunnus alalunga*) using three methodologies. *Fishery Bulletin, 91*(4), 649–663.

Lai, C. C. (2009). *Total and organic mercury concentrations in white muscles of albacore (Thunnus alalunga) and bigeye tuna (Thunnus obesus) in Pacific Ocean.* Master Thesis, National Sun Yat-sen University, Kaohsiung.

Laurs, R. M. (1983). The North Pacific albacore—an important visitor to California Current waters. *California Cooperative Oceanic Fisheries Investigations Reports, 24*, 99–106.

Laurs, R. M., Fiedler, P. C., & Montgomery, D. R. (1984). Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep Sea Research Part A. Oceanographic Research Papers, 31*(9), 1085–1099. doi: 10.1016/0198-0149(84)90014-1

Laurs, R. M., & Lynn, R. J. (1977). Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: Distribution, relative abundance, and association with transition zone waters. *Fishery Bulletin, 75*(4), 795–822.

Laurs, R. M., & Lynn, R. J. (1991). North Pacific albacore ecology and oceanography. In J. A. Wetherall (Ed.), *Biology, oceanography, and fisheries of the North Pacific Transition Zone and Subarctic Frontal Zone. U.S. Department of Commerce, NOAA Technical Report NMFS* (Vol. 105, pp. 69–87).

Laurs, R. M., Nishimoto, R., & Wetherall, J. A. (1985). Frequency of increment formation on sagittae of North Pacific albacore (*Thunnus alalunga*). *Canadian Journal of Fisheries and Aquatic Sciences, 42*(9), 1552–1555. doi: 10.1139/f85-194

Laurs, R. M., & Wetherall, J. A. (1981). Growth rates of North Pacific albacore, *Thunnus alalunga*, based on tag returns. *Fishery Bulletin, 79*(2), 293–302.

Laurs, R. M., Yuen, H. S. H., & Johnson, J. H. (1977). Small-scale movements of albacore, *Thunnus alalunga*, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. *Fishery Bulletin, 75*(2), 347–355.

Le Gall, J. Y. (1974). Expose synoptique des donnees biologiques sur le germon *Thunnus alalunga* de l'Ocean Atlantique. *FAO Fisheries Synopsis, 109*, 1–73.

Lee, J. U., Hue, J. S., & Kim, B. A. (1978). A study on the relative growth of albacore, *Thunnus alalunga* Bonnaterre, caught by pole and line fishery in the Pacific Ocean. *Bulletin of Fisheries Research & Development Agency, 20*, 77–83.

Lee, L. K., & Yeh, S. Y. (1993). Studies on the age and growth of South Atlantic albacore (*Thunnus alalunga*) specimens collected from Taiwanese longliners. *Collective Volume of Scientific Papers ICCAT, 40*(2), 354–360.

Lee, Y. C., & Liu, H. C. (1992). Age determination, by vertebra reading, in Indian albacore, *Thunnus alalunga* (Bonnaterre). *Journal of the Fisheries Society of Taiwan, 19*(2), 89–102.

Lu, H.-J., Lee, K.-T., & Liao, C.-H. (1998). On the relationship between El Niño/Southern oscillation and South Pacific albacore. *Fisheries Research, 39*(1), 1–7. doi: 10.1016/S0165-7836(98)00174-X

Maddala, G. S. (1983). *Limited-dependent and qualitative variables in economics*. New York: Cambridge University Press.

Manly, B. F. J. (1997). *Randomization, bootstrap and Monte Carlo methods in biology* (2nd ed.). New York: Chapman & Hall.

Maxwell, M. R. (2002). *Reproductive biology of albacore (Thunnus alalunga).* Paper presented at the The Eighteenth North Pacific Albacore Workshop,NOAA/NMFS, Southwest Fisheries Science Center, La Jolla, California, USA, December 4–11, 2002

Megalofonou, P. (2000). Age and growth of Mediterranean albacore. *Journal of Fish Biology, 57*(3), 700–715. doi: 10.1006/jfbi.2000.1345

Morrissey, M. T., Rasmussen, R., & Okada, T. (2004). Mercury content in Pacific troll-caught albacore tuna (*Thunnus alalunga*). *Journal of Aquatic Food Product Technology, 13*(4), 41–52. doi: 10.1300/J030v13n04_04

Motulsky, H., & Christopoulos, A. (2004). *Fitting models to biological data using linear and nonlinear regression: A practical guide to curve fitting*. Oxford: Oxford University Press.

Murphy, G. I. (1959). Effect of water clarity on albacore catches. *Limnology and Oceanography, 4*(1), 86–93.

Murray, T. (1993). A review of the biology and fisheries for albacore, *Thunnus alalunga*, in the South Pacific Ocean. In R. S. Shomura, J. Majkowski & S. Langi (Eds.), *Interactions of Pacific tuna fisheries. Proceedings of the first FAO Expert Consultation on Interactions of Pacific Tuna Fisheries. December 3–11 , 1991. Noumea, New Caledonia. Volume 2: papers on biology and fisheries.*

FAO Fisheries Technical Papers, No. 336, Vol. 2 (pp. 188–206). Rome: FAO.

Nagelkerke, N. J. D. (1991). A note on a general definition of the coefficient of determination. *Biometrika, 78*(3), 691–692. doi: 10.1093/biomet/78.3.691

Nakamura, E. L., & Uchiyama, J. H. (1966). Length-weight relations of Pacific tunas. In T. A. Manar (Ed.), *Proceedings of the Governor's Conference on Central Pacific Fishery Resources, Honolulu—Hilo, February 28–March 12, 1966* (pp. 197–201).

Nakamura, H. (1969). *Tuna distribution and migration*. London: Fishing News.

Neill, J. W. (1988). Testing for lack of fit in nonlinear regression. *The Annals of Statistics, 16*(2), 733–740. doi: 10.1214/aos/1176350831

Neilson, J. D., & Campana, S. E. (2008). A validated description of age and growth of western Atlantic bluefin tuna (*Thunnus thynnus*). *Canadian Journal of Fisheries and Aquatic Sciences, 65*(8), 1523–1527. doi: 10.1139/F08-127

Nishikawa, Y., Honma, M., Ueyanagi, S., & Kikawa, S. (1985). Average distribution of larvae of oceanic species of Scombroid fishes, 1956–1981. *Far Seas Fisheries Research Laboratory, S Series, 12*, 1–99.

Nishikawa, Y., Kikawa, S., Honma, M., & Ueyanagi, S. (1978). Distribution atlas of larval tunas, billfishes and related species—Results of larval surveys by R/V Shunyo Maru and Shoyo Maru (1956–1975). *Far Seas Fisheries Research Laboratory, S Series, 9*, 1–99.

Nose, Y., Kawatsu, H., & Hiyama, Y. (1957). Age and growth of Pacific tunas by scale reading. In Y. Suehiro, Y. Oshima & Y. Hiyama (Eds.), *Suisangaku Shusei* (pp. 701–716). Tokyo: Tokyo University Press.

Ortiz de Zárate, V., & C-Parrack, N. (1996). Note on updated tag-recapture growth analyses from North Atlantic albacore. *Collective Volume of Scientific Papers ICCAT, 43*(1), 247–253.

Otsu, T. (1960). Albacore migration and growth in the North Pacific Ocean as estimated from tag recoveries. *Pacific Science, 14*(3), 257–266.

Otsu, T., & Hansen, R. J. (1962). Sexual maturity and spawning of the albacore in the central South Pacific Ocean. *Fishery Bulletin of the Fish and Wildlife Service, 62*(204), 147–161.

Otsu, T., & Sumida, R. F. (1968). Distribution, apparent abundance, and size composition of albacore (*Thunnus alalunga*) taken in the longline fishery based in American Samoa, 1954–65. *Fishery Bulletin of the Fish and Wildlife Service, 67*(1), 47–69.

Otsu, T., & Sumida, R. F. (1970). Albacore of Hawaiian waters (*Thunnus alalunga*). *Commercial Fisheries Review, 32*(5), 18–26.

Otsu, T., & Uchida, R. N. (1959a). Sexual maturity and spawning of albacore in the Pacific Ocean. *Fishery Bulletin of the Fish and Wildlife Service, 59*(148), 283–305.

Otsu, T., & Uchida, R. N. (1959b). Study of age determination by hard parts of albacore from central north Pacific and Hawaiian waters. *Fishery Bulletin of the Fish and Wildlife Service, 59*(150), 349–363.

Otsu, T., & Uchida, R. N. (1963). Model of the migration of albacore in the North Pacific Ocean. *Fishery Bulletin of the Fish and Wildlife Service, 63*(1), 33–44.

Parrish, R. H., Bartoo, N. W., Herrick, S. F., Kleiber, P. M., Laurs, R. M., & Wetherall, J. A. (1989). Albacore management information document. *U.S. Department of Commerce, NOAA Technical Memorandum NMFS, NOAA-TM-NMFS-SWFC-126* (pp. 1–56).

Partlo, J. M. (1955a). Distribution, age and growth of Eastern Pacific albacore (*Thunnus alalunga* Gmelin). *Journal of the Fisheries Research Board of Canada, 12*(1), 35–60.

Partlo, J. M. (1955b). Histological studies on albacore (*Thunnus alalunga*) gonads from the Eastern Pacific. *Journal of the Fisheries Research Board of Canada, 12*(1), 61–67.

Pascual, M. A., & Iribarne, O. O. (1993). How good are empirical predictions of natural mortality? *Fisheries Research, 16*(1), 17–24.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer, 39*(2), 175–192. doi: 10.1093/icesjms/39.2.175

Pearcy, W. G. (1973). Albacore oceanography off Oregon—1970. *Fishery Bulletin, 71*(2), 489–504.

Punt, A. E., Campbell, R. A., & Smith, A. D. M. (2001). Evaluating empirical indicators and reference points for fisheries management: application to the broadbill swordfish fishery off eastern Australia. *Marine and Freshwater Research, 52*(6), 819–832. doi: 10.1071/MF00095

Quinn, T. J., & Deriso, R. B. (1999). *Quantitative fish dynamics*. Oxford: Oxford University Press.

Ramon, D., & Bailey, K. (1996). Spawning seasonality of albacore, *Thunnus alalunga*, in the South Pacific Ocean. *Fishery Bulletin, 94*(4), 725–733.

Ratty, F. J., Laurs, R. M., & Kelly, R. M. (1990). Gonad morphology, histology, and spermatogenesis in South Pacfiic albacore tuna *Thunnus alalunga* (Scombridae). *Fishery Bulletin, 88*(1), 207–216.

Richards, F. J. (1959). A flexible growth function for empirical use. *Journal of Experimental Botany, 10*(29), 290–300.

Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada, 191*, 1–382.

Saito, S. (1973). Studies on fishing of albacore, *Thunnus alalunga* (Bonnaterre) by experimental deep-sea tuna long-line. *Memoirs of the Faculty of Fisheries, Hokkaido University, 21*(2), 107–185.

Santiago, J. (2004). *Dinámica de la población de atún blanco (Thunnus alalunga Bonaterre 1788) del Atlántico Norte.* Thèse de Doctorat, Euskal Herriko Unibertsitatea, Bilbao.

Santiago, J., & Arrizabalaga, H. (2005). An integrated growth study for North Atlantic albacore (*Thunnus alalunga* Bonn. 1788). *ICES Journal of Marine Science 62*(4), 740–749. doi: 10.1016/j.icesjms.2005.01.015

Schaefer, K. M. (1998). Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. *Inter-American Tropical Tuna Commission, Bulletin, 21*(5), 201–272.

Schaefer, K. M. (2001). Reproductive biology of tunas. In B. A. Block & S. E. Donald (Eds.), *Tuna: physiology, ecology, and evolution* (Vol. 19, pp. 225–270). San Diego: Academic Press.

Schaefer, K. M., & Fuller, D. W. (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*(2), 33–76.

Schnute, J. T., & Richards, L. J. (1990). A unified approach to the analysis of fish growth, maturity, and survivorship data. *Canadian Journal of Fisheries and Aquatic Sciences, 47*(1), 24–40. doi: 10.1139/f90-003

Secor, D. H., Wingate, R. L., Neilson, J. D., Rooker, J. R., & Campana, S. E. (2009). Growth of Atlantic bluefin tuna: direct age estimates. *Collective Volume of Scientific Papers ICCAT, 64*(2), 405–416.

Sharp, G. D., & Dotson, R. C. (1977). Energy for migration in albacore, *Thunnus alalunga*. *Fishery Bulletin, 75*(2), 447–450.

Shih, C. L. (2008). *Study on the age and growth of Indian albacore (Thunnus alalunga).* Master Thesis, National Kaohsiung Marine University, Kaohsiung.

Shimose, T., Tanabe, T., Chen, K. S., & Hsu, C. C. (2009). Age determination and growth of Pacific bluefin tuna, *Thunnus orientalis*, off Japan and Taiwan. *Fisheries Research, 100*(2), 134–139. doi: 10.1016/j.fishres.2009.06.016

Shomura, R. S. (1966). Age and growth studies of four species of tunas in the Pacific Ocean. In T. A. Manar (Ed.), *Proceedings of the Governor's Conference on Central Pacific Fishery Resources, Honolulu—Hilo, February 28–March 12, 1966* (pp. 203–219). Honolulu: State of Hawaii.

Squire, J. L. (1981). Observations of albacore (*Thunnus alalunga*) fishing off California in relation to sea surface temperature isotherms as measured by an airborne infrared radiometer *U.S. Department of Commerce, NOAA Technical Memorandum NMFS, NOAA-TM-NMFS-SWFC-11* (pp. 1–15).

Srebocan, E., Pompe-Gotal, J., Prevendar-Crnic, A., & Ofner, E. (2007). Mercury concentrations in captive Atlantic bluefin tuna (*Thunnus thynnus*) farmed in the Adriatic Sea. *Veterinarni Medicina, 52*(4), 175–177.

Stéquert, B., Panfili, J., & Dean, J. M. (1996). Age and growth of yellowfin tuna, *Thunnus albacares*, from the western Indian Ocean, based on otolith microstructure. *Fishery Bulletin, 94*(1), 124–134.

Stevens, E. D., & Neill, W. H. (1978). Body temperature relations of tunas, especially skipjack. In W. S. Hoar & D. J. Randall (Eds.), *Fish physiology* (Vol. VII. Locomotion, pp. 315–359). New York: Academic Press.

Suda, A. (1954a). Average year's fishing condition of tuna longline fisheries. 1952 edition, albacore section. In N. R. F. R. Laboratory (Ed.), *(English translation) U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 169* (pp. 1–131). Tokyo: Nippon Katsuo-Maguro Gyogyokumiai Rengokai.

Suda, A. (1954b). Studies on the albacore—I. Size composition in the North Pacific Ground between the period of it's southward migration. *Bulletin of the Japanese Society of Scientific Fisheries, 20*(6), 460–468.

Suda, A. (1956). Studies on the albacore—III. Size compositions classified by ocean current. *Bulletin of the Japanese Society of Scientific Fisheries, 21*(12), 1194–1198.

Suda, A. (1958). Catch variations in the North Pacific albacore. I. Recruitment and dispersion of the North Pacific albacore. *Report of Nankai Regional Fisheries Research Laboratory, 9*, 103–116.

Suda, A. (1966). Catch variations in the North Pacific albacore VI. *Report of Nankai Regional Fisheries Research Laboratory, 24*, 1–14.

Suda, A., & Warashina, Y. (1961). Studies on the albacore—VI. Some considerations on the condition factor of albacore in the North West Pacific, especially on the differences between albacore caught by the long-line and Pole and line methods. *Report of Nankai Regional Fisheries Research Laboratory, 13*, 21–34.

Sun, C. L., Ehrhardt, N. M., Porch, C. E., & Yeh, S. Z. (2002). Analyses of yield and spawning stock biomass per recruit for the South Atlantic albacore (*Thunnus alalunga*). *Fisheries Research, 56*(2), 193–204.

Sun, C. L., Wang, S. P., Porch, C. E., & Yeh, S. Z. (2005). Sex-specific yield per recruit and spawning stock biomass per recruit for the swordfish, *Xiphias gladius*, in the waters around Taiwan. *Fisheries Research, 71*(1), 61–69. doi: 10.1016/j.fishres.2004.07.010

Sund, P. N., Blackburn, M., & Williams, F. (1981). Tunas and their environment in the Pacific Ocean: a review. *Oceanography and Marine Biology, An Annual Review, 19*, 443–512.

Tauti, M. (1940). On the stock of *Germo germo* (Lacépède). *Bulletin of the Japanese Society of Scientific Fisheries, 9*(4), 139–141.

Taylor, C. C. (1958). Cod growth and temperature. *Journal du Conseil International pour l'Exploration de la Mer, 23*(3), 366–370. doi: 10.1093/icesjms/23.3.366

Thompson, M. J. (2005). *Integrating traceability with onboard handling to enhance product quality and marketability of eastern Pacific troll-caught albacore tuna (Thunnus alalunga).* Master Thesis, Oregon State University, Corvallis.

Thompson, W. F., & Bell, F. H. (1934). Biological statistics of the Pacific halibut fishery. (2) Effect of changes in intensity upon total yield and yield per unit of gear. *Report of the International Fisheries Commission, 8*, 8–49.

Tzeng, W. N. (1990). Relationship between growth rate and age at recruitment of *Anguilla japonica* elvers in a Taiwan estuary as inferred from otolith growth increments. *Marine Biology, 107*(1), 75–81. doi: 10.1007/BF01313244

Uchiyama, J. H., & Kazama, T. K. (2003). Updated weight-on-length relationships for pelagic fishes caught in the central North Pacific Ocean and bottomfishes from the Northwestern Hawaiian Islands *U.S. Department of Commerce, NOAA National Marine Fisheries Service, Pacific Islands Fisheries Science Center Administrative Report H-03-01* (pp. 1–46).

Uda, M. (1973). Pulsative fluctuation of oceanic fronts in association with the tuna fishing grounds and fisheries. *Journal of the Faculty of Marine Science and Technology, Tokai University, 7*, 245–266.

Ueyanagi, S. (1955). On the ripe ovary of the albacore, *Germo germo* (Lacépède), taken from the Indian Ocean. *Bulletin of the Japanese Society of Scientific Fisheries, 20*(12), 1050–1053.

Ueyanagi, S. (1957). Spawning of the albacore in the Western Pacific. *Report of Nankai Regional Fisheries Research Laboratory, 6*, 113–124.

Ueyanagi, S. (1969). Observations on the distribution of tuna larvae in the Indo-Pacific Ocean with emphasis on the delineation of the spawning areas of albacore, *Thunnus alalunga*. *Bulletin of Far Seas Fisheries Research Laboratory, 2*, 177–256.

Uno, M. (1936). *Germo germo* (Lacepede) in the waters east of Nozima Promontory, Tiba Prefecture. (Preliminary reprot II). *Bulletin of the Japanese Society of Scientific Fisheries, 5*(4), 235.

Uosaki, K., & Bayliff, W. H. (1999). A review of the Japanese longline fishery for tunas and billfishes in the eastern Pacific Ocean, 1988–1992. *Inter-American Tropical Tuna Commission, Bulletin, 21*(6), 273–488.

Vetter, E. F. (1988). Estimation of natural mortality in fish stocks: a review. *Fishery Bulletin, 86*(1), 25–43.

Weisberg, S. (2005). *Applied linear regression* (3rd ed.). Hoboken, NJ: John Wiley & Sons.

Wetherall, J. A., Laurs, R. M., Nishimoto, R. N., & Yong, M. Y. Y. (1987). *Growth variation and stock structure in North Pacific albacore*. Paper presented at the the 10th North Pacific Albacore Workshop, Far Seas Fisheries Research Laboratory, Shimizu, Shizuoka, Japan.

Wu, C. L., & Kuo, C. L. (1993). Maturity and fecundity of albacore, *Thunnus alalunga* (Bonnaterre), from the Indian Ocean. *Journal of the Fisheries Society of Taiwan, 20*(2), 135–151.

Wu, G. C. C., Chiang, H. C., Chen, K. S., Hsu, C. C., & Yang, H. Y. (2009). Population structure of albacore (*Thunnus alalunga*) in the Northwestern Pacific Ocean inferred from mitochondrial DNA. *Fisheries Research, 95*(1), 125–131. doi: 10.1016/j.fishres.2008.07.014

Yabuta, Y., & Yukinawa, M. (1963). Growth and age of albacore. *Report of Nankai Regional Fisheries Research Laboratory, 17*, 111–120.

Yang, R. T. (1970). Progress report on study of tuna resources. II Study of tuna resources in the Atlantic Ocean. (1) Studies of age and growth of Atlantic albacore and a critical review on the stock structure. *China Fisheries Monthly, 213*, 3–16.

Yoneta, K., & Saito, S. (1973). Studies on the large-sized albacore and its vertical distribution in the western South Pacific Ocean. *Bulletin of the Japanese Society of Scientific Fisheries, 39*(6), 617–624.

Yoshida, H. O. (1968). Early life history and spawning of the albacore, *Thunnus alalunga*, in Hawaiian waters. *Fishery Bulletin of the Fish and Wildlife Service, 67*(2), 205–211.

Yoshida, H. O. (1971). Distribution, apparent abundance, and length composition of juvenile albacore, *Thunnus alalunga*, in the South Pacific Ocean. *Fishery Bulletin, 69*(4), 821–827.

Yoshida, H. O. (1975). The American Samoa longline fishery, 1966–71. *Fishery Bulletin, 73*(4), 747–765.

Yoshida, H. O., & Otsu, T. (1962). *Synopsis of biological data on albacore, Thunnus germo (Lacepede), 1880 (Pacific and Indian Oceans). Proceedings of the World Scientific Meeting on the Biology of Tunas and Related Species, La Jolla, California, July 2–14, 1962* (FAO Species Synopsis, No. 9). Rome: FAO.

Zainuddin, M., Kiyofuji, H., Saitoh, K., & Saitoh, S. I. (2006). Using multi-sensor satellite remote sensing and catch data to detect ocean hot spots for albacore (*Thunnus alalunga*) in the northwestern North Pacific. *Deep-Sea Research Part II, 53*(3–4), 419–431. doi: 10.1016/j.dsr2.2006.01.007

Zar, J. H. (1999). *Biostatistical analysis* (4th ed.). Upper Saddle River, NJ: Prentice-Hall.

Figures

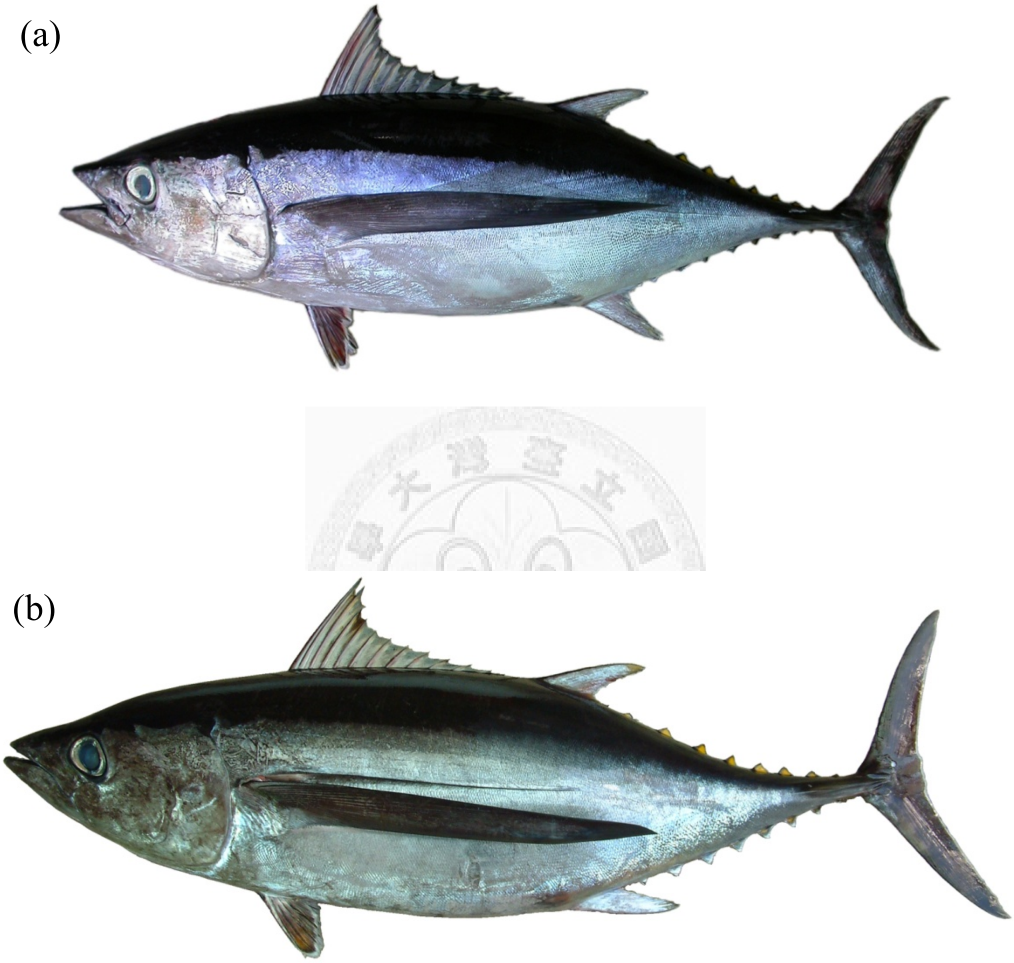

Figure 1.1. Images of albacore (*Thunnus alalunga*) from the North Pacific Ocean. (a) A female (91 cm in fork length; 15.7 kg in body weight). (b) A male (104 cm in fork length; 22.9 kg in body weight).

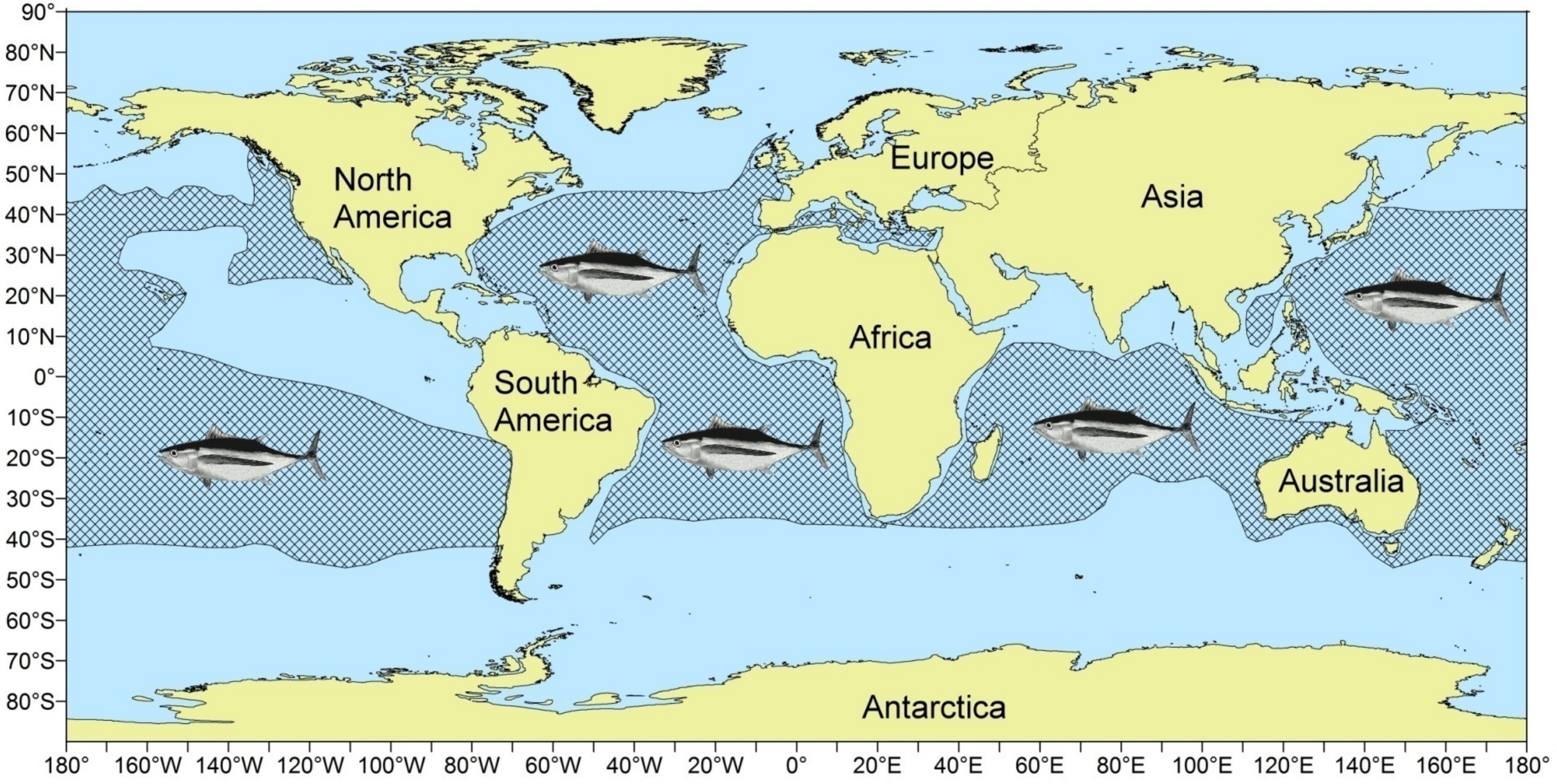

Figure 1.2. Distribution of albacore (*Thunnus alalunga*) in the world's oceans from Collette & Nauen (1983).

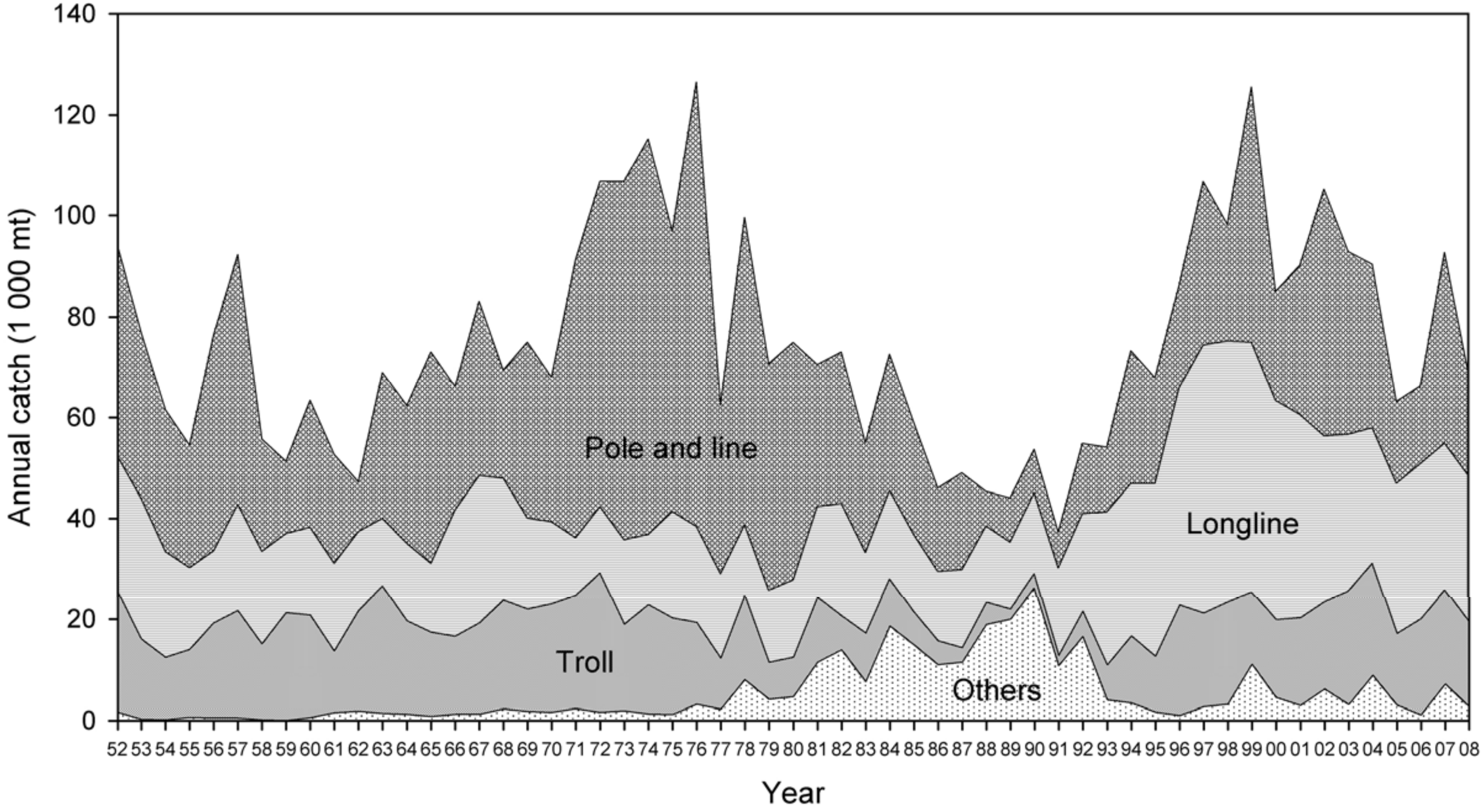

Figure 1.3. Annual fisheries production of North Pacific albacore (*Thunnus alalunga*) by fishing gear during the period of 1952 to 2008. The catch data used in this figure are from ISC (2010).

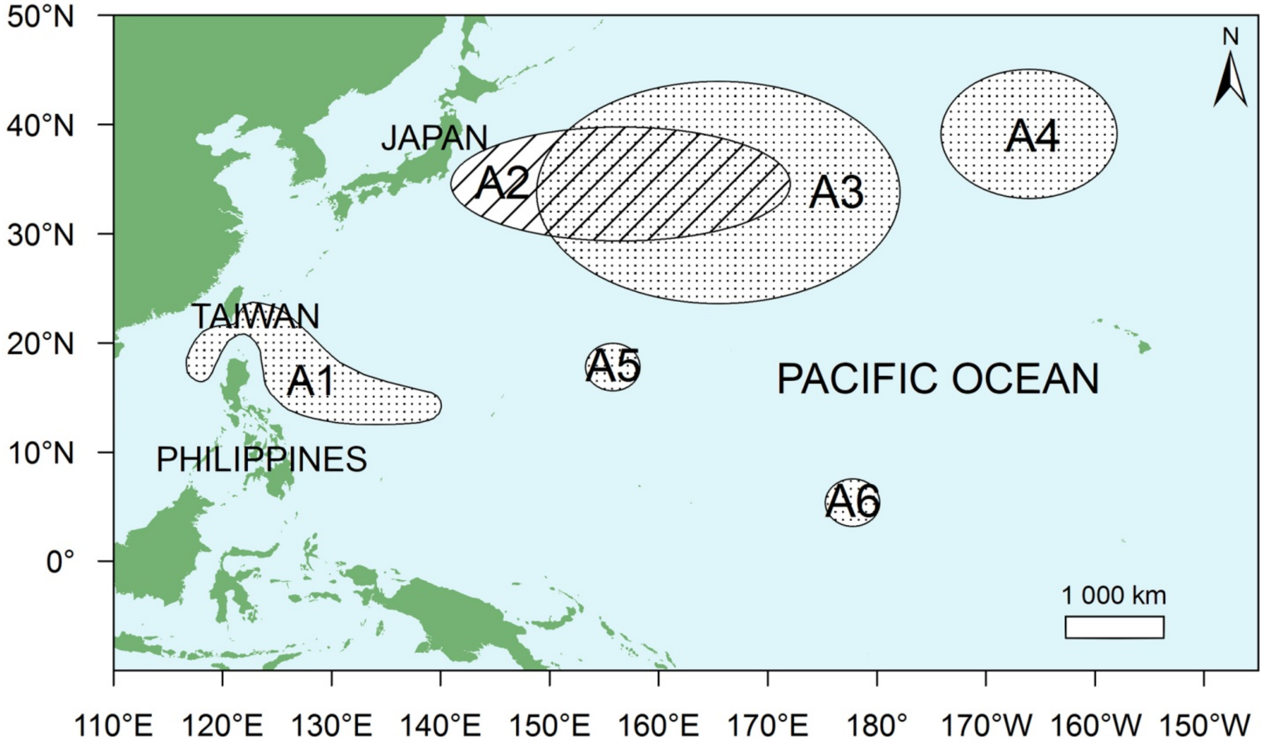

Figure 2.1. Sampling areas for the albacore (*Thunnus alalunga*) specimens collected in this study from October 2001 to January 2008. The dotted areas (A1, A3, A4, A5, and A6) indicate the fishing-operation areas for Taiwanese longline vessels. The hatched area (A2) indicates the fishing-operation area for Japanese pole-and-line vessels. The numbers of fish collected in the six areas are shown below: 136 in A1; 49 in A2; 71 in A3; 30 in A4; 6 in A5; 1 in A6.

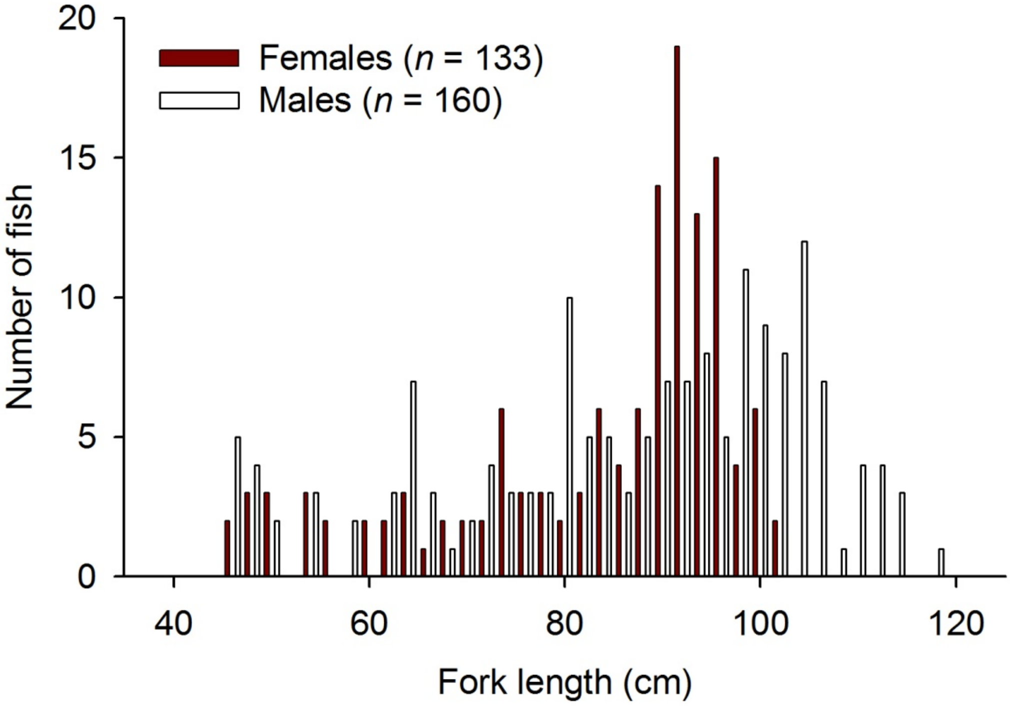

Figure 2.2. Length-frequency distribution (in 2-cm intervals) of the North Pacific albacore (*Thunnus alalunga*) specimens collected for biological investigations in this study. These specimens were collected from catches of Taiwanese longline vessels and Japanese pole-and-line vessels operated in the central and western North Pacific Ocean from 2001 to 2008.

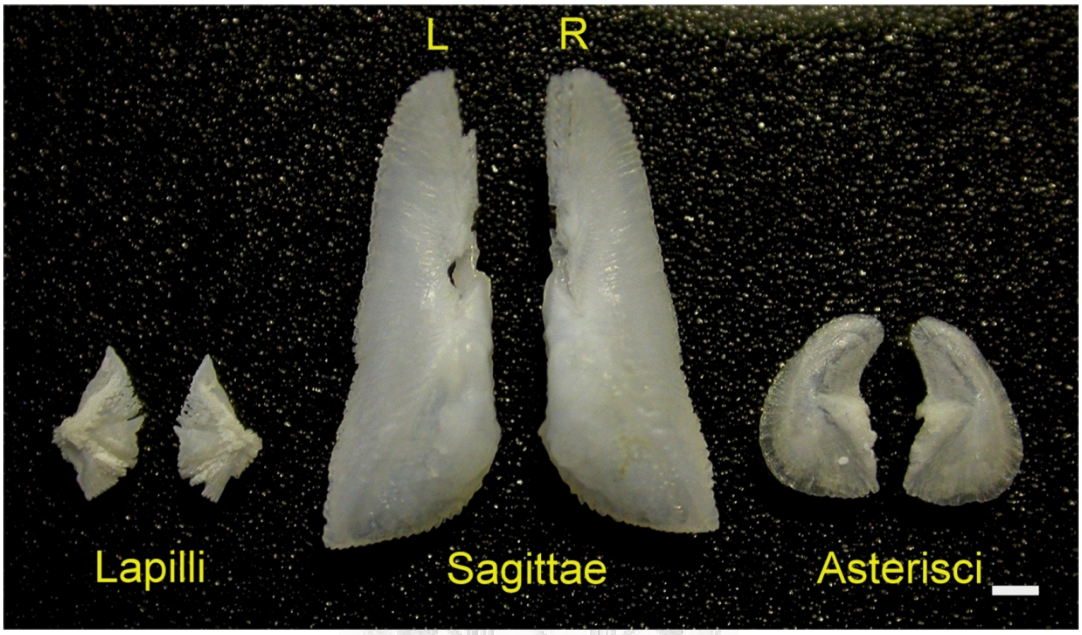

Figure 2.3. The three pairs of otoliths from a male North Pacific albacore (88 cm in fork length; 15.3 kg in body weight). L, left otolith; R, right otolith. Scale bar = 1 mm.

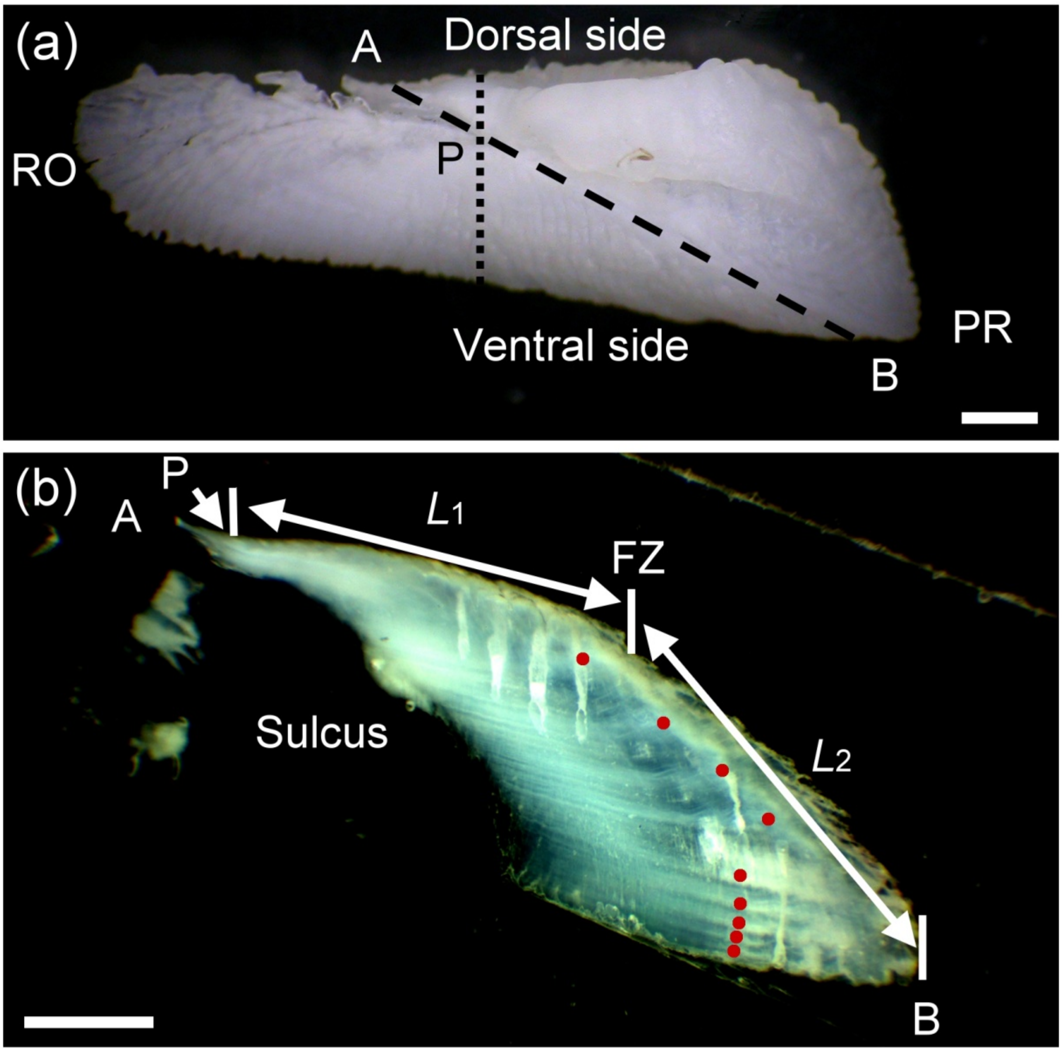

Figure 2.4. Images of a left sagittal otolith [(a), outer view] and an obliquely sectioned slice (b) of the otolith from a female North Pacific albacore (101 cm in fork length). The obliquely sectioned slice is indicated by “– – –” in (a). For comparison, the transversely sectioned slice is indicated by “▪▪▪▪▪▪” in (a). The sample was photographed using a light microscope with reflected light and a black background. RO, rostrum; P, primordium; PR, postrostrum. A, the dorsal edge of “– – –” in (a); B, the posterior-ventral edge of “– – –” in (a). FZ, the first zone composed of relatively compact micro-increments (i.e., the first annulus); L_1, the length from P to the outer-ventral margin of FZ; L_2, the length from the outer-ventral margin of FZ to B. The solid circles in (b) indicate the annual growth marks (annuli) identified. Scale bar = 1 mm.

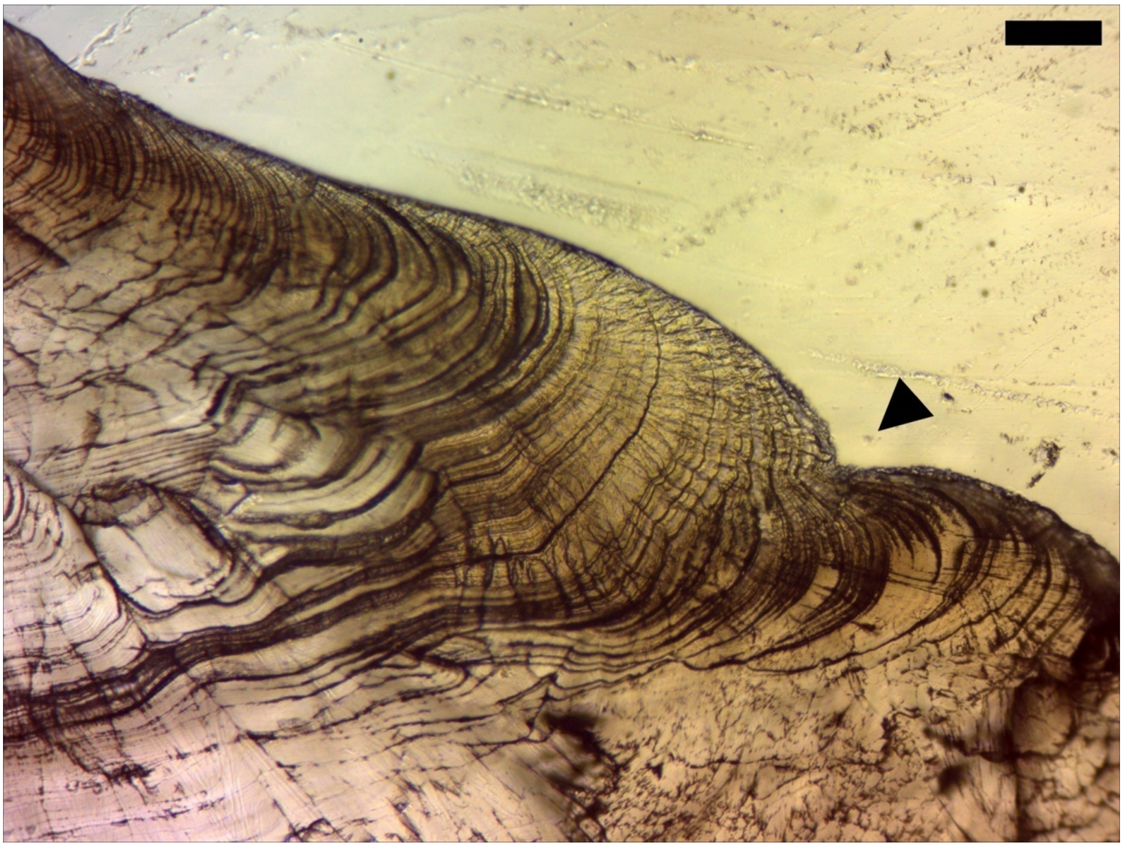

Figure 2.5. An image showing the microstructure of an annulus identified in a sagittal otolith slice. The image was obtained using a digital camera attached to a light microscope with transmitted light. The arrowhead indicates the crenulation associated with the annulus. Scale bar = 0.1 mm.

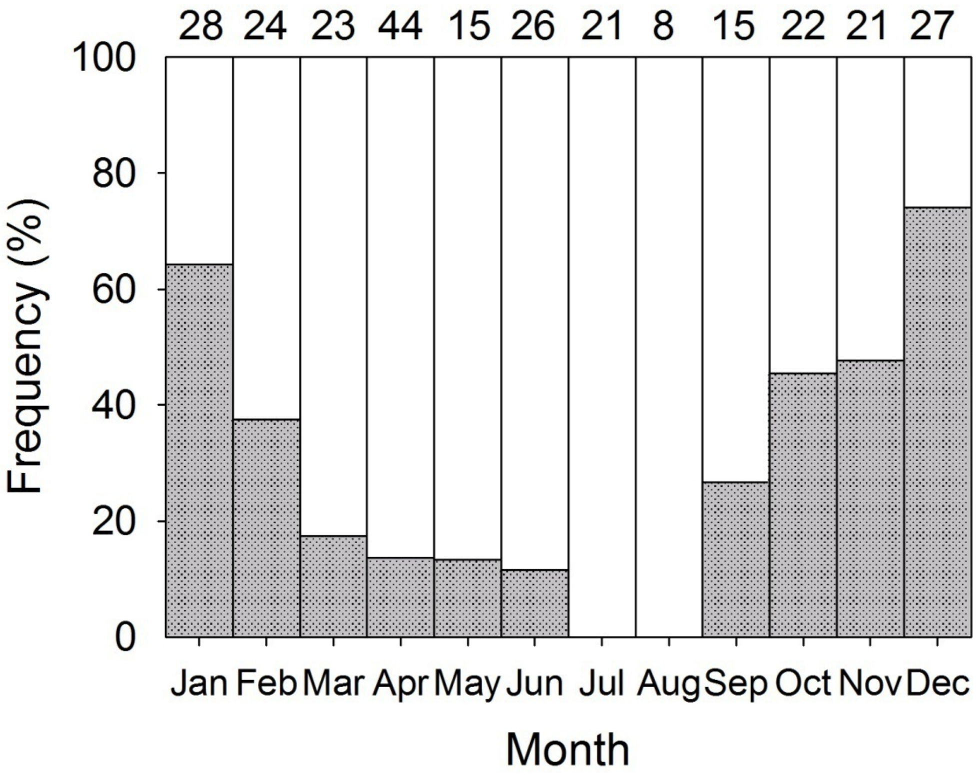

Figure 2.6. Frequency distribution (▓) of North Pacific albacore (*Thunnus alalunga*) with an annulus on the posterior-ventral otolith edge. The number above each bar indicates the sample size.

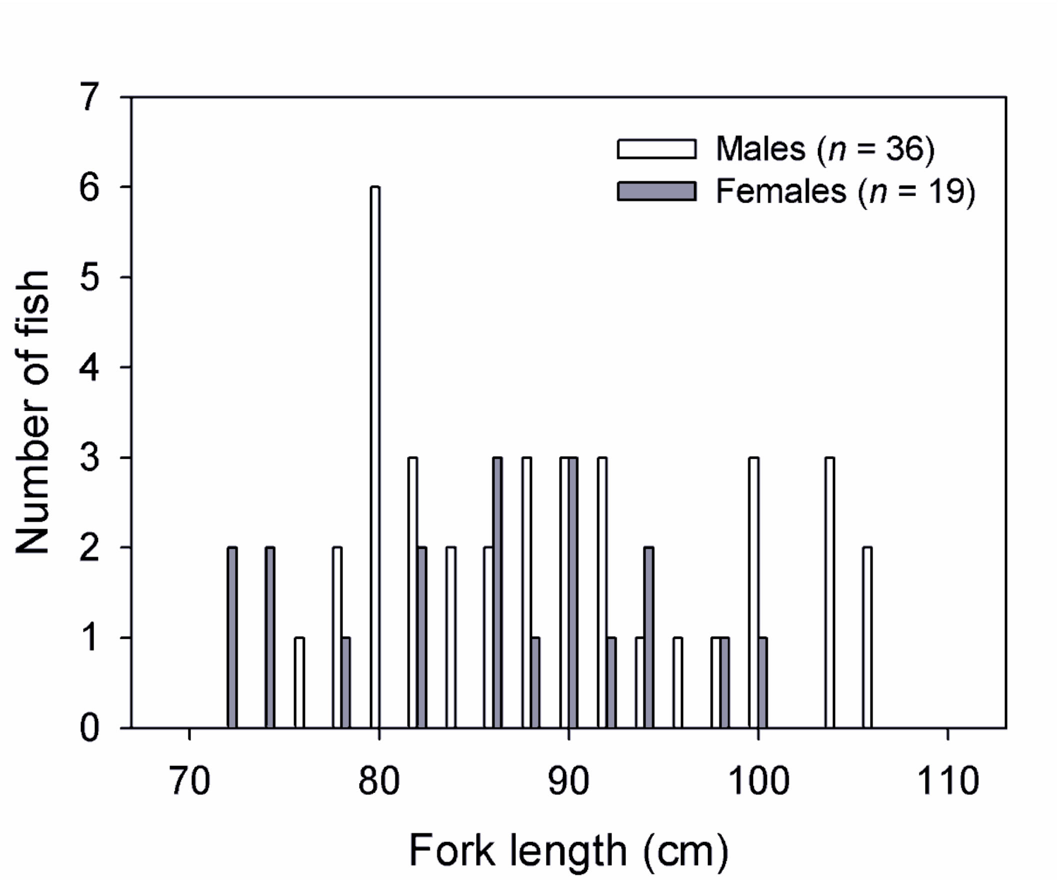

Figure 2.7. Length-frequency distribution of the 55 North Pacific albacore (*Thunnus alalunga*) used for the age assessments of first annulus formation in this study.

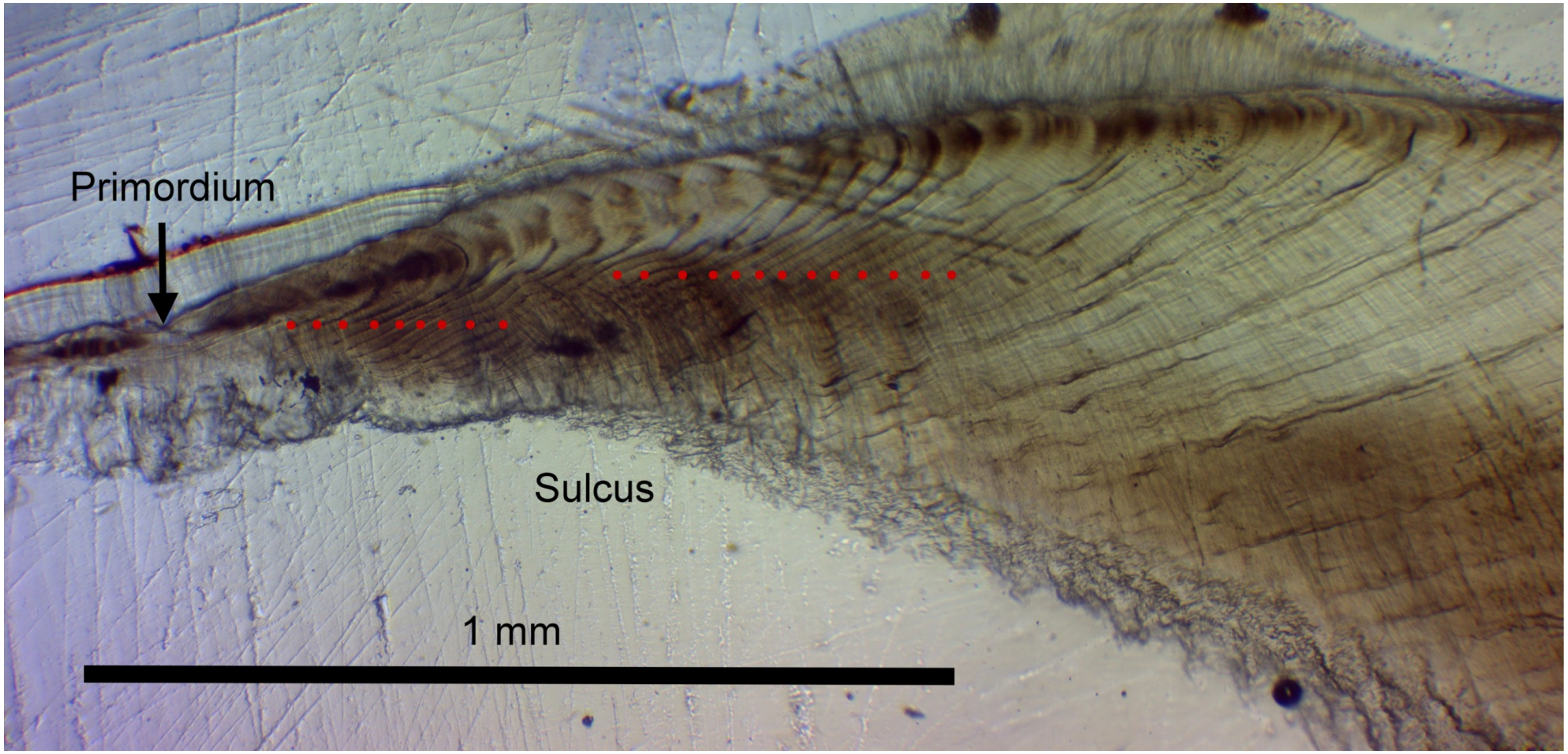

Figure 2.8. An image showing the microstructure close to the primordium in an obliquely sectioned sagittal otolith from a female North Pacific albacore (100 cm in fork length). This otolith slice was photographed using transmitted light. The solid circles indicate some of the micro-increments identified.

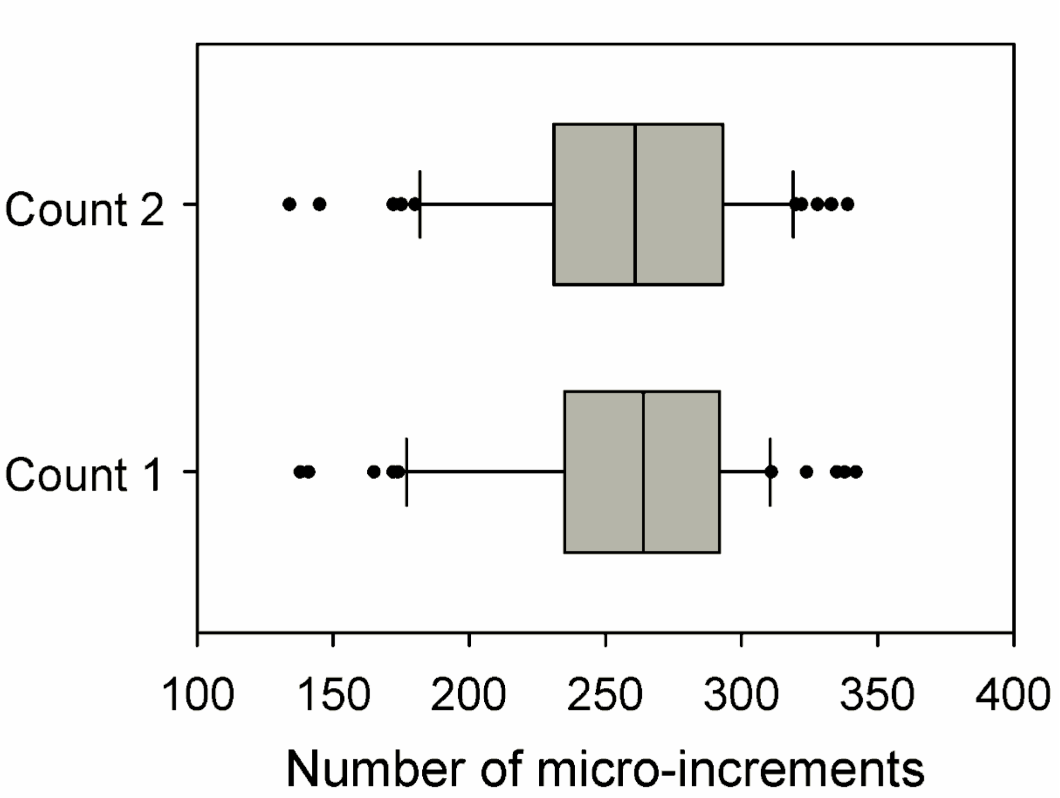

Figure 2.9. Box plots for two counts of micro-increments from the primordium to the end of the first annulus in obliquely sectioned sagittal otoliths of 55 North Pacific albacore (*Thunnus alalunga*). Whiskers (error bars) in each box plot indicate the 10th and 90th percentiles.

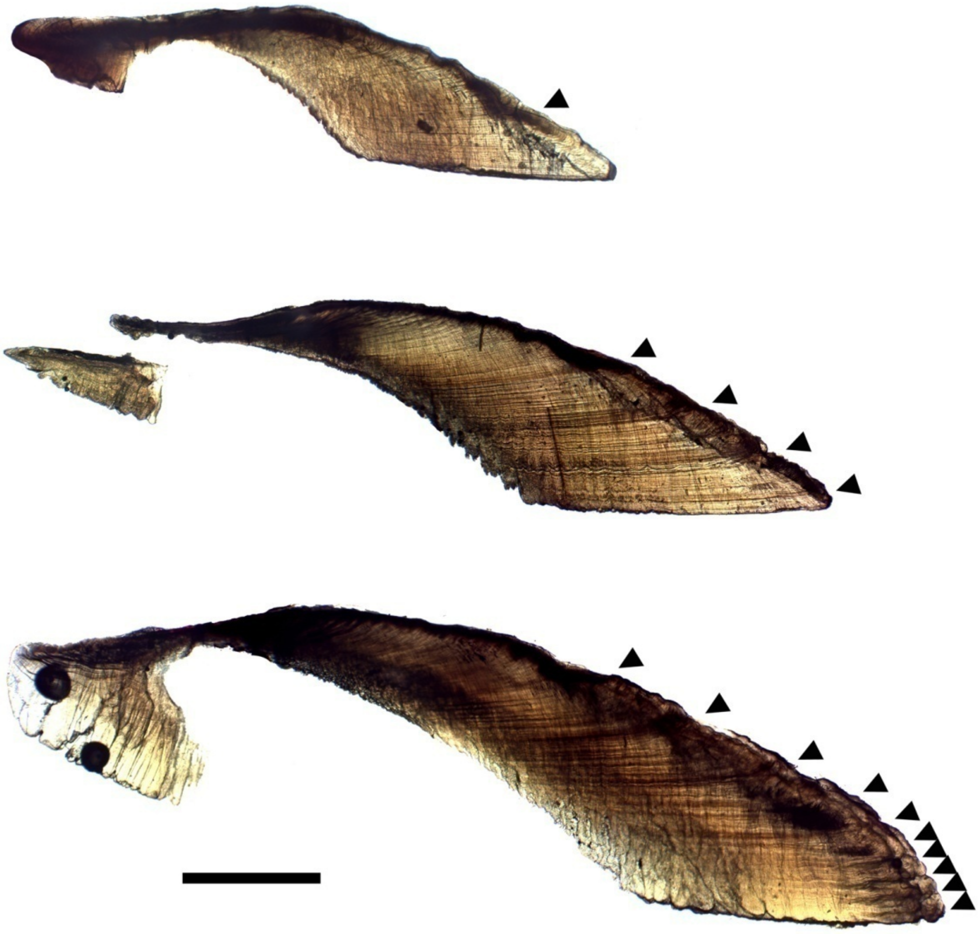

Figure 2.10. Images of three obliquely sectioned otolith slices of North Pacific albacore (*Thunnus alalunga*). These images were photographed using transmitted light. The size (in fork length) and gender of the fish are shown below: (a) 50-cm female, (b) 79-cm male, (c) 100-cm female. Arrowheads indicate the annuli identified. Scale bar = 1 mm.

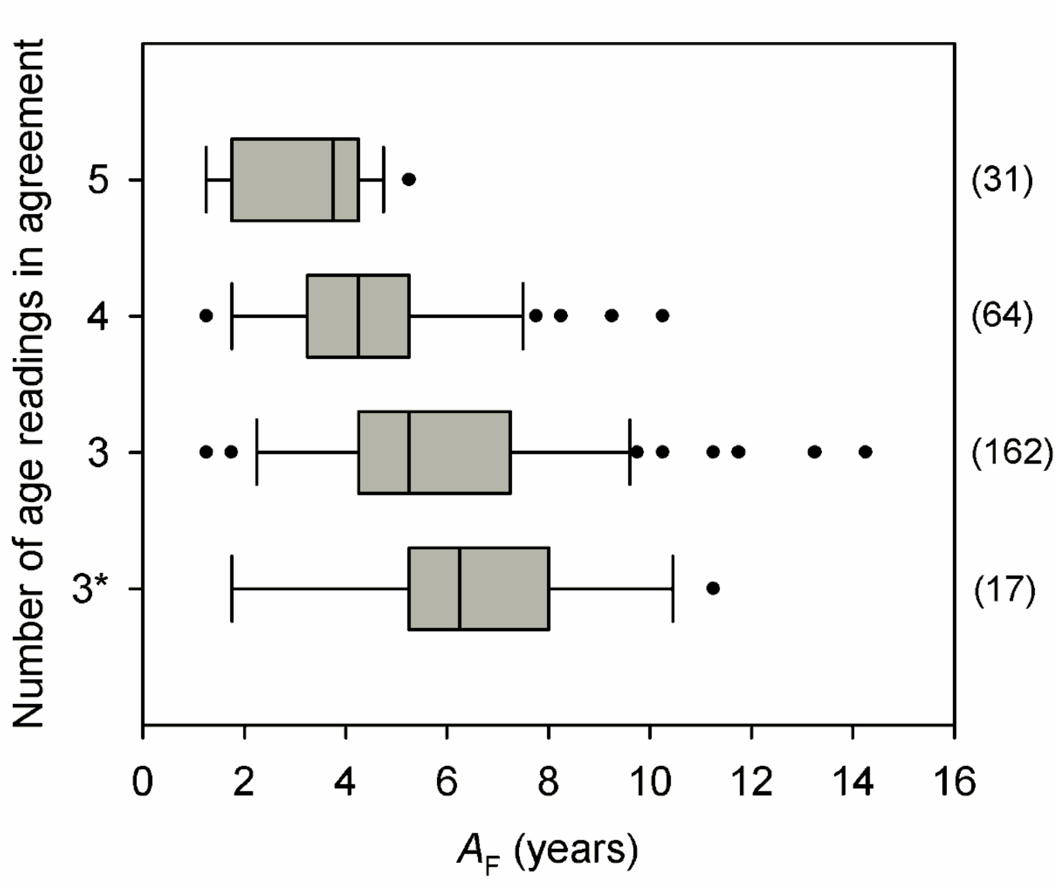

Figure 2.11. Box plots for the distributions of fish ages (A_F) determined by various criteria for North Pacific albacore (*Thunnus alalunga*). The numbers 3, 4, and 5 on the vertical axis represent the number of identical readings among five age readings, and the sign 3* denotes three identical readings among six age readings. The number in parentheses indicates the sample size of the corresponding dataset. Whiskers (error bars) in each box plot indicate the 10th and 90th percentiles.

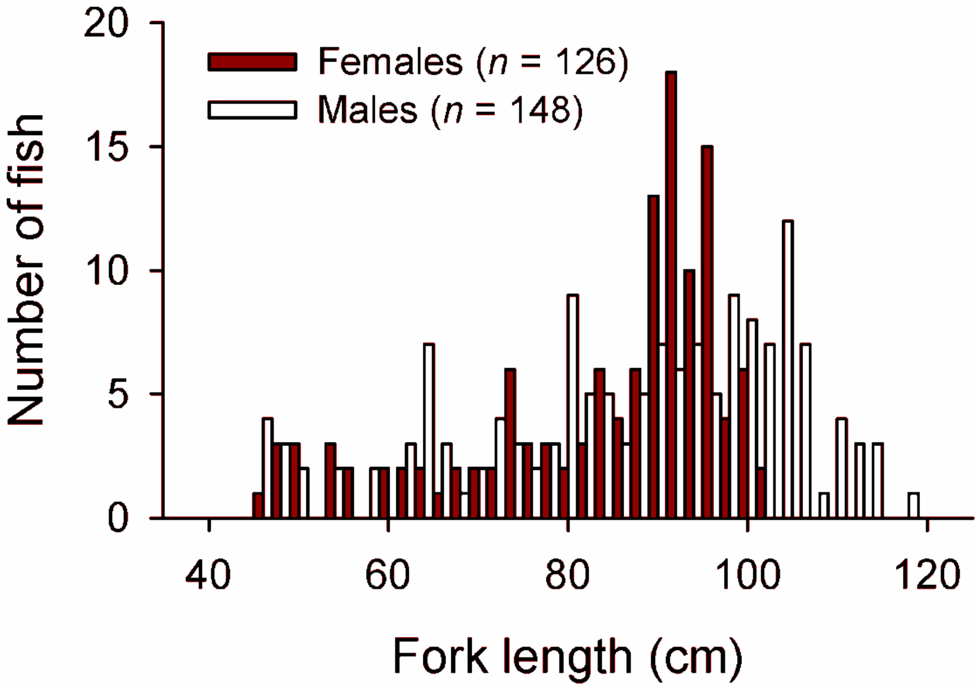

Figure 2.12. The length-frequency distribution of the age-determined North Pacific albacore (*Thunnus alalunga*) in this study.

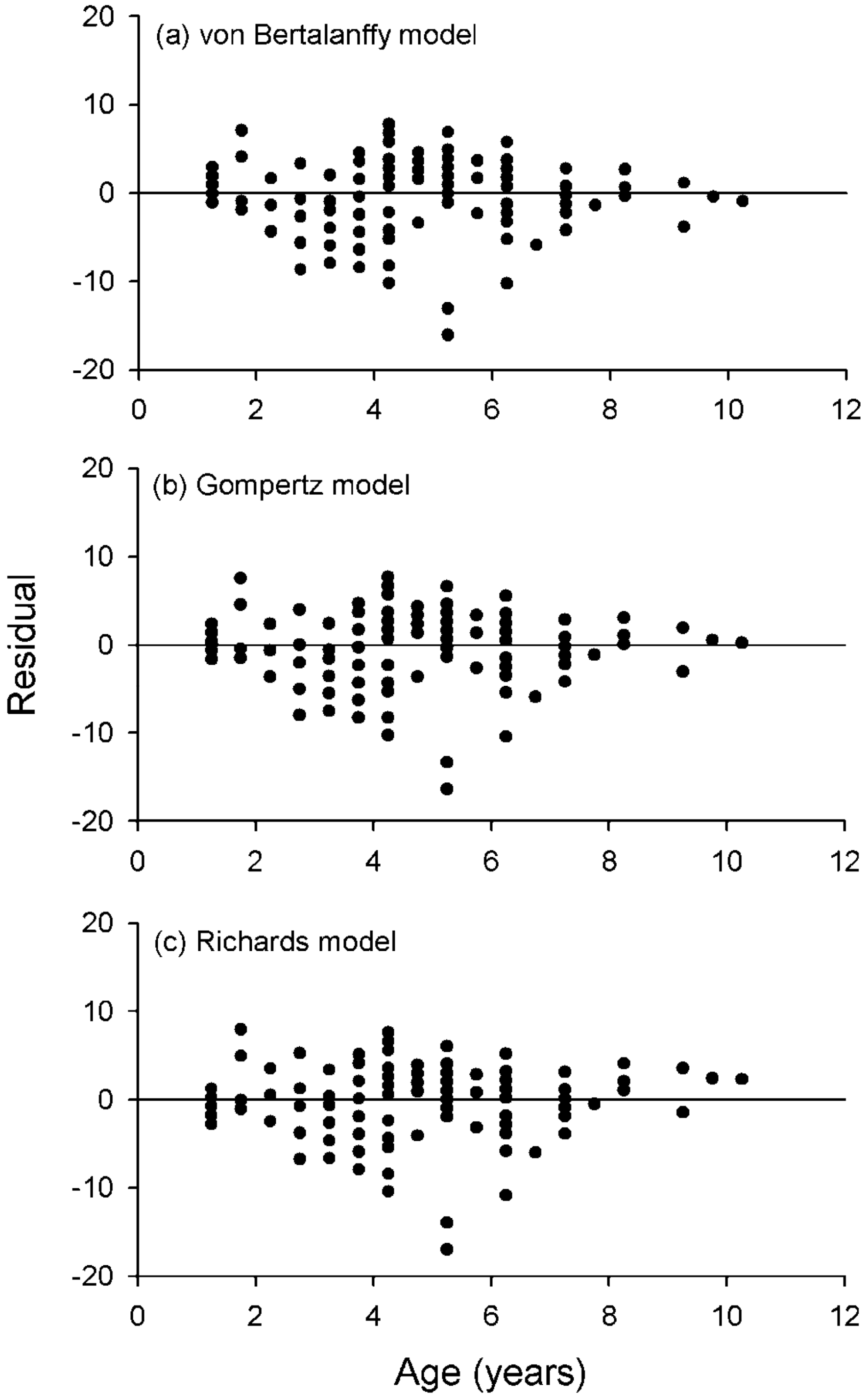

Figure 2.13. Residual plots for female North Pacific albacore (*Thunnus alalunga*) at the fitting of the three growth models (von Bertalanffy, Gompertz, and Richards).

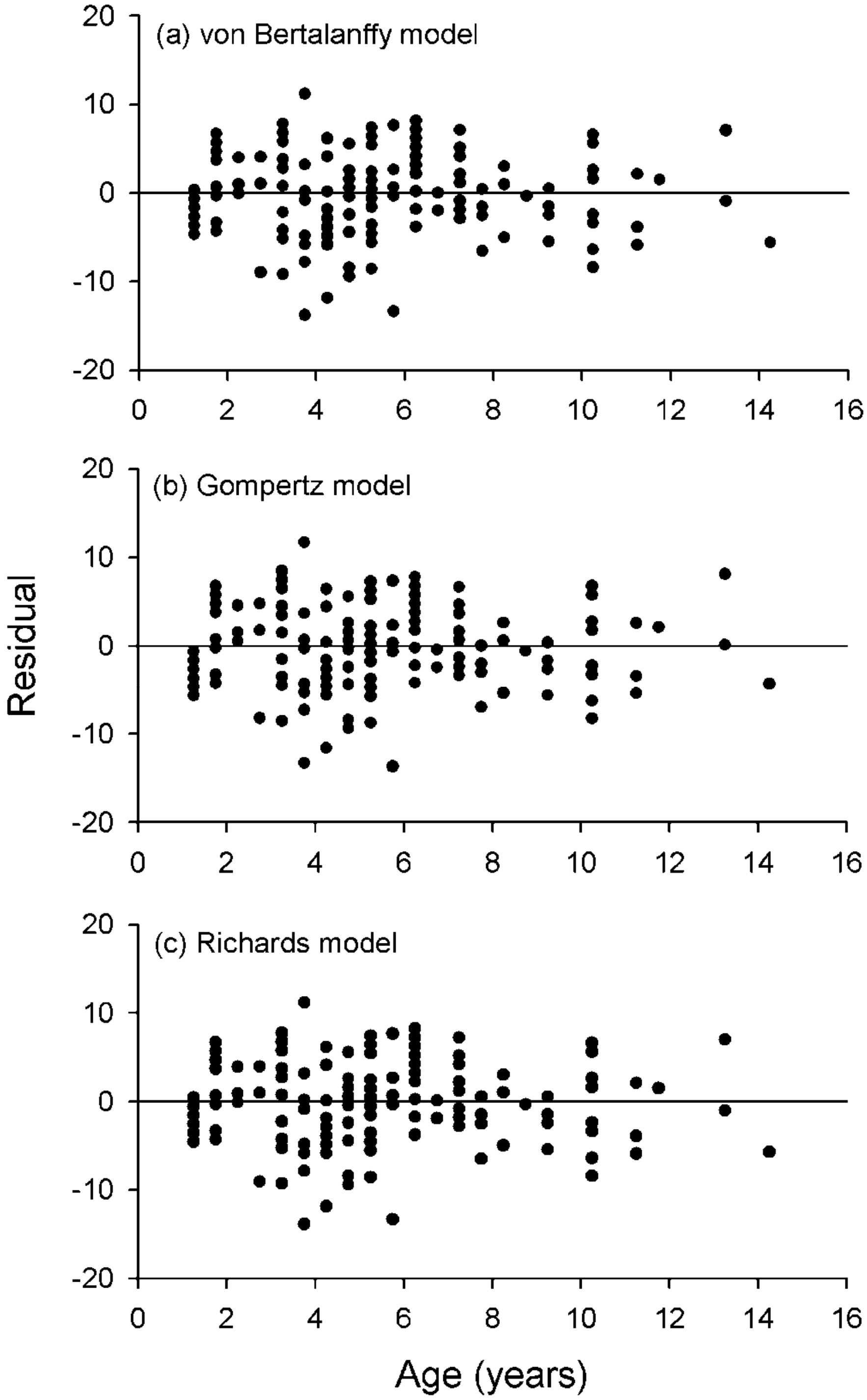

Figure 2.14. Residual plots for male North Pacific albacore (*Thunnus alalunga*) at the fitting of the three growth models (von Bertalanffy, Gompertz, and Richards).

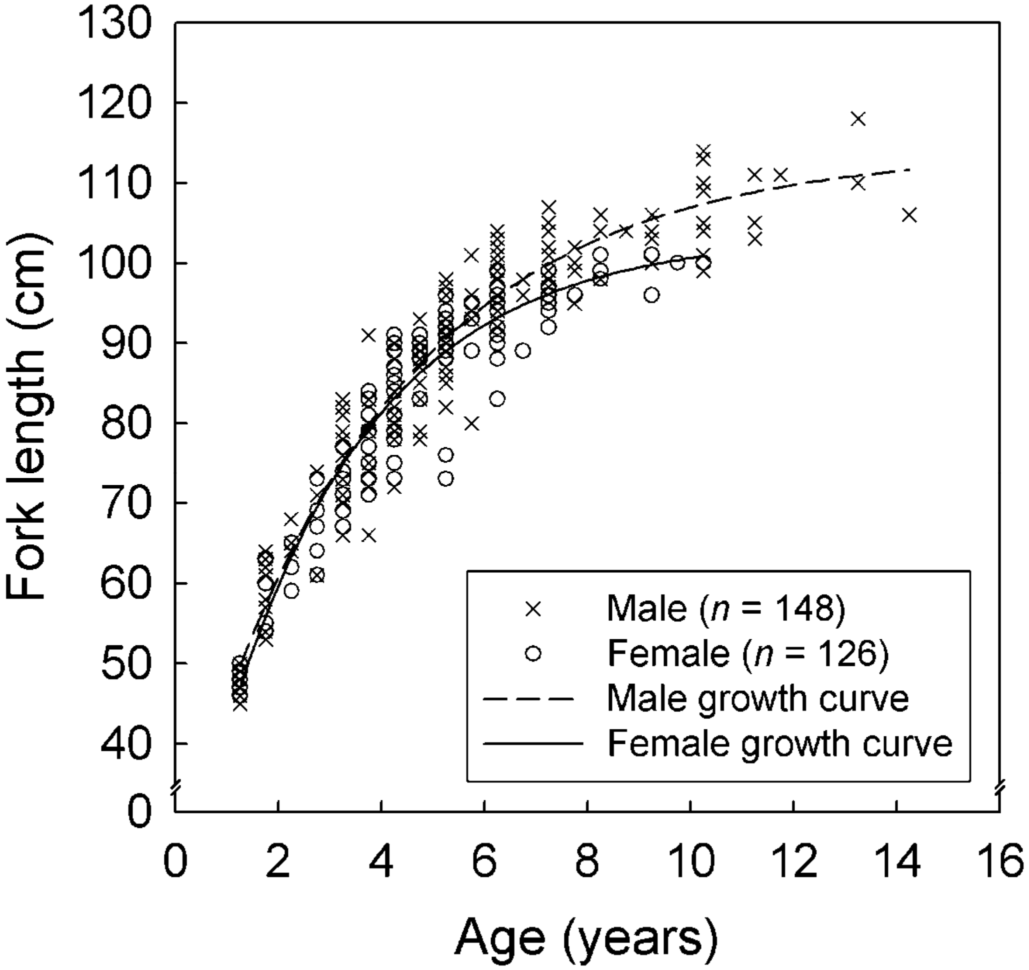

Figure 2.15. A diagram showing the sex-specific age-length data and von Bertalanffy growth curves of North Pacific albacore (*Thunnus alalunga*). The von Bertalanffy growth parameters estimated for males were L_∞ = 114.0 cm, K = 0.253 year^{-1}, and t_0 = −1.01 years; the parameters for females were L_∞ = 103.5 cm, K = 0.340 year^{-1}, and t_0 = −0.53 years.

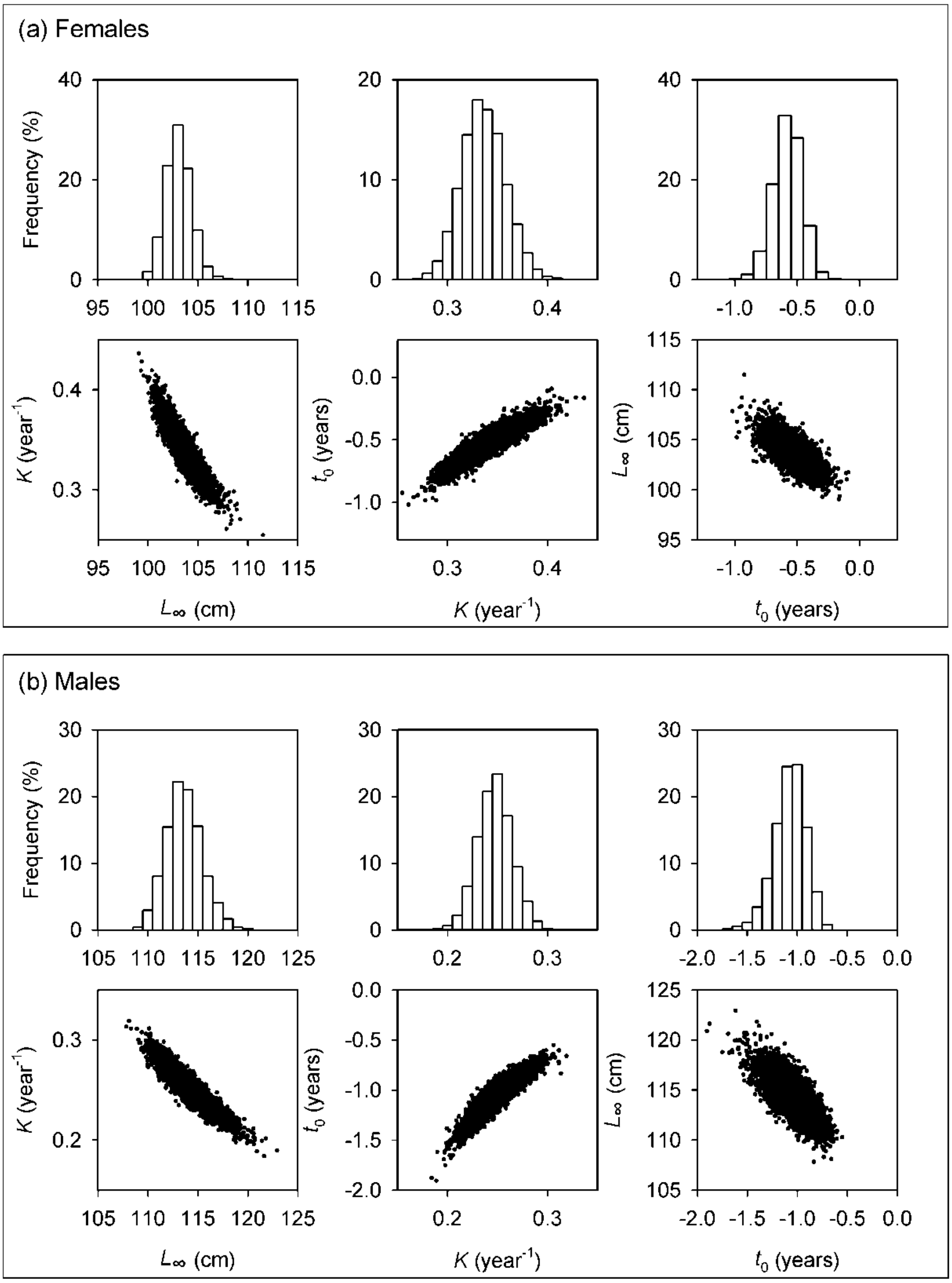

Figure 2.16. Results of the bootstrapping (*n* = 5 000) of age-length data for North Pacific albacore (*Thunnus alalunga*) at the fitting of the von Bertalanffy growth model. Histograms represent the frequency (%) distributions of the bootstrap estimates of growth parameters (L_∞, K, and t_0); scatter plots illustrate correlations between the parameters.

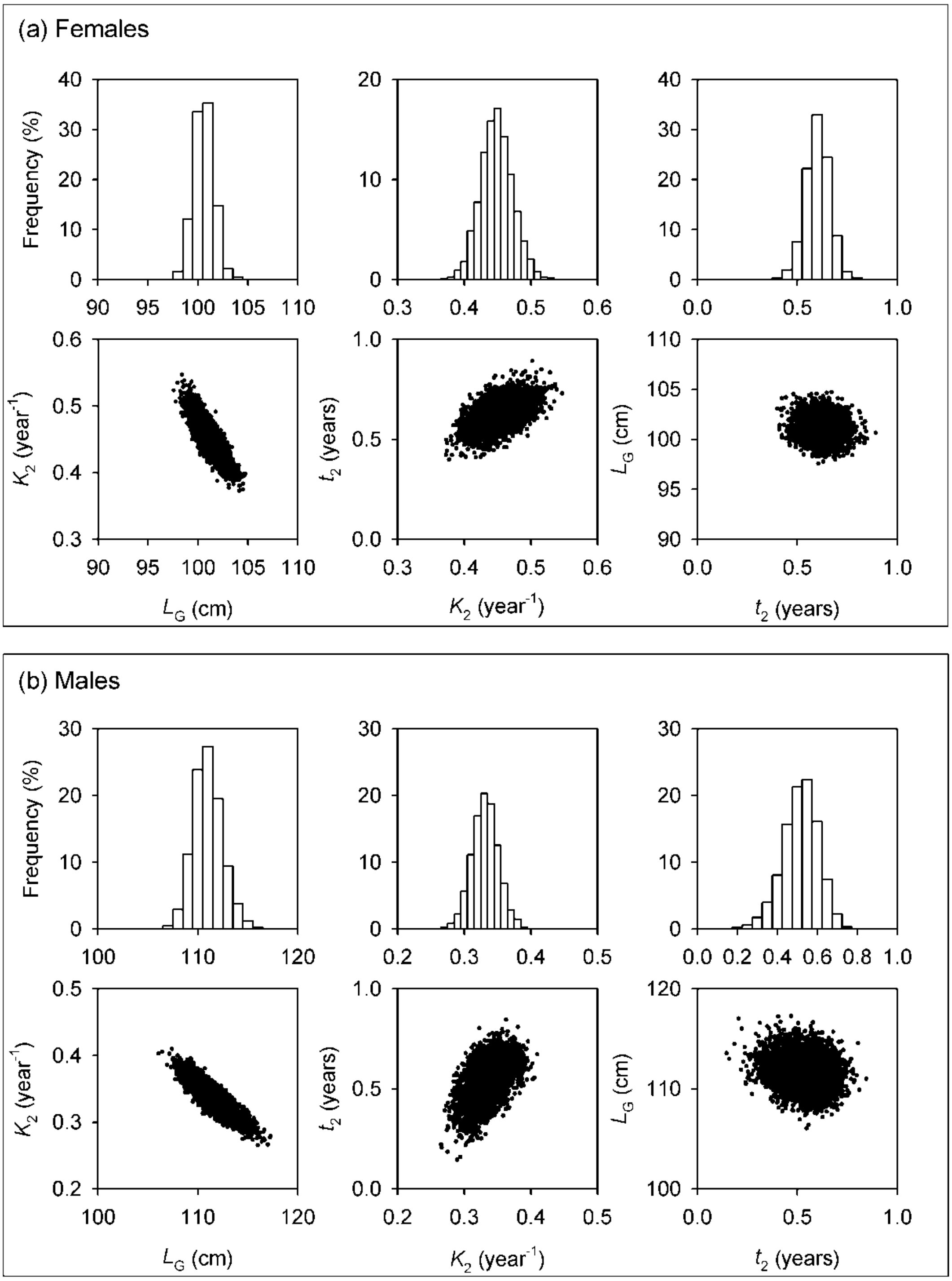

Figure 2.17. Results of the bootstrapping (*n* = 5 000) of age-length data for North Pacific albacore (*Thunnus alalunga*) at the fitting of the Gompertz growth model. Histograms represent the frequency distributions (%) of the bootstrap estimates of growth parameters (L_G, K_2, and t_2); scatter plots illustrate correlations between the parameters.

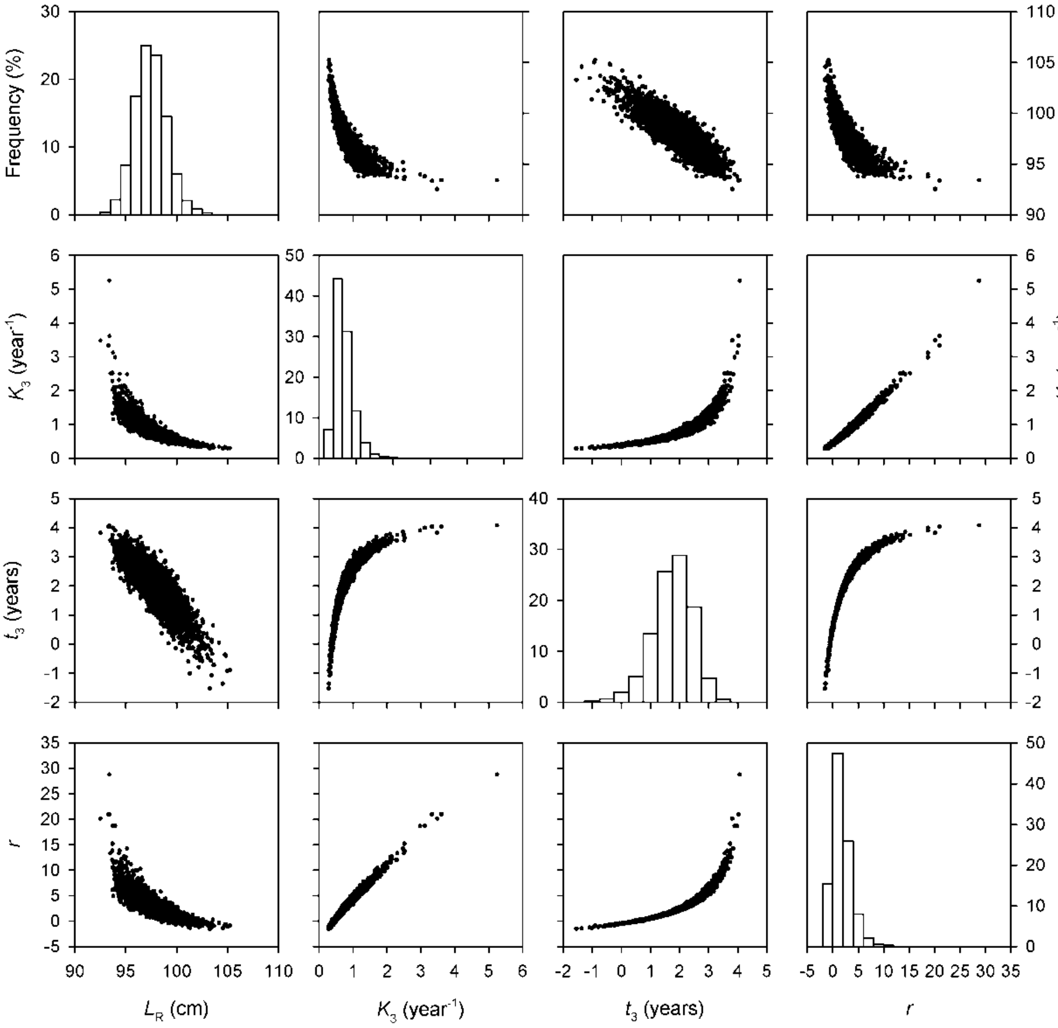

Figure 2.18. Results of the bootstrapping (n = 5 000) of female age-length data for North Pacific albacore (*Thunnus alalunga*) at the fitting of the Richards growth model. Histograms represent the frequency (%) distributions of the bootstrap estimates of growth parameters (L_R, K_3, t_3, and r); scatter plots illustrate correlations between the parameters.

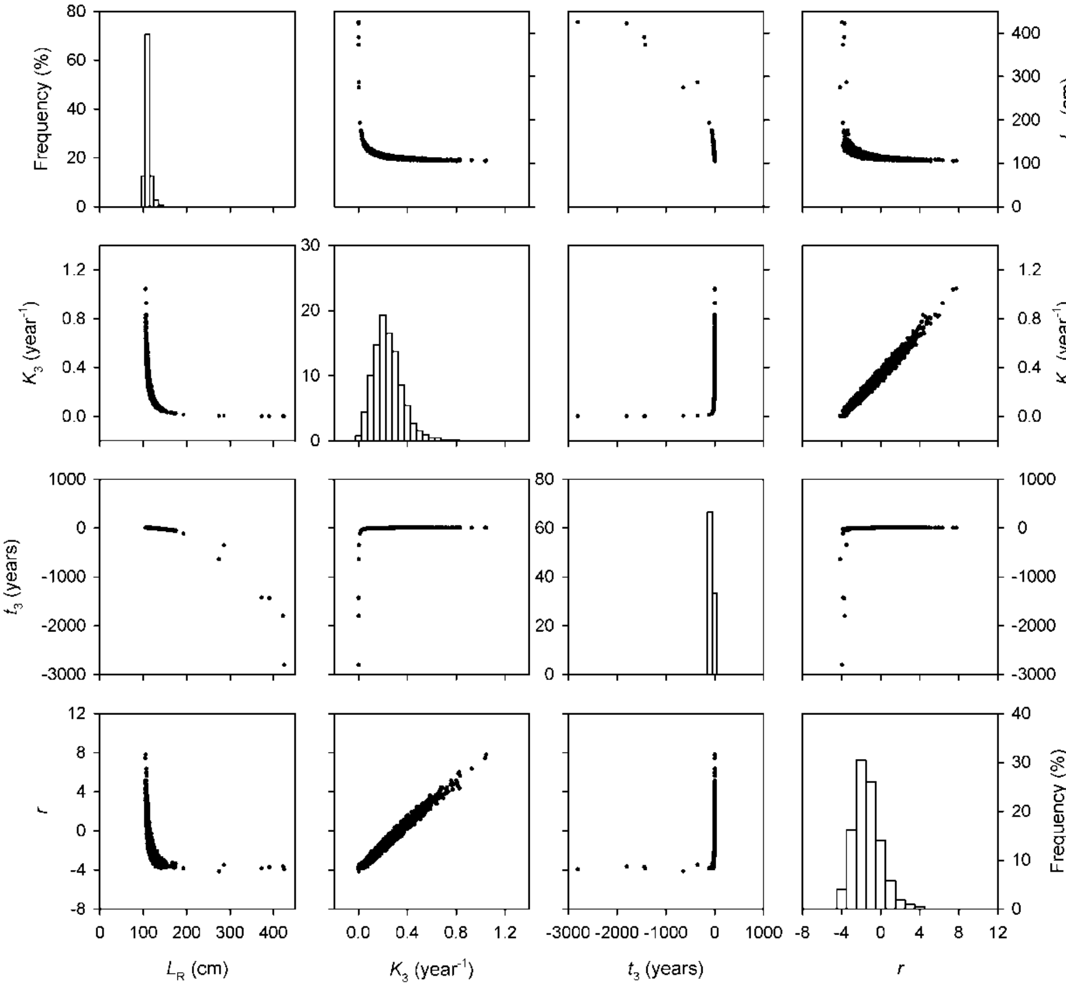

Figure 2.19. Results of the bootstrapping (n = 5 000) of male age-length data for North Pacific albacore (*Thunnus alalunga*) at the fitting of the Richards growth model. Histograms represent the frequency (%) distributions of the bootstrap estimates of growth parameters (L_R, K_3, t_3, and r); scatter plots illustrate correlations between the parameters.

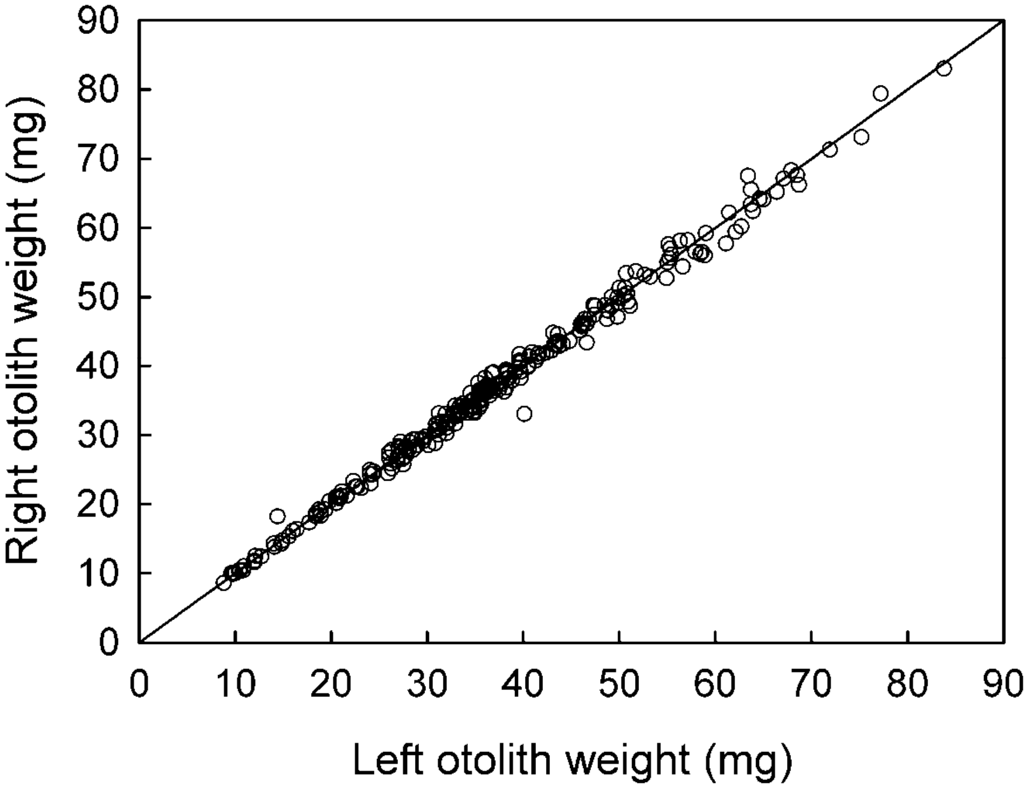

Figure 2.20. Right otolith weight versus left otolith weight for sagittae from 245 North Pacific albacore (*Thunnus alalunga*). The straight line represents y = x.

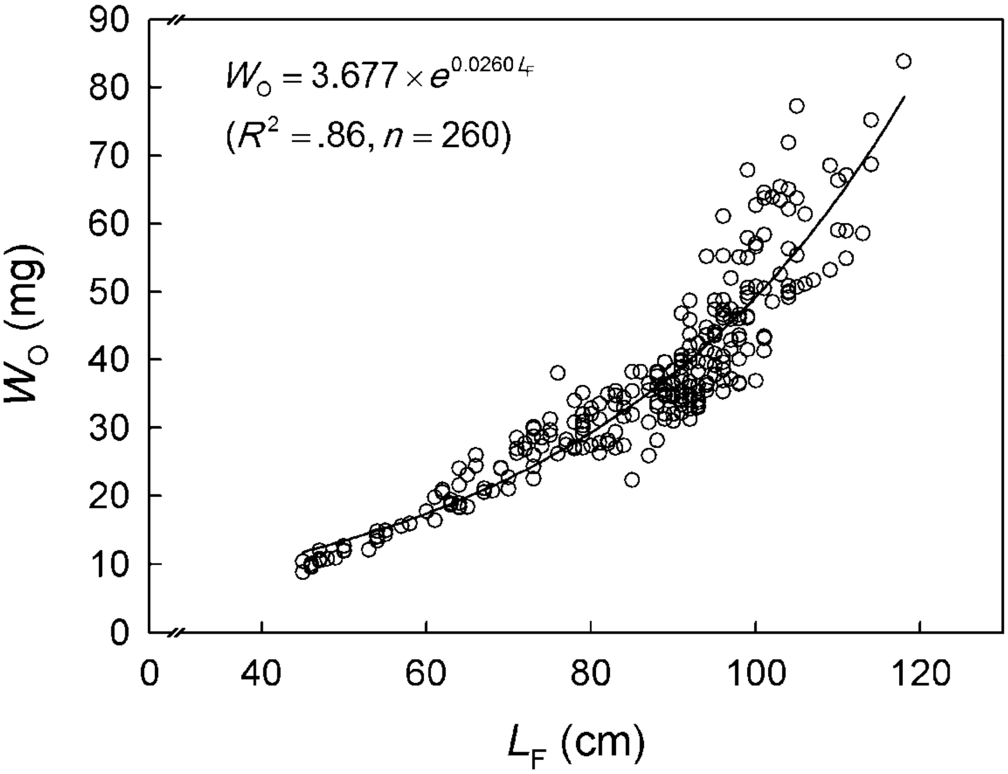

Figure 2.21. The relationship between left otolith weight (W_O) and fork length (L_F) for North Pacific albacore (*Thunnus alalunga*). The curve indicates the regression function fitted using sex-pooled data.

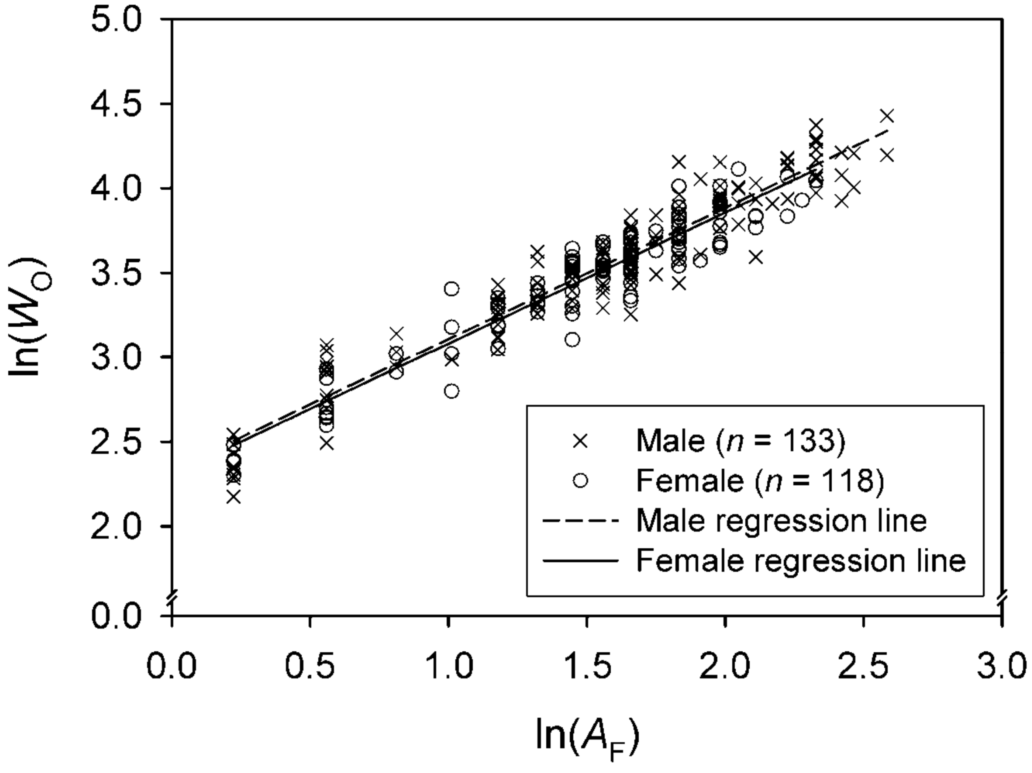

Figure 2.22. The relationships between the log-transformed data of the left otolith weight (W_O, in milligrams) and fish age (A_F, in years) for male and female North Pacific albacore (*Thunnus alalunga*). For males, the simple linear regression function and the standard errors (*SE*) of the bootstrap parameters (n = 5 000) were as follows: $\ln(M_O) = a + b \times \ln(A_F)$, a = 2.331 (*SE* = 0.041), b = 0.777 (*SE* = 0.024), and r^2 = .91. For females, the parameters of the regression function were as follows: a = 2.305 (*SE* = 0.036), b = 0.776 (*SE* = 0.023), and r^2 = .91.

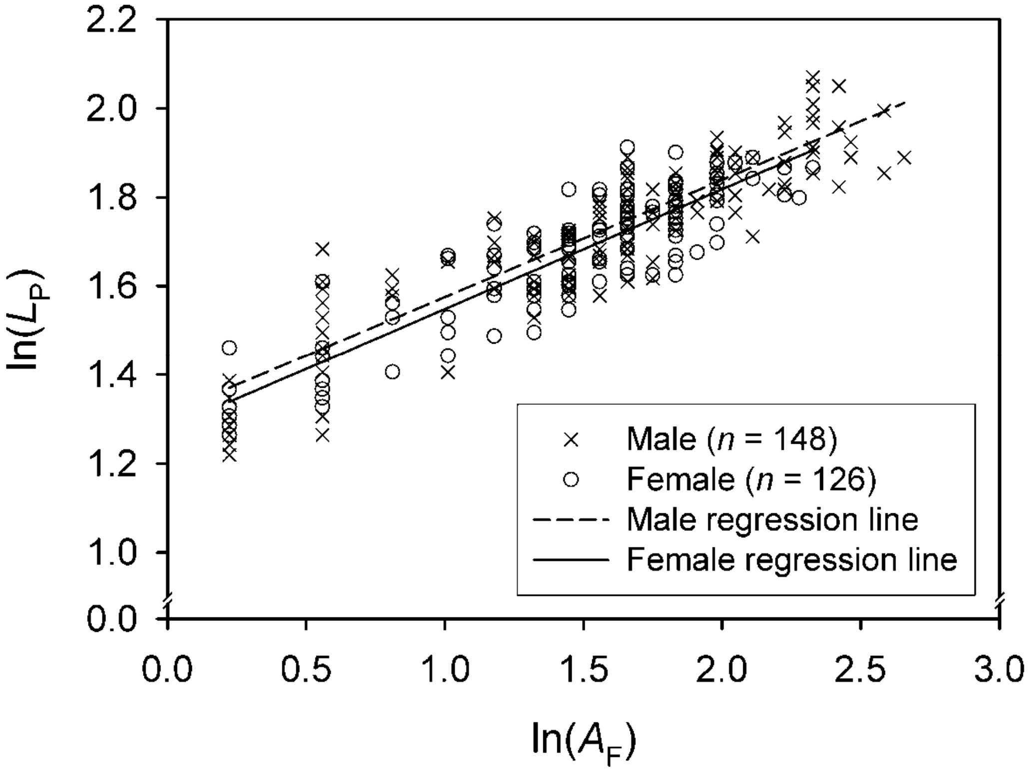

Figure 2.23. The relationships between the log-transformed data of the postrostral otolith length (L_P, in millimeters) and fish age (A_F, in years) for male and female North Pacific albacore (*Thunnus alalunga*). For males, the simple linear regression function and the standard errors (*SE*) of the bootstrap parameters (n = 5 000) were as follows: $\ln(L_P) = a + b \times \ln(A_F)$, a = 1.311 (*SE* = 0.023), b = 0.264 (*SE* = 0.013), and r^2 = .81. For females, the parameters of the regression function were as follows: a = 1.278 (*SE* = 0.021), b = 0.270 (*SE* = 0.013), and r^2 = .78.

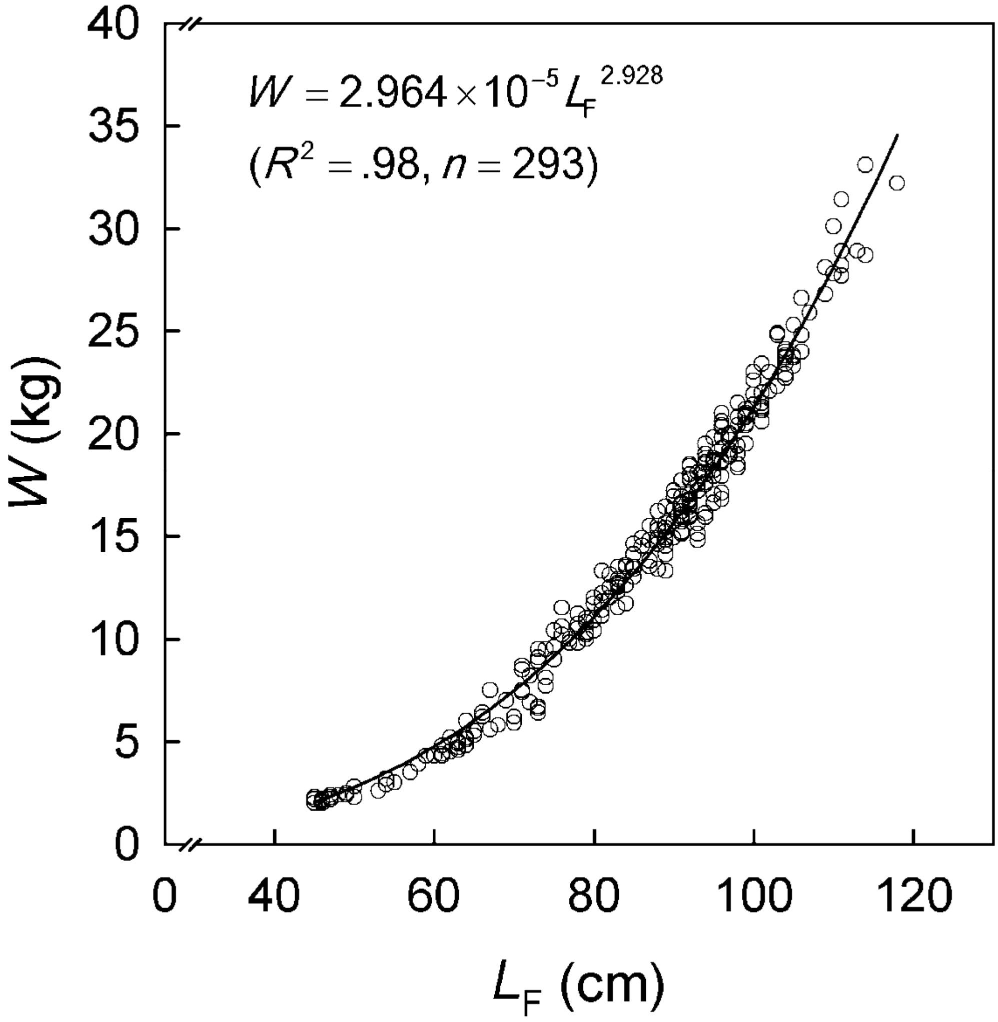

Figure 2.24. The relationship between body weight (*W*) and fork length (L_F) in North Pacific albacore (*Thunnus alalunga*).

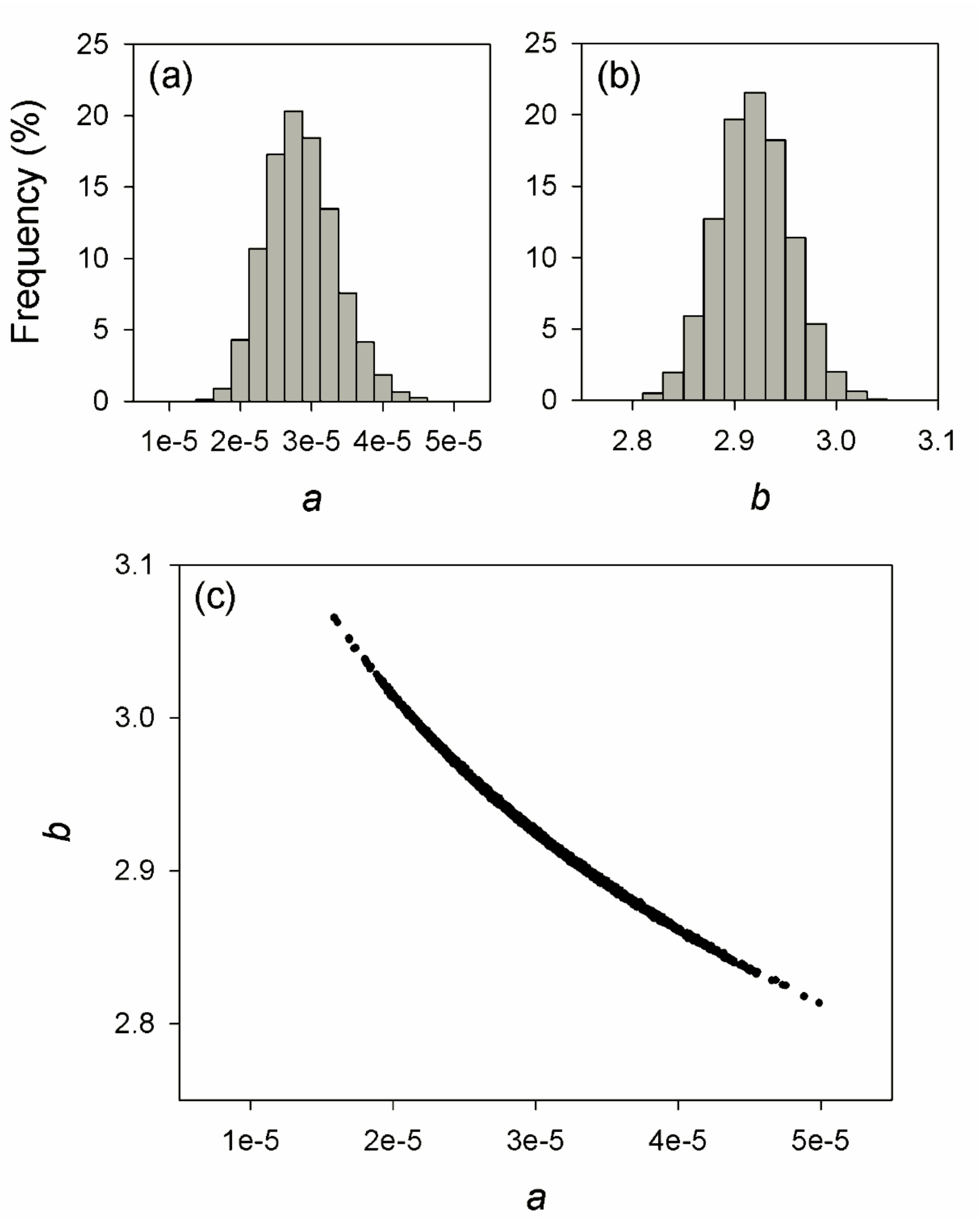

Figure 2.25. Results of bootstrapping (n = 5 000) for the length-weight parameters (a and b) of North Pacific albacore (*Thunnus alalunga*) at fitting the power function, $W = a \times L_F{}^b$ [where W is the body weight (kg) and L_F is the fork length (cm)], by the nonlinear least-squares method.

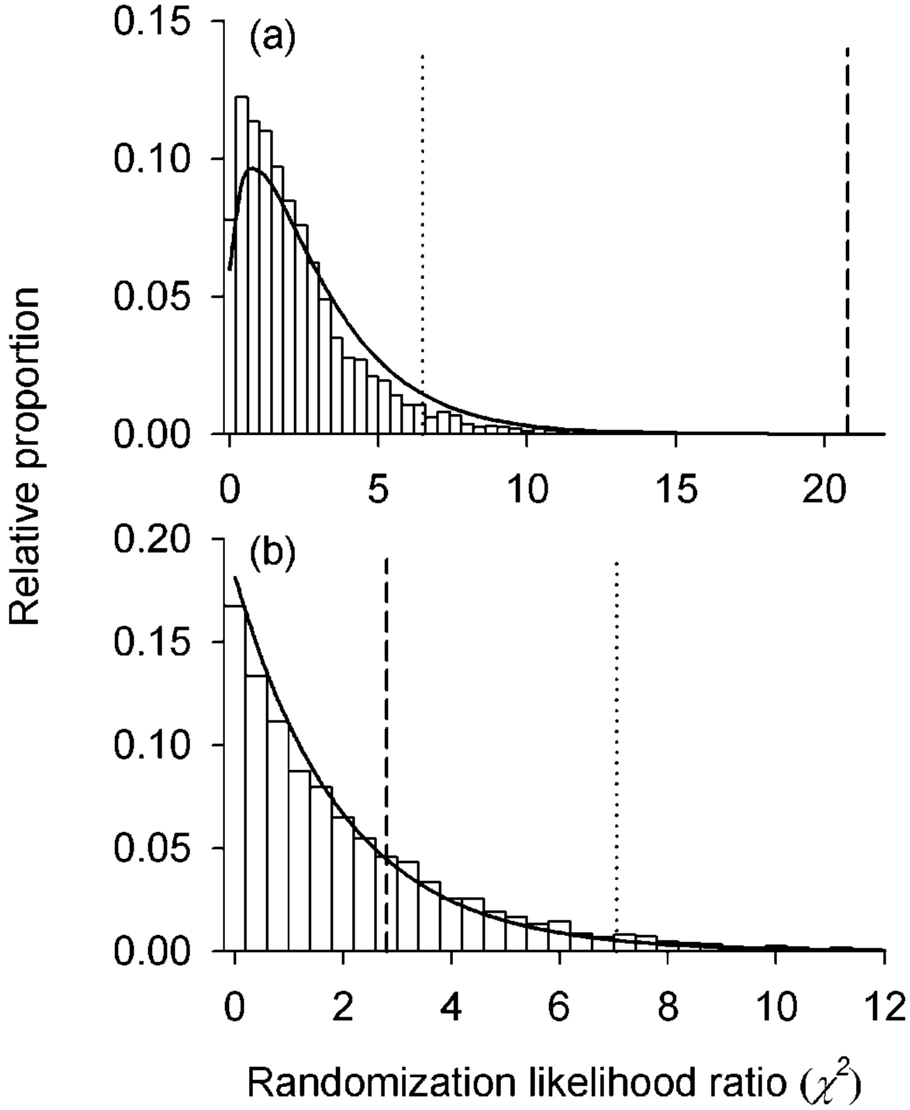

Figure 2.26. Randomized likelihood ratio tests (open columns, n = 5 000) for comparing the sex-specific (a) growth and (b) allometric functions of North Pacific albacore (*Thunnus alalunga*). The solid curve represents the chi-square distribution with 3 degrees of freedom (*df*) in (a) and with *df* = 2 in (b). For both (a) and (b), the dashed line indicates the χ^2 value calculated by the original data, and the dotted line indicates the critical value of the randomization test at a 5% level of significance.

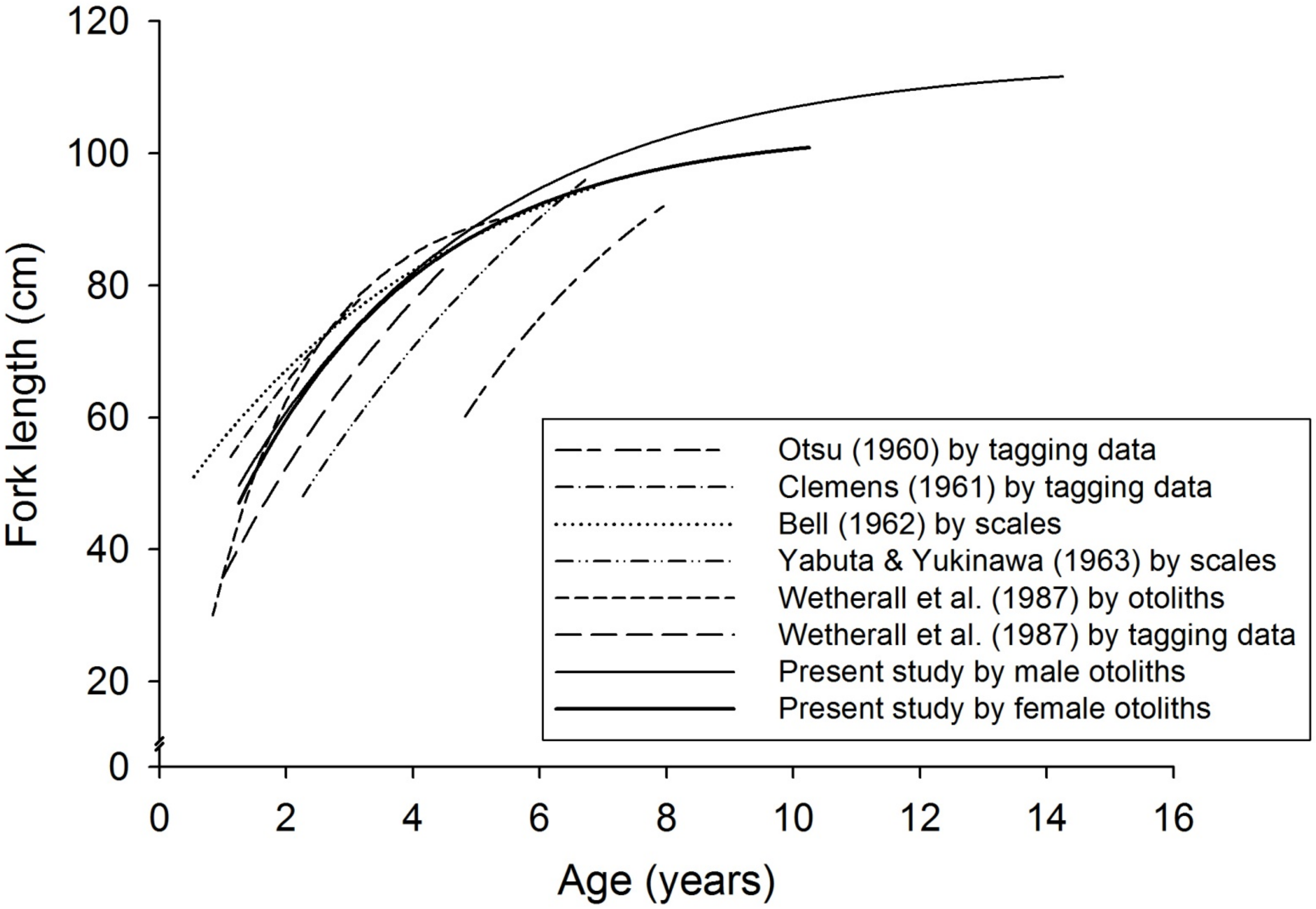

Figure 2.27. Curves for the von Bertalanffy growth parameters reported for North Pacific albacore (*Thunnus alalunga*). The parameters for plotting the curves are presented in Table 2.7. The curves for Wetherall et al. (1987) are for the north albacore data in that article.

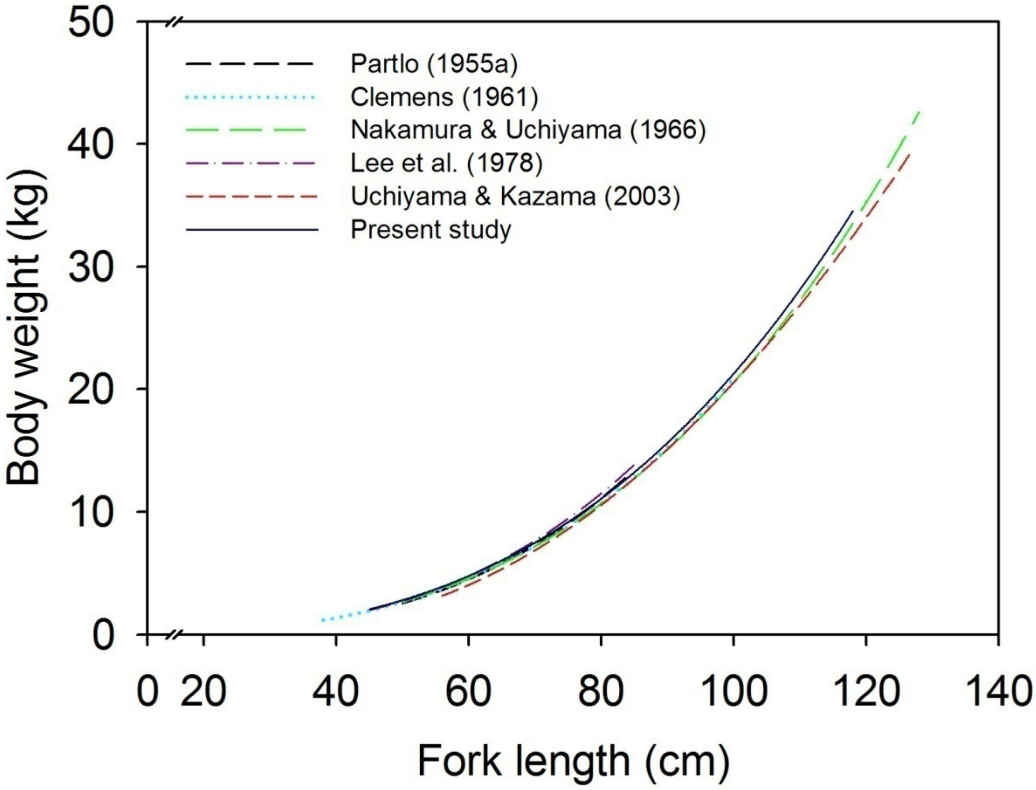

Figure 2.28. Curves for the length-weight functions reported for North Pacific albacore (*Thunnus alalunga*). The parameters for plotting these curves are presented in Table 2.9.

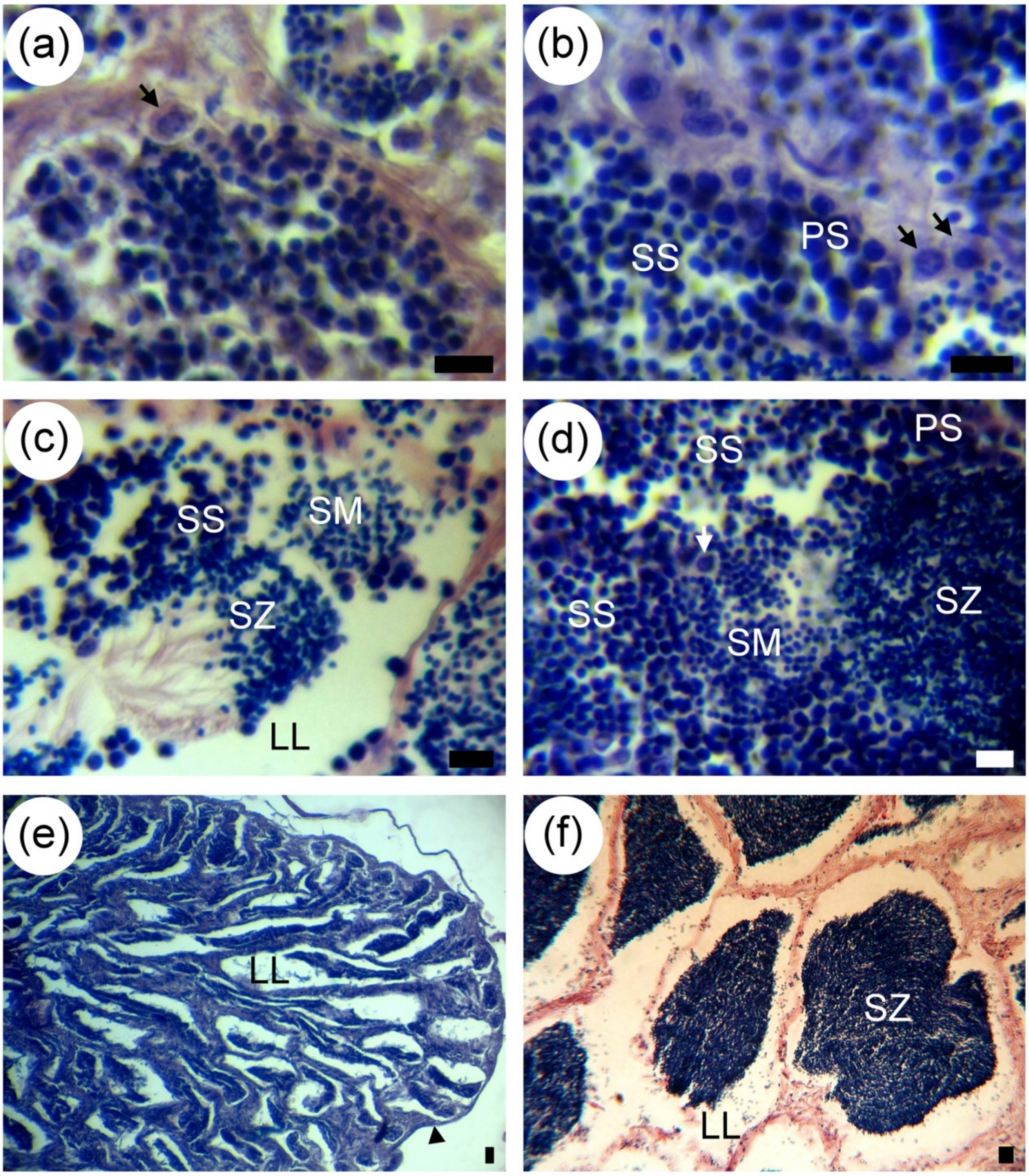

Figure 3.1. Spermatogenic cells during spermatogenesis observed in North Pacific albacore (*Thunnus alalunga*) testes. Histological sections were stained with Mayer's hematoxylin and eosin. (a) Spermatogonium (arrow). (b) Primary spermatocytes (PS); secondary spermatocytes (SS); spermatogonia (arrows). (c) Spermatids (SM); spermatozoa (SZ). (d) Spermatogenic cells in various stages in the lobule lumen (spermatogonium, indicated by an arrow). (e) A section of an immature testis (fish size of 79 cm in fork length) showing no spermatozoa in the LL (testicular wall, indicated by an arrowhead). (f) A section of a mature testis (fish size of 90 cm in fork length). Scale bar = 10 μm.

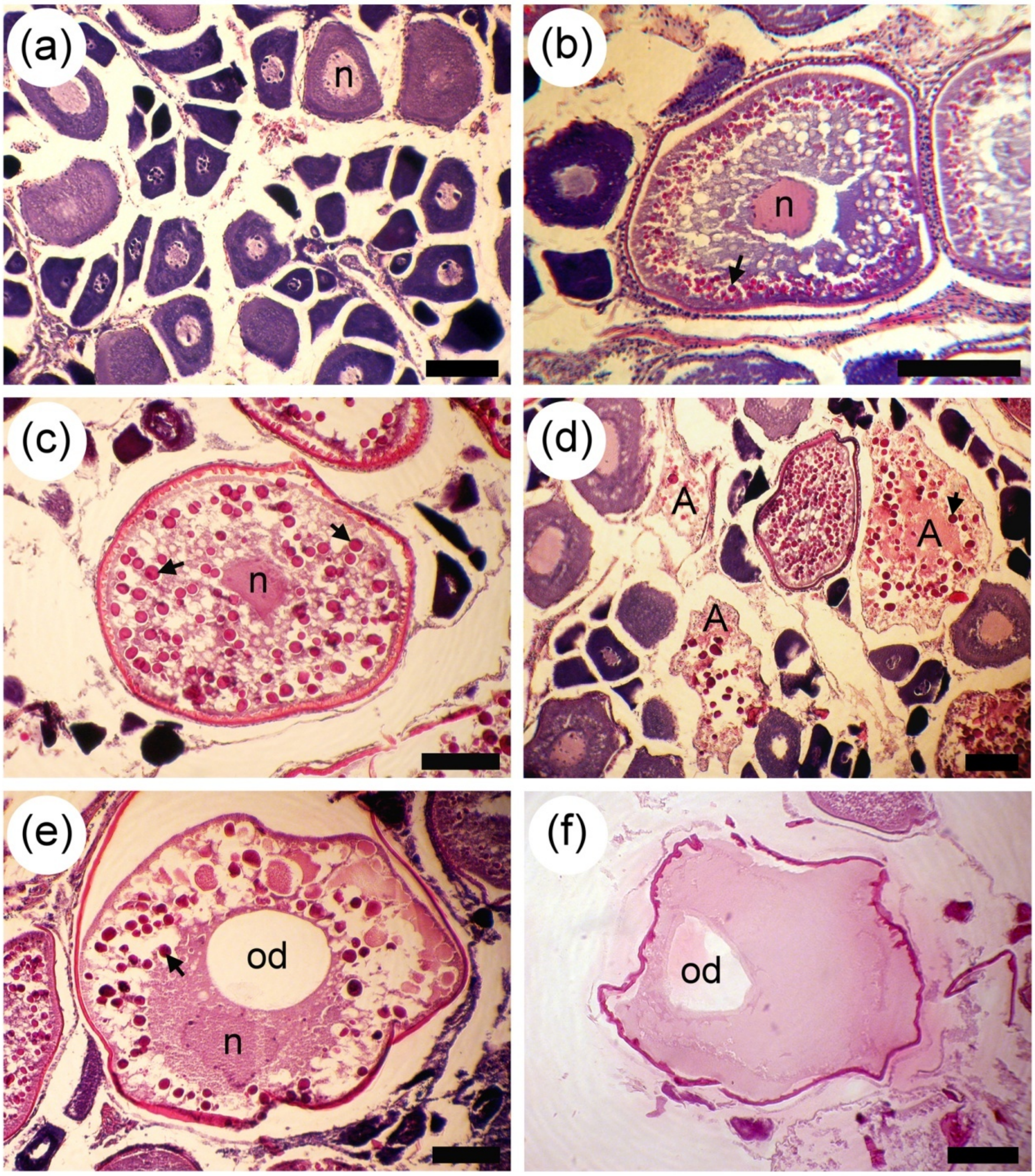

Figure 3.2. Oocytes during oogenesis observed in North Pacific albacore (*Thunnus alalunga*) ovaries. Histological sections were stained with Mayer's hematoxylin and eosin. (a) Unyolked oocytes. (b) Early yolked oocyte. (c) Advanced yolked oocyte. (d) Atretic yolked oocytes (indicated by A). (e) Migratory-nucleus-stage oocyte. (f) Hydrated oocyte. The arrows indicate examples of yolk granules. n, nucleus; od, oil droplet. Scale bar = 100 μm.

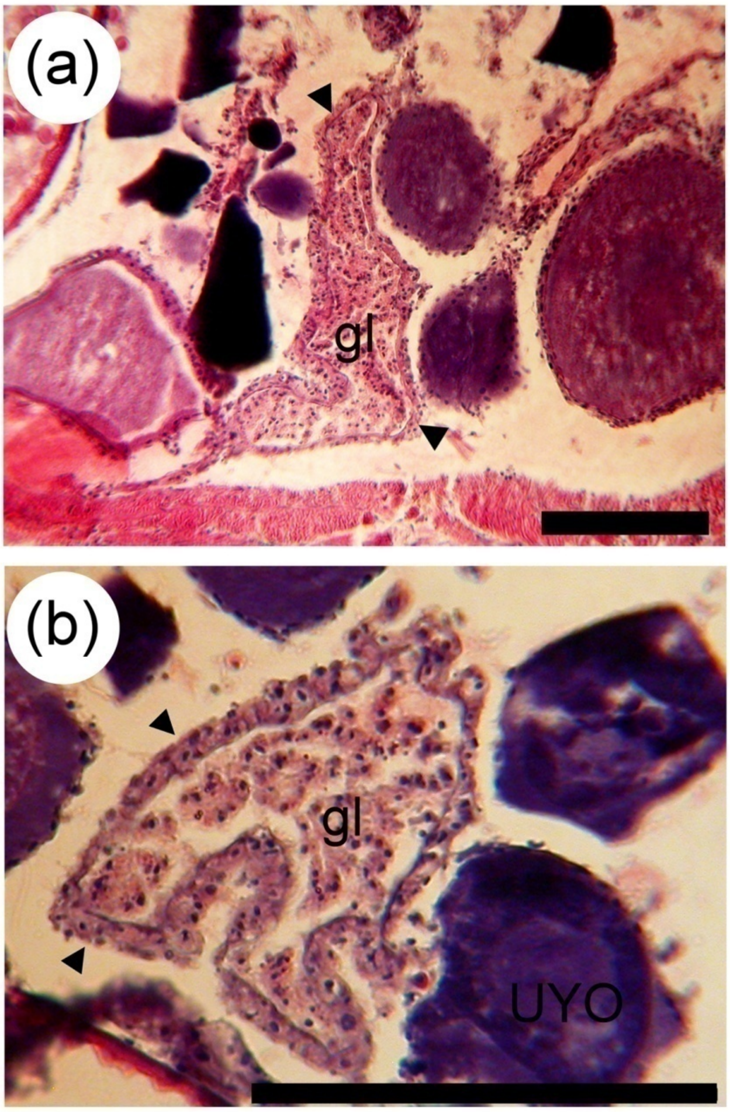

Figure 3.3. Newly formed postovulatory follicles observed in a running-ripe ovary of North Pacific albacore (*Thunnus alalunga*). Histological sections were stained with Mayer's hematoxylin and eosin. Arrowheads [in (a) and (b)] indicate the thecal layer. gl, granulosa layer; UYO, unyolked oocyte. Scale bar = 100 µm.

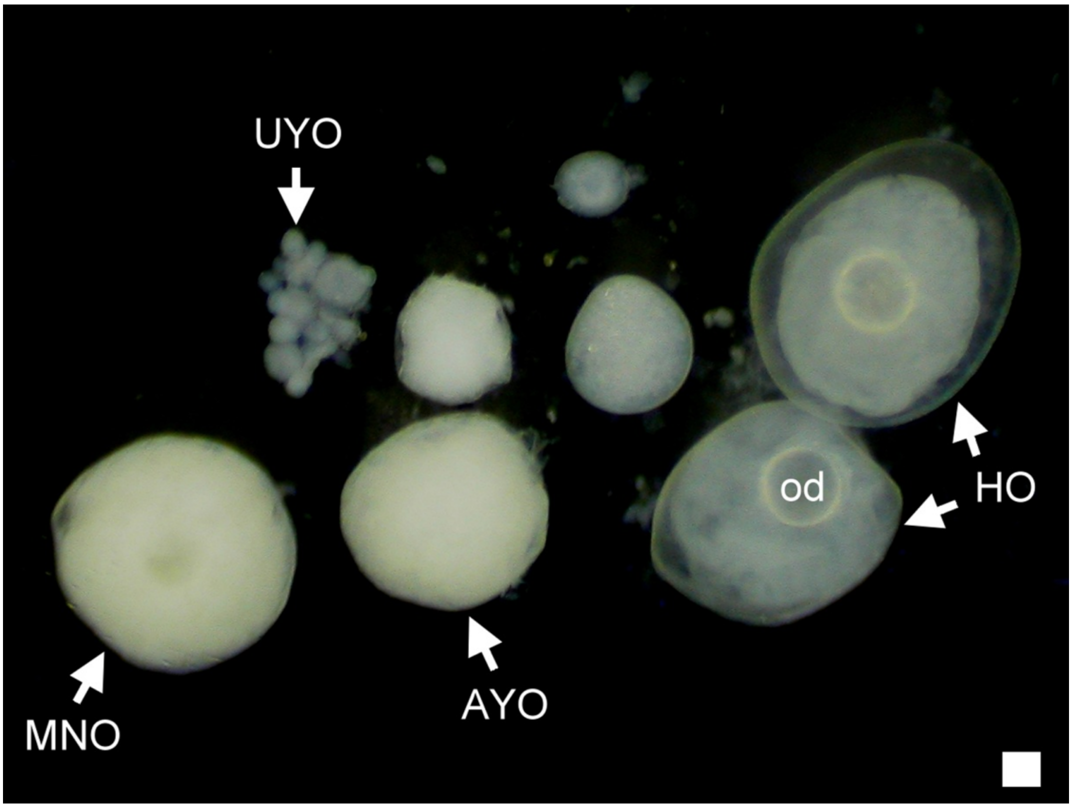

Figure 3.4. A microscopic image showing the external appearances of oocytes from North Pacific albacore (*Thunnus alalunga*) ovaries. UYO, unyolked oocytes; MNO, migratory nucleus oocyte; AYO, advanced yolked oocyte; HO, hydrated oocyte; od, oil droplet. Scale bar = 0.1 mm.

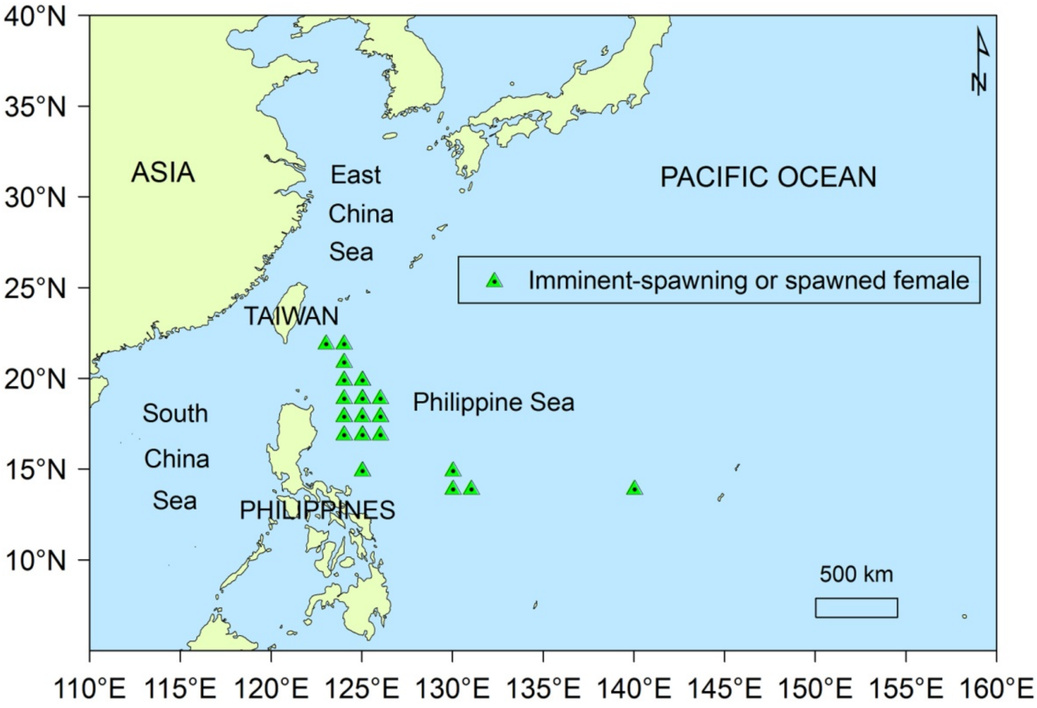

Figure 3.5. The locations of imminent-spawning or spawned female North Pacific albacore (*Thunnus alalunga*) that possessed at least one of the following types of oocytes or oocyte remnants: migratory nucleus oocytes, hydrated oocytes, or postovulatory follicles.

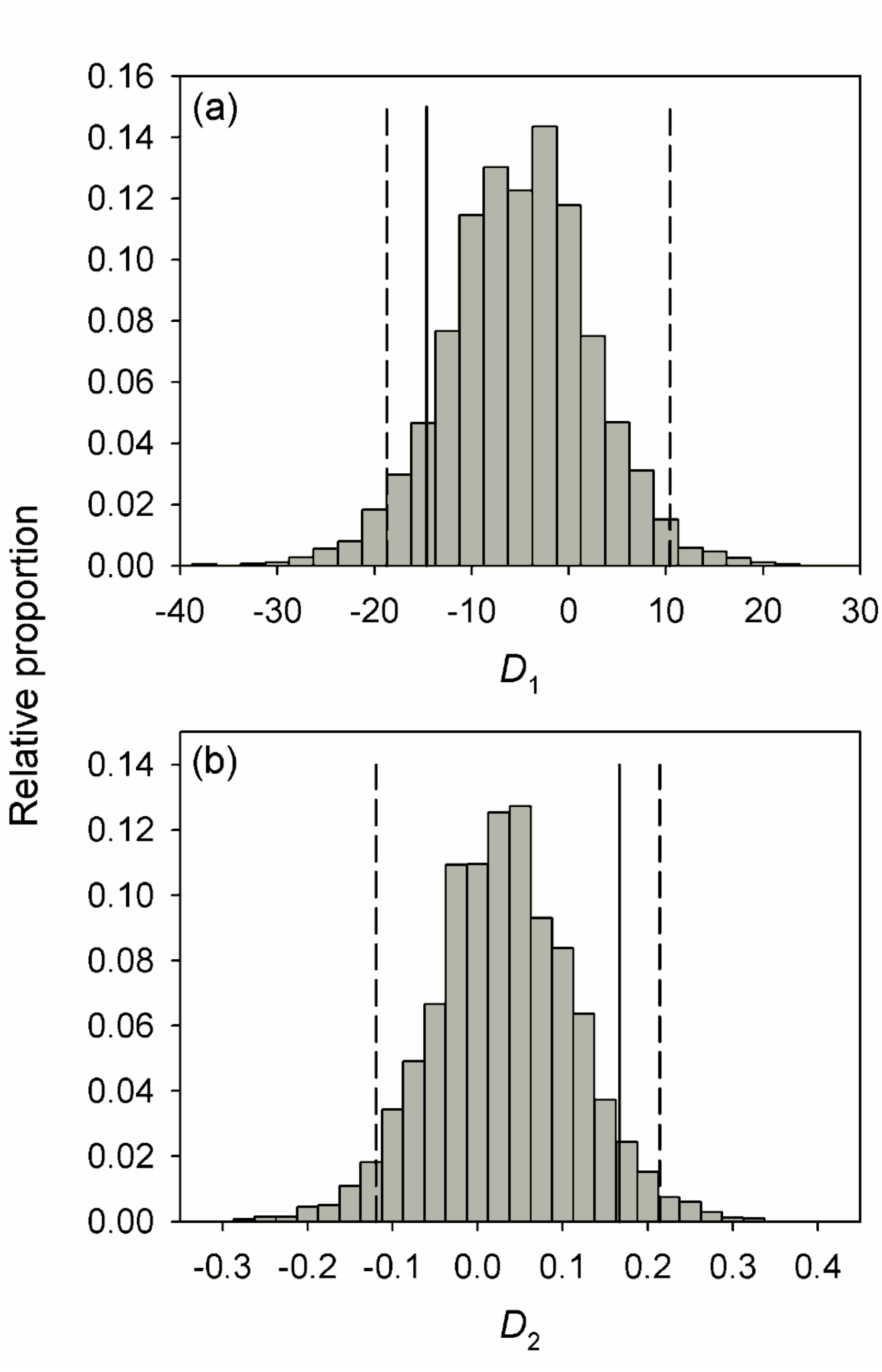

Figure 3.6. Histogram plots showing the results of the randomization test (n = 5 000) for comparing the sex-specific maturity ogives of North Pacific albacore (*Thunnus alalunga*). Both in (a) and in (b), the dashed line indicates the critical points at the 5% level of significance, and the solid line indicates the value of the parameter difference between males and females, calculated from the original data. The variables D_1 and D_2 are parameter differences (i.e., $D_1 = \beta_{0\mathrm{F}} - \beta_{0\mathrm{M}}$ and $D_2 = \beta_{1\mathrm{F}} - \beta_{1\mathrm{M}}$).

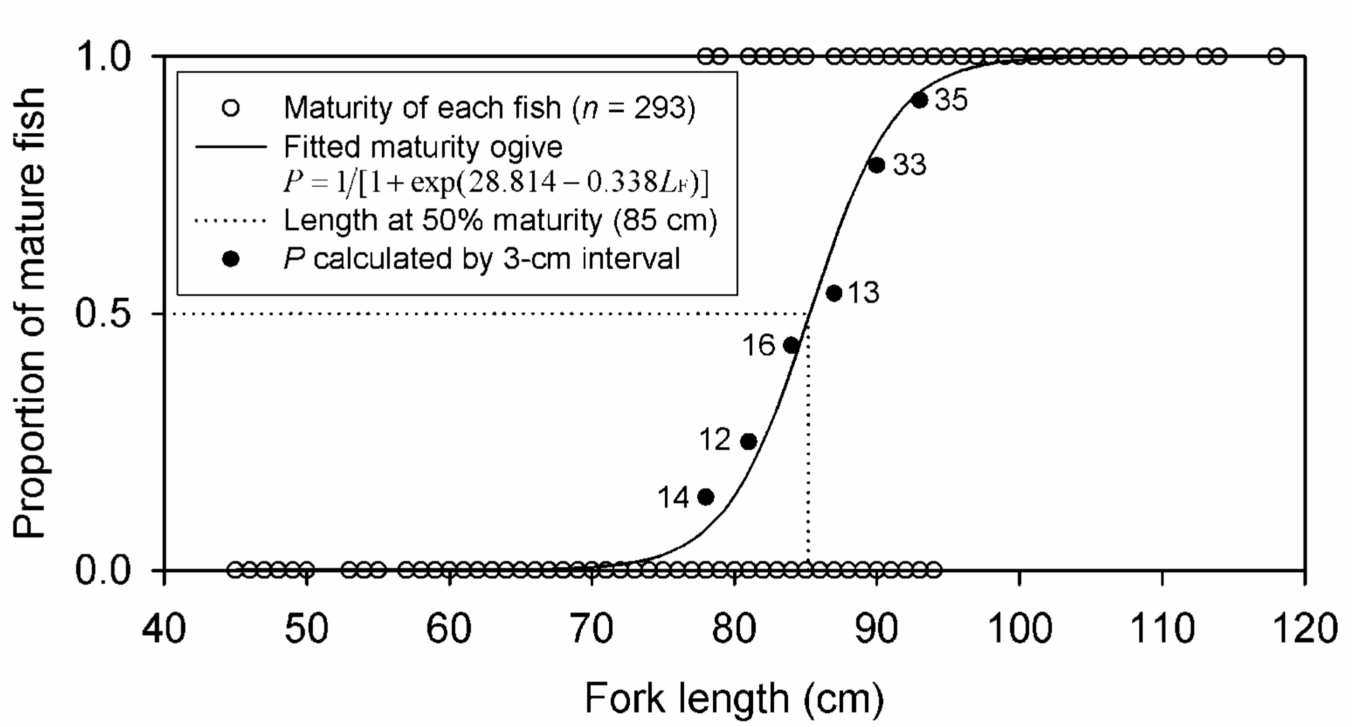

Figure 3.7. The estimated length-maturity ogive for North Pacific albacore (*Thunnus alalunga*) using sex-pooled data. The results of the Hosmer and Lemeshow goodness-of-fit test were as follows: $\chi^2(8) = 1.21$, $p = .99$. For comparison, the proportions of mature fish calculated using the original data divided into 3-cm intervals are shown in solid circles. The number close to each solid circle indicates the sample size. P, proportion of mature fish; L_F, fork length.

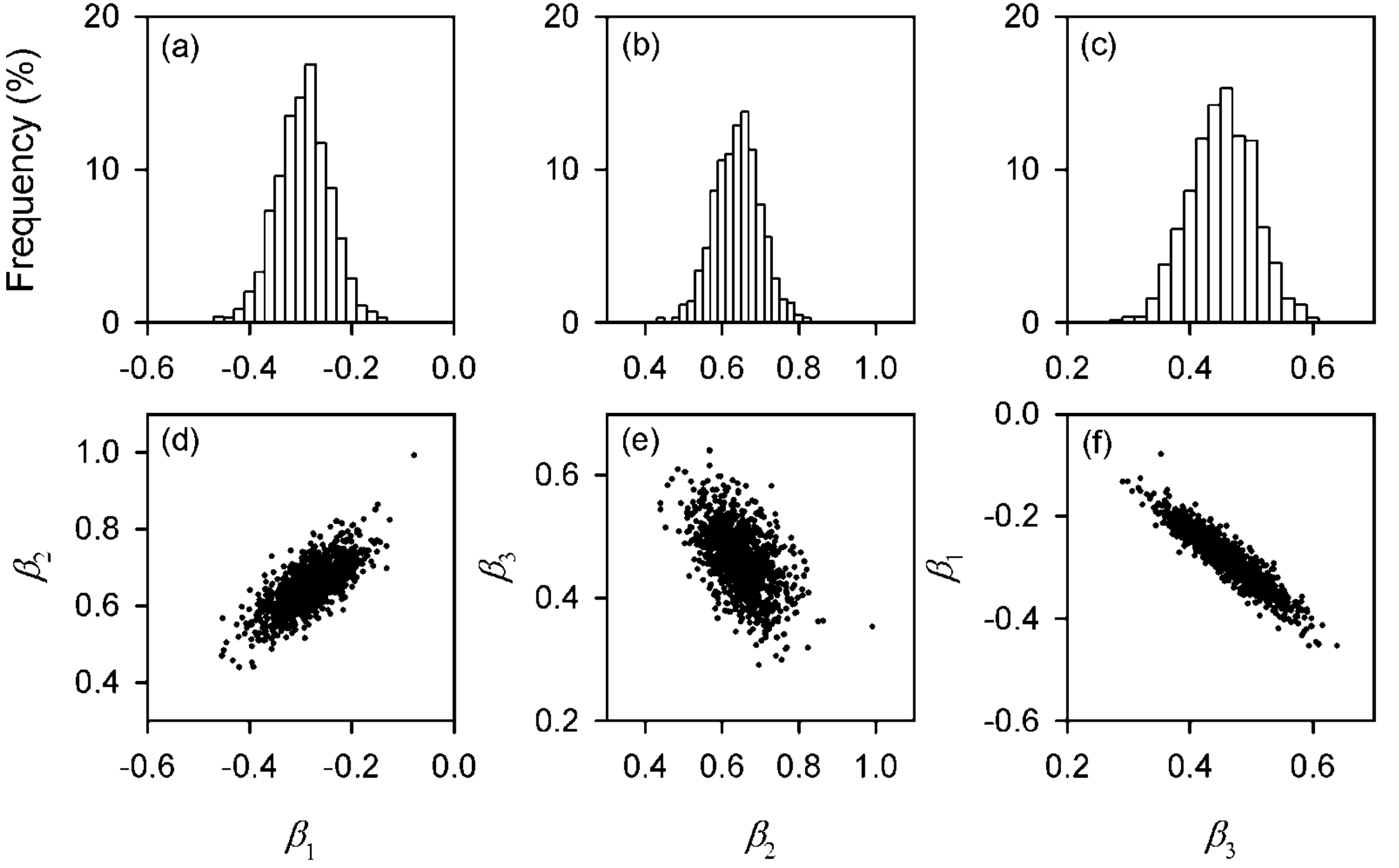

Figure 4.1. Results of bootstrapping (1 000 replicates) for the parameters of a modified Pauly equation (see also Table 4.2). The modified Pauly equation is $\log_{10}(M) = \beta_1 \log_{10}(L_\infty) + \beta_2 \log_{10}(K) + \beta_3 \log_{10}(T)$, where L_∞ = the asymptotic length in the von Bertalanffy growth model, K = the growth coefficient in the von Bertalanffy growth model, and T = seawater temperature (°C).

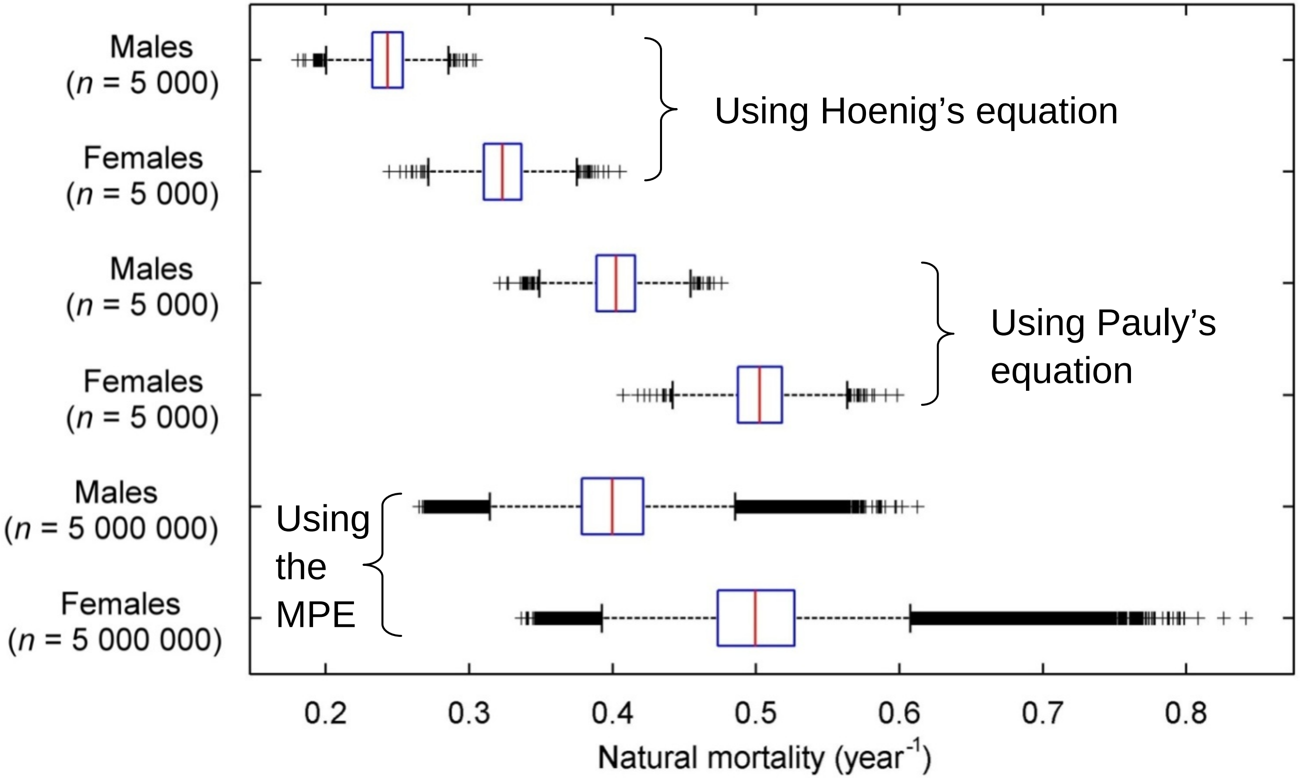

Figure 4.2. Box plots for the natural mortality estimates obtained with the three equations (Hoenig's, Pauly's, and modified Pauly equations) using the bootstrap von Bertalanffy growth parameters (5 000 sets for each sex) presented in Chapter 2. The bootstrap parameters (1 000 sets) of the modified Pauly equation (MPE) are shown in Fig. 4.1 and Table 4.2. In the natural-mortality estimation, the seawater temperature used in the Pauly and modified Pauly equations is 17.5 °C; the maximum fish ages used in Hoenig's equation are estimated with Taylor's equation (Taylor, 1958). Whiskers (error bars) in each box plot indicate 1.5 times the interquartile range.

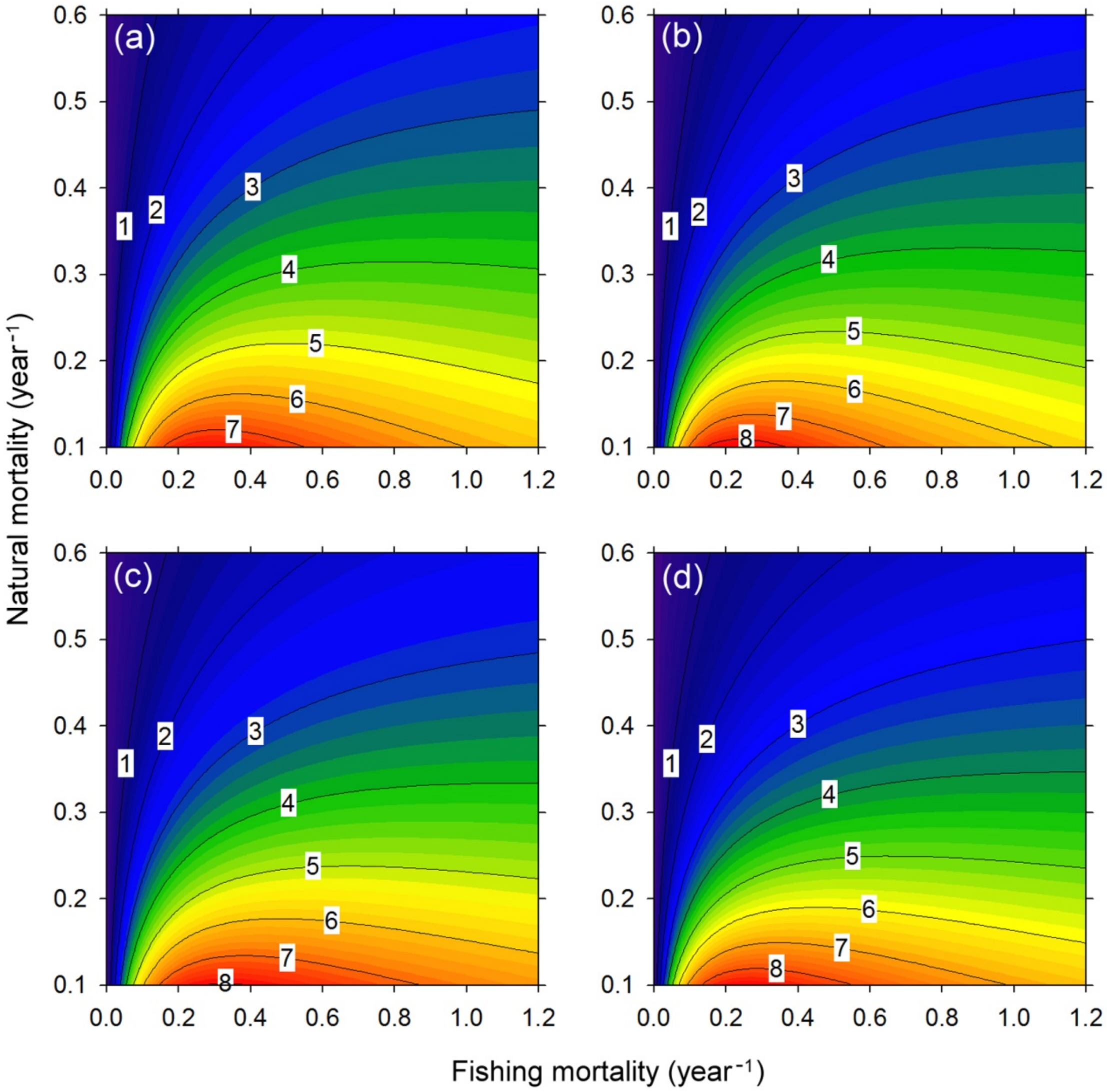

Figure 4.3. Isopleths of the yield-per-recruit values obtained by simulating combinations of natural and fishing mortality rates for North Pacific albacore (*Thunnus alalunga*). (a) Females with Model Scenario 1. (b) Males with Model Scenario 1. (c) Females with Model Scenario 2. (d) Males with Model Scenario 2.

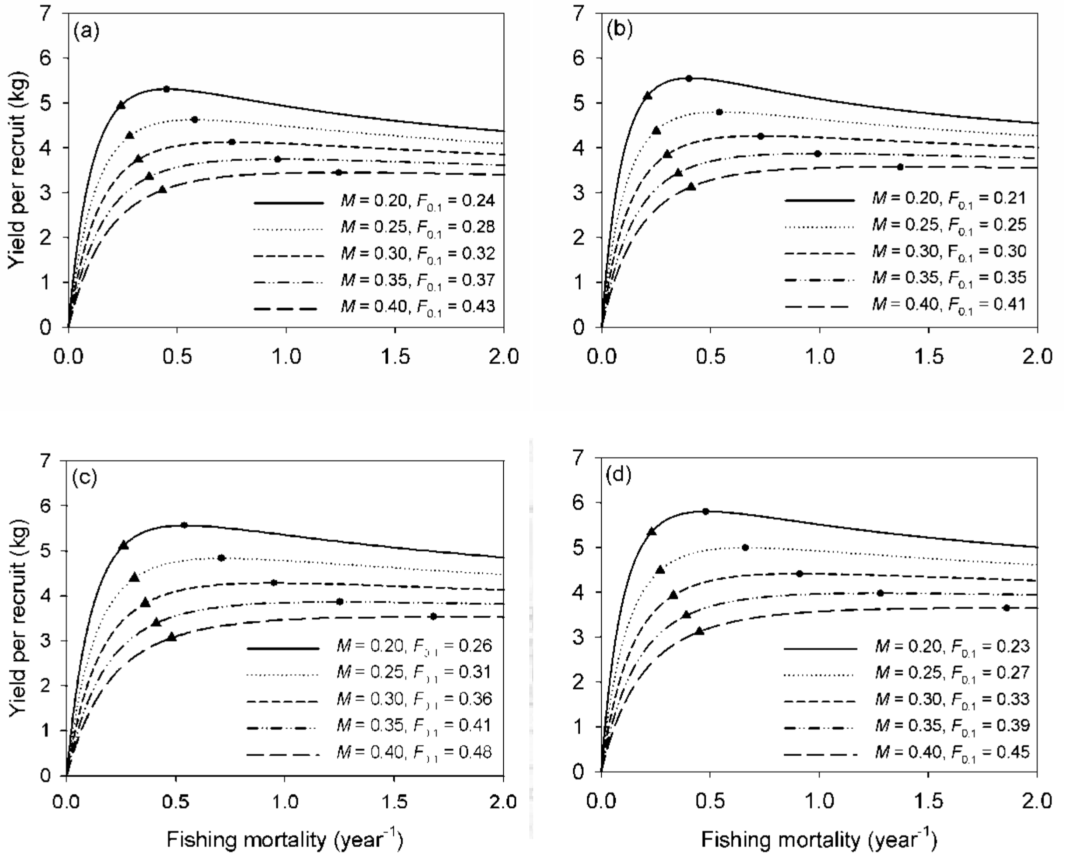

Figure 4.4. Curves for the yield-per-recruit values obtained by simulations using fixed values (0.2, 0.25, 0.3, 0.35, and 0.4) for the instantaneous rate of natural mortality (M, year^{-1}) for North Pacific albacore (*Thunnus alalunga*). (a) Female data with Model Scenario 1. (b) Male data with Model Scenario 1. (c) Female data with Model Scenario 2. (d) Male data with Model Scenario 2. The $F_{\max}$ values estimated are indicated by filled circles, and the $F_{0.1}$ values estimated are shown by filled triangles.

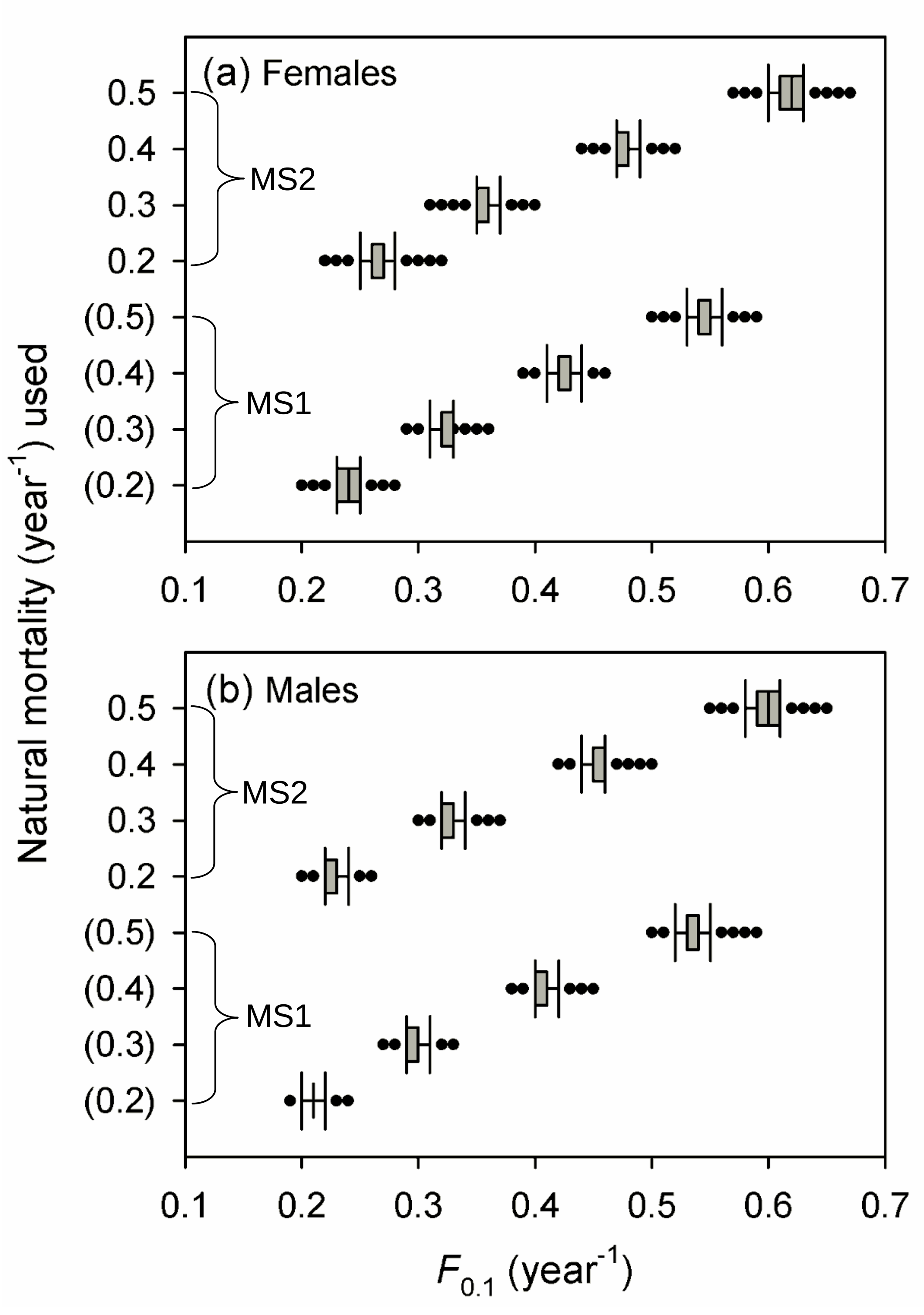

Figure 4.5. Box plots for the $F_{0.1}$ values estimated by 5 000 sets of bootstrap von Bertalanffy growth parameters and 50 sets of bootstrap length-weight parameters in the yield-per-recruit analyses of North Pacific albacore (*Thunnus alalunga*). Each dataset has 250 000 values. Whiskers (error bars) in each box plot indicate the 10th and 90th percentiles. MS1, Model Scenario 1; MS2, Model Scenario 2.

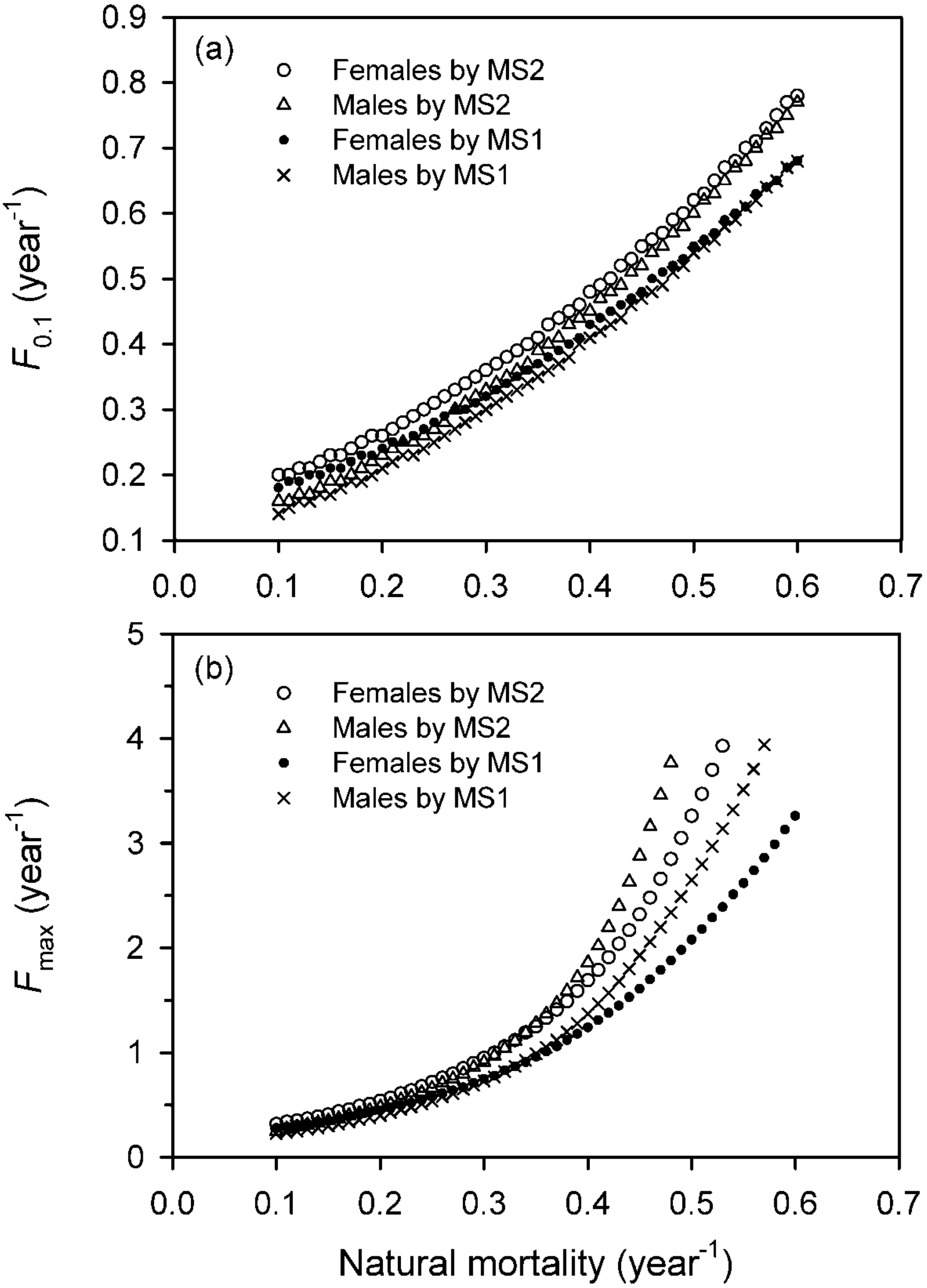

Figure 4.6. Scatter plots for the relationship between the biological reference point ($F_{0.1}$ or $F_{\max}$) and instantaneous rate of natural mortality (*M*) for North Pacific albacore (*Thunnus alalunga*). The degree 3 polynomials estimated are presented in Table 4.5. (a) $F_{0.1}$; (b) $F_{\max}$. MS2, Model Scenario 2; MS1, Model Scenario 1.

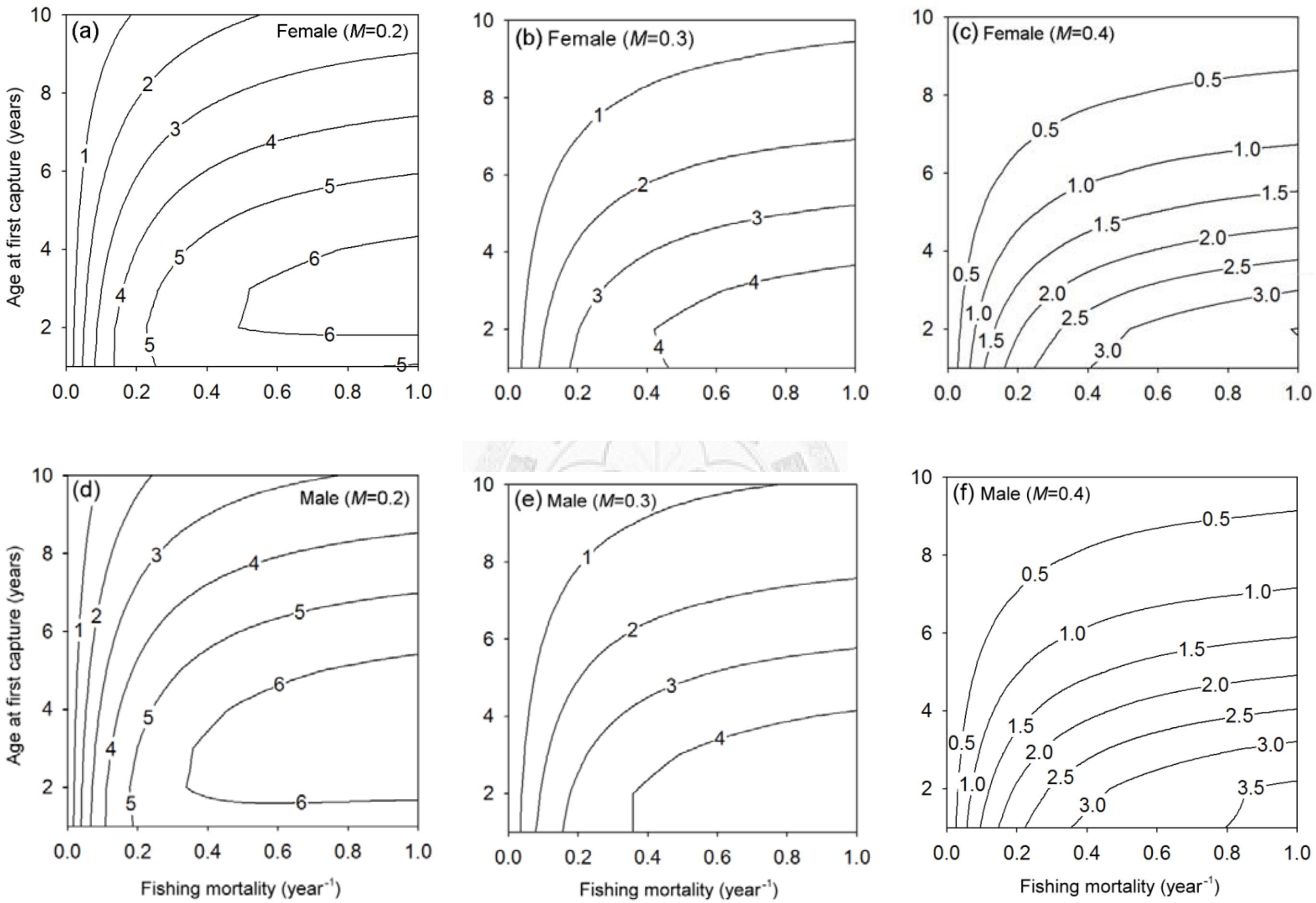

Figure 4.7. Isopleths of the yield-per-recruit values obtained by Model Scenario 1 for North Pacific albacore (*Thunnus alalunga*) for assessing the optimal age at first capture. *M*, instantaneous rate of natural mortality (in year^{-1}).

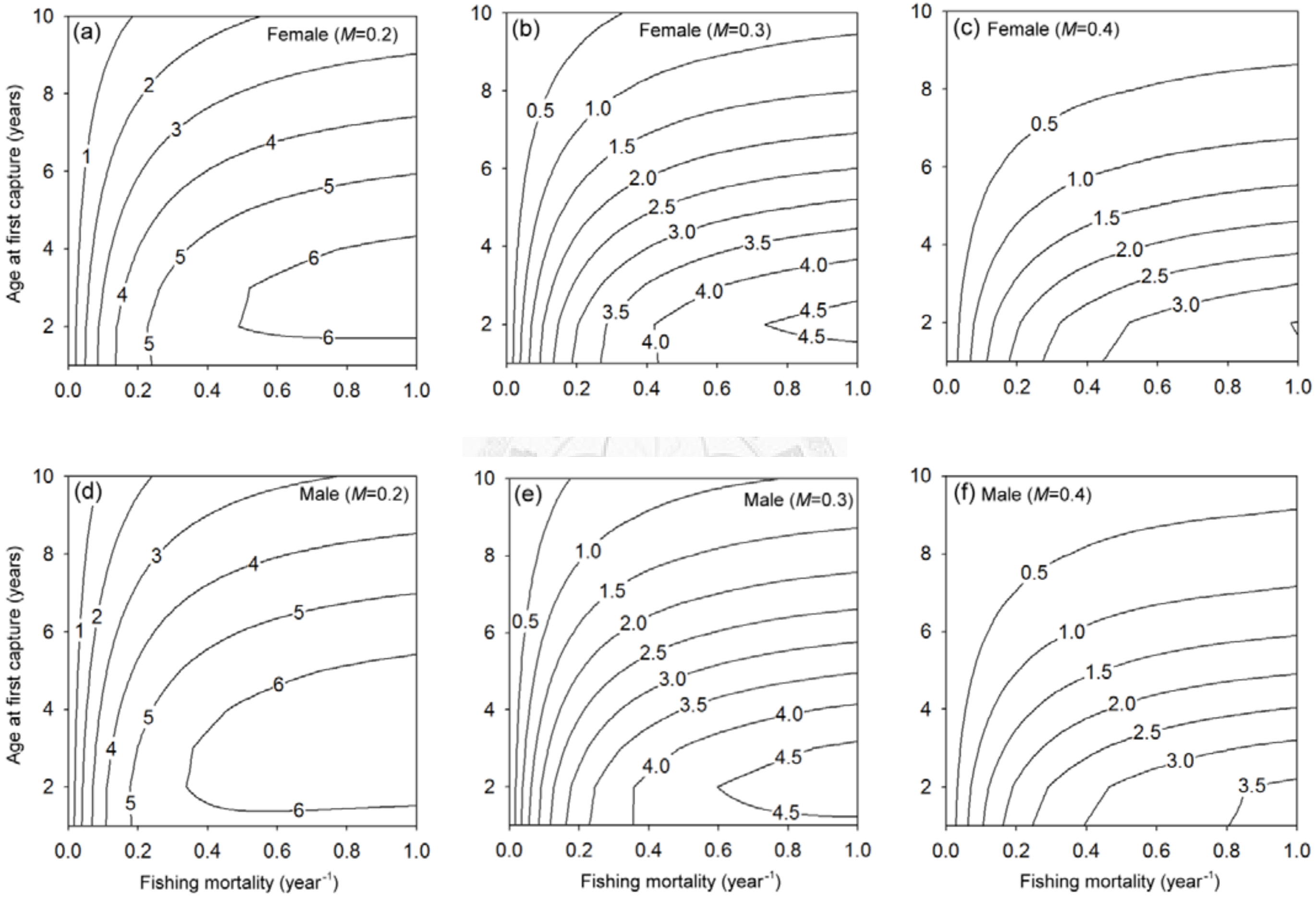

Figure 4.8. Isopleths of the yield-per-recruit values obtained by Model Scenario 2 for North Pacific albacore (*Thunnus alalunga*) for assessing the optimal age at first capture. M, instantaneous rate of natural mortality (in year^{-1}).

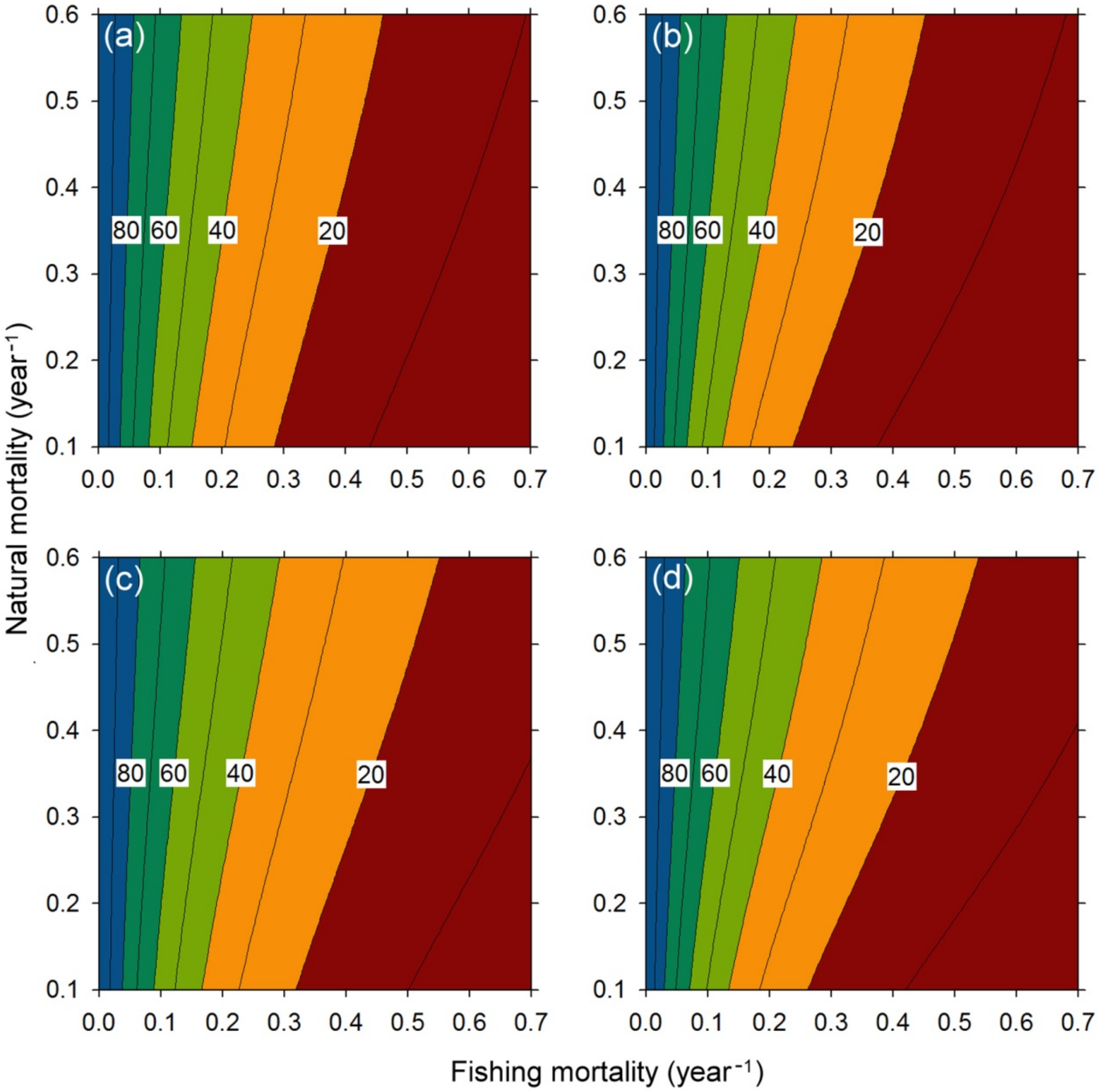

Figure 4.9. Isopleths of the spawning-potential-ratio values obtained by simulations with combinations of natural and fishing mortality rates for North Pacific albacore (*Thunnus alalunga*). (a) Female data using Model Scenario 1. (b) Male data using Model Scenario 1. (c) Female data using Model Scenario 2. (d) Male data using Model Scenario 2.

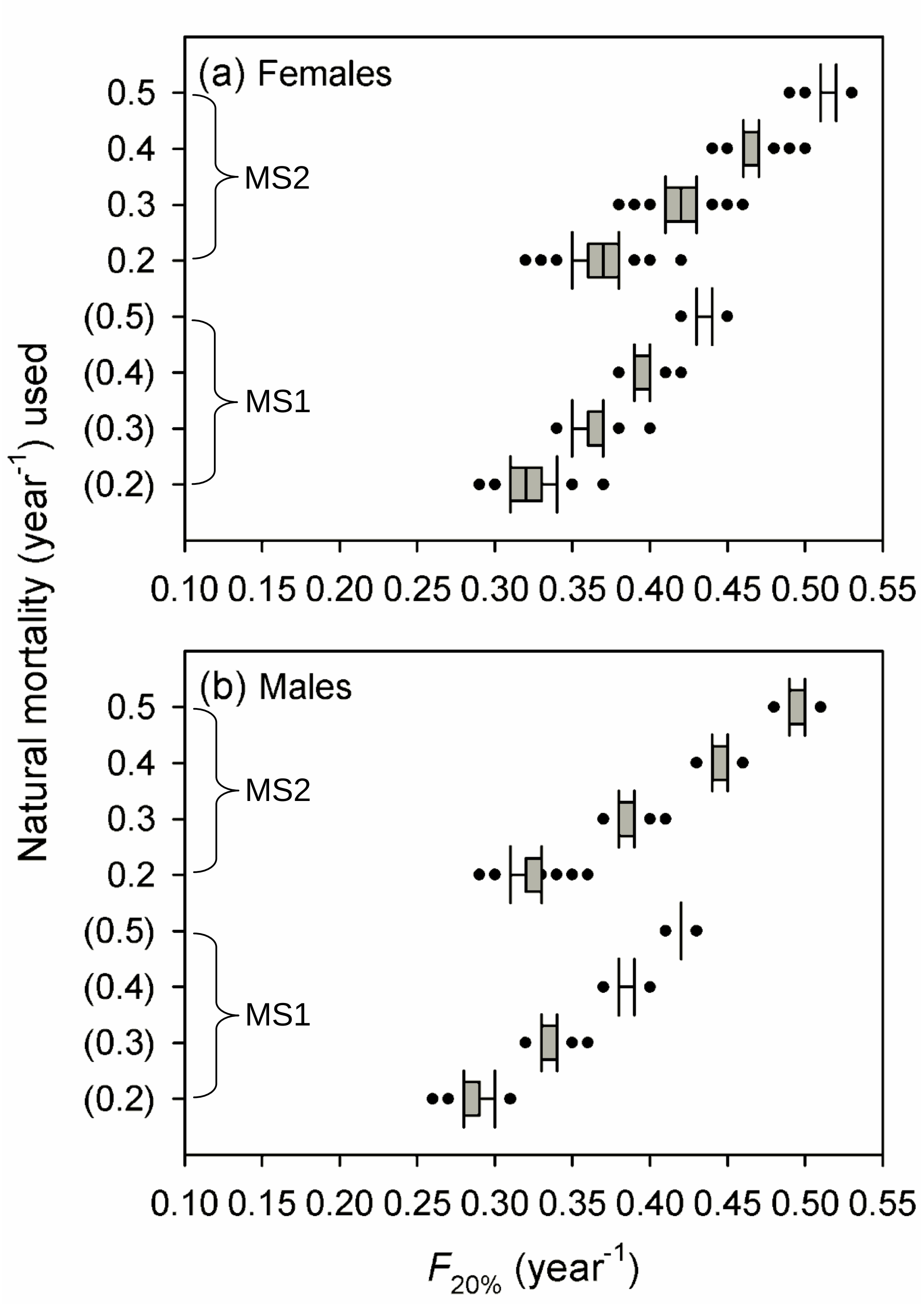

Figure 4.10. Box plots for the $F_{20\%}$ values estimated by 5 000 sets of bootstrap von Bertalanffy growth parameters and 50 sets of bootstrap length-weight parameters in the analysis of spawning potential ratios for North Pacific albacore (*Thunnus alalunga*). Each dataset has 250 000 values. Whiskers (error bars) in each box plot indicate the 10th and 90th percentiles. MS1, Model Scenario 1; MS2, Model Scenario 2.

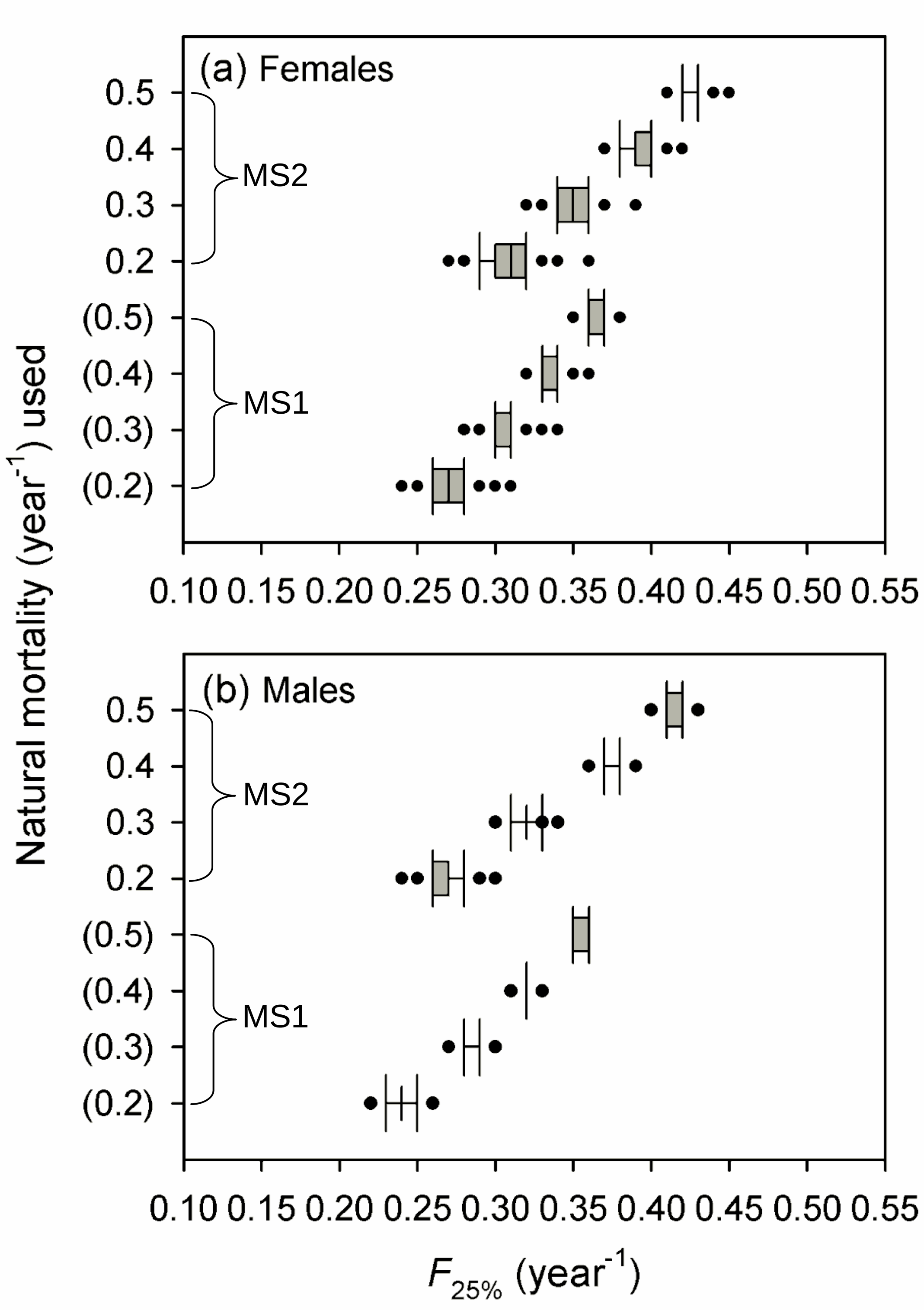

Figure 4.11. Box plots for the $F_{25\%}$ values estimated by 5 000 sets of bootstrap von Bertalanffy growth parameters and 50 sets of bootstrap length-weight parameters in the analysis of spawning potential ratios for North Pacific albacore (*Thunnus alalunga*). Each dataset has 250 000 values. Whiskers (error bars) in each box plot indicate the 10th and 90th percentiles. MS1, Model Scenario 1; MS2, Model Scenario 2.

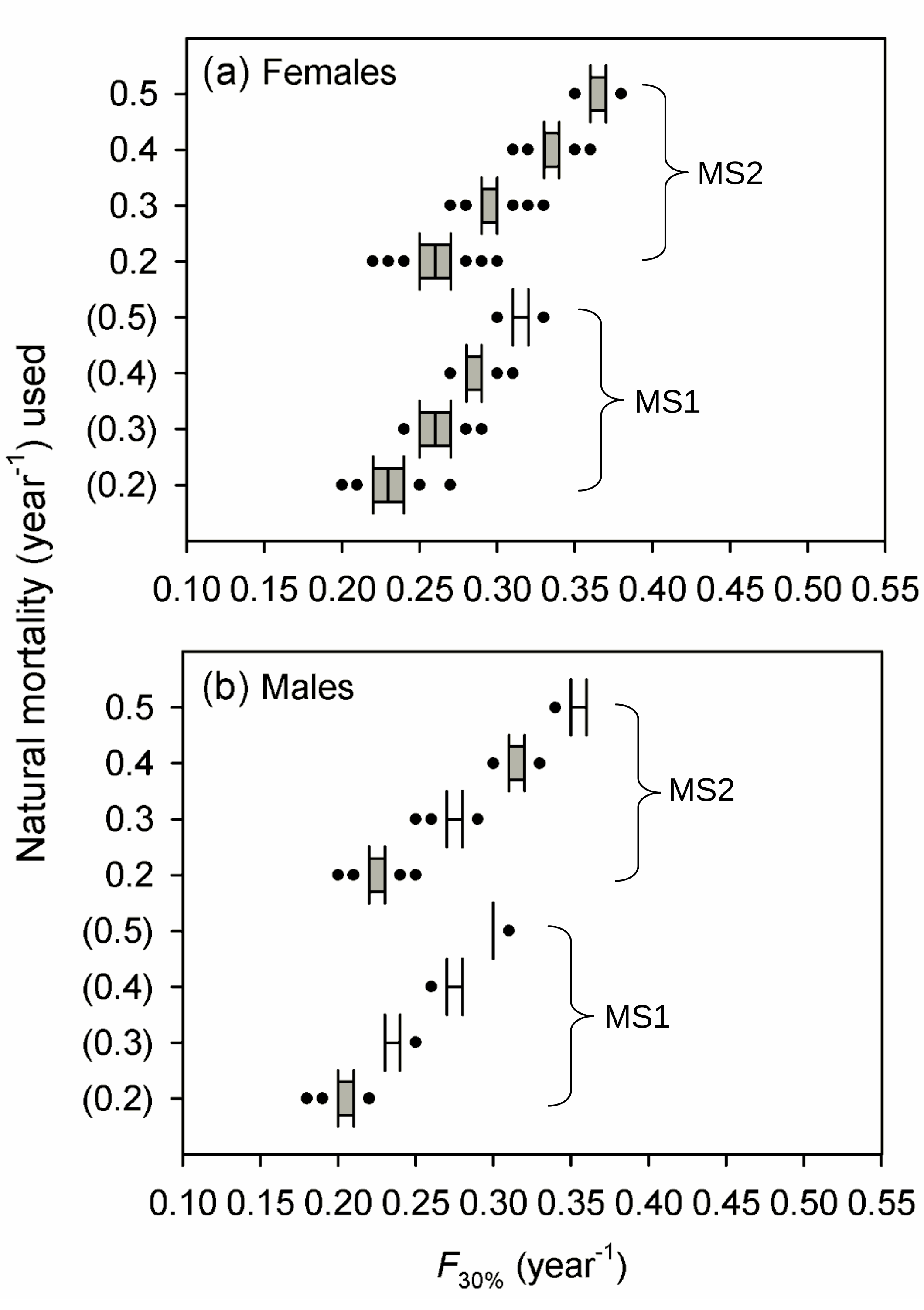

Figure 4.12. Box plots for the $F_{30\%}$ values estimated by 5 000 sets of bootstrap von Bertalanffy growth parameters and 50 sets of bootstrap length-weight parameters in the analysis of spawning potential ratios for North Pacific albacore (*Thunnus alalunga*). Each dataset has 250 000 values. Whiskers (error bars) in each box plot indicate the 10th and 90th percentiles. MS1, Model Scenario 1; MS2, Model Scenario 2.

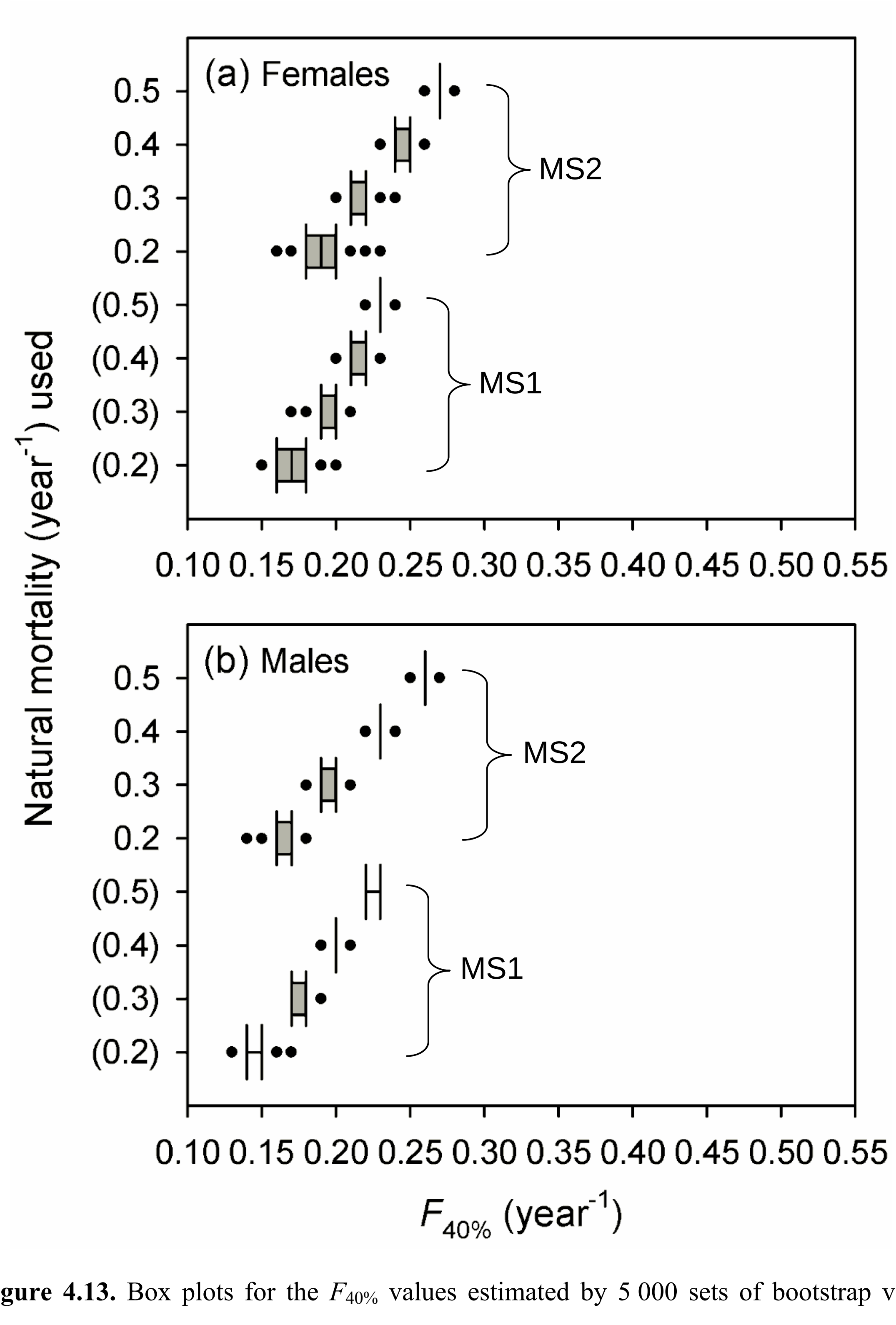

Figure 4.13. Box plots for the $F_{40\%}$ values estimated by 5 000 sets of bootstrap von Bertalanffy growth parameters and 50 sets of bootstrap length-weight parameters in the analysis of spawning potential ratios for North Pacific albacore (*Thunnus alalunga*). Each dataset has 250 000 values. Whiskers (error bars) in each box plot indicate the 10th and 90th percentiles. MS1, Model Scenario 1; MS2, Model Scenario 2.

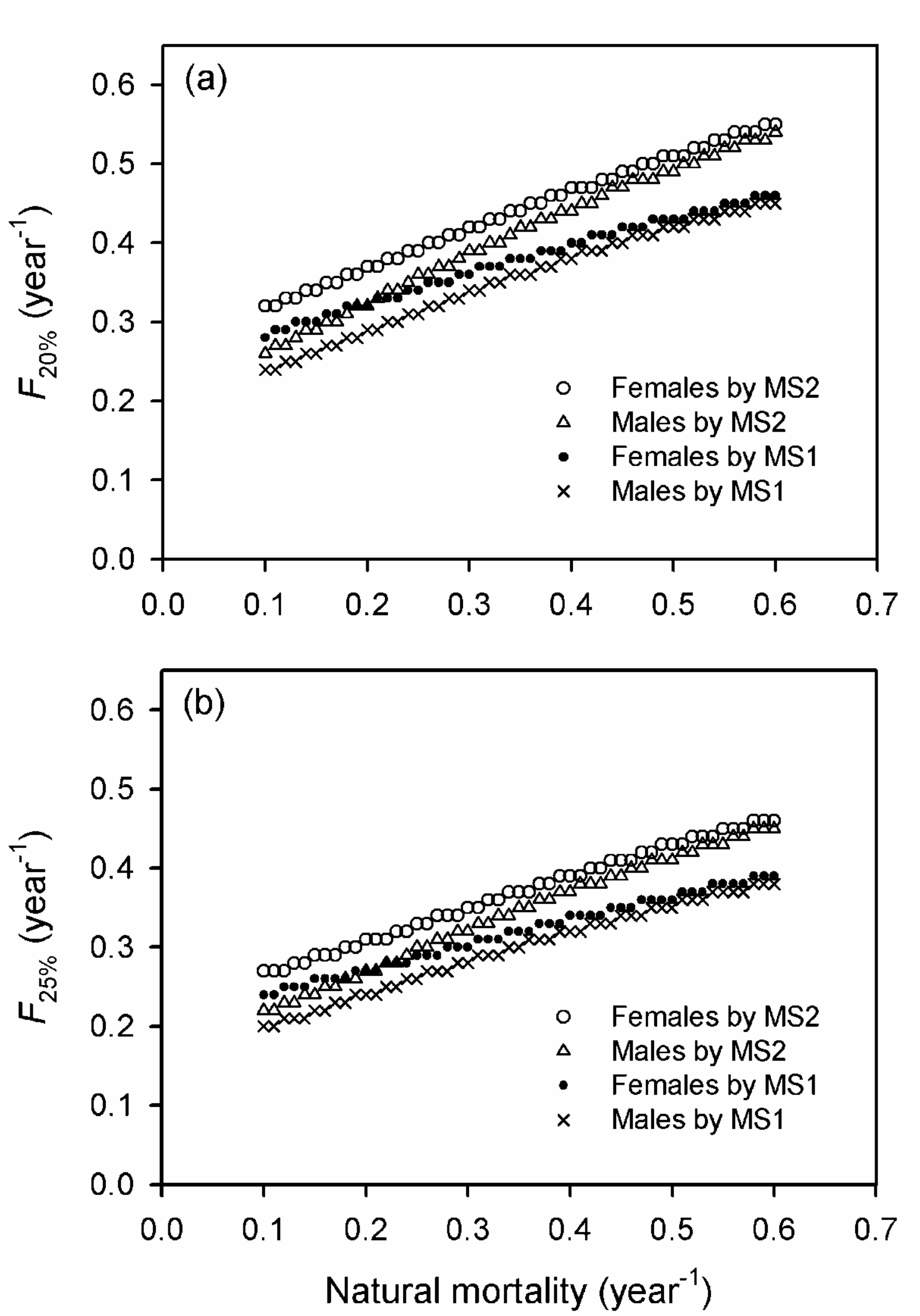

Figure 4.14. Scatter plots for the relationship between the biological reference point ($F_{20\%}$ or $F_{25\%}$) and the instantaneous rate of natural mortality (M, ranging between 0.1 and 0.6 with an increment of 0.01) for North Pacific albacore (*Thunnus alalunga*). The degree 3 polynomials estimated are presented in Table 4.5. (a) $F_{20\%}$; (b) $F_{25\%}$. MS2, Model Scenario 2; MS1, Model Scenario 1.

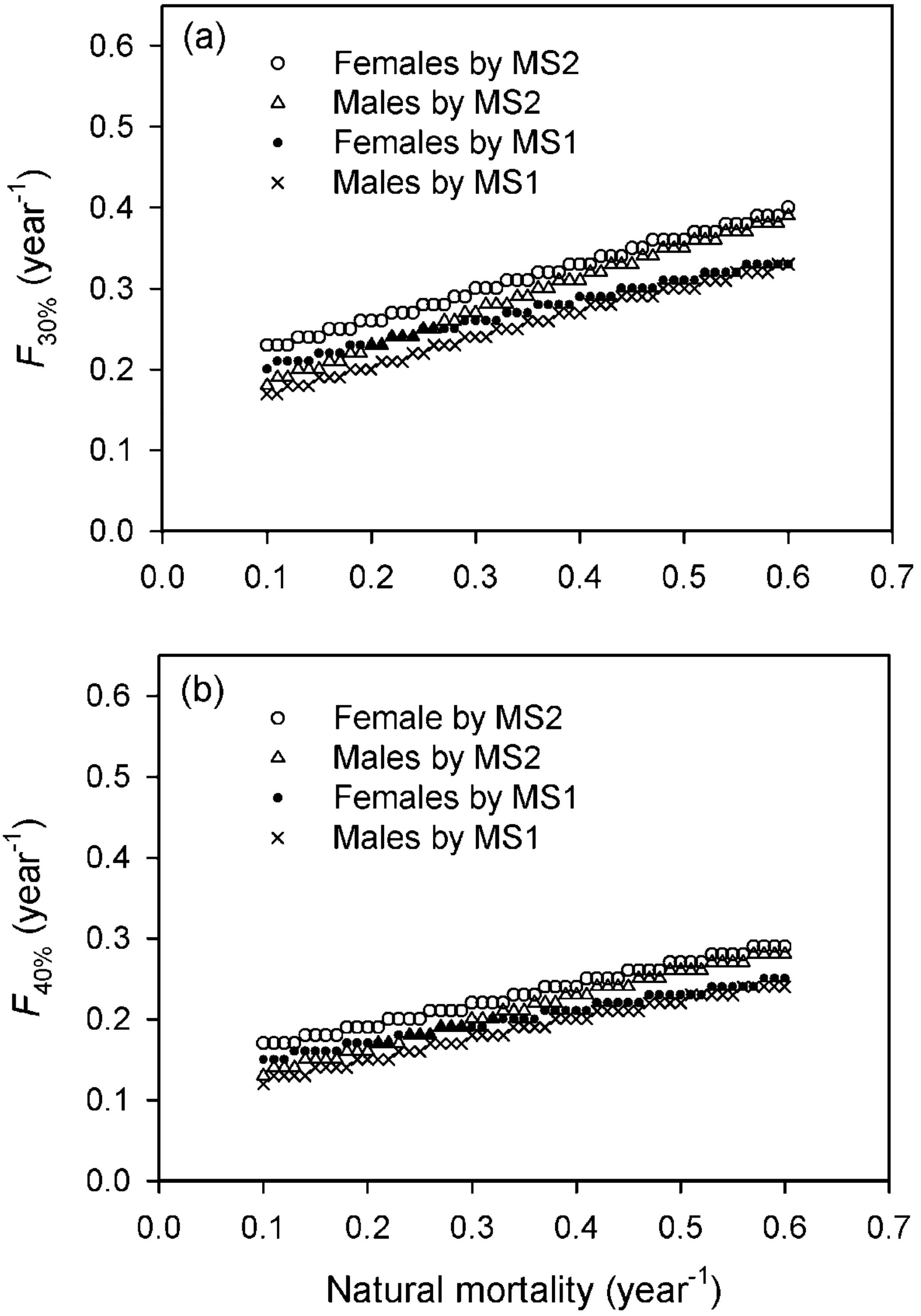

Figure 4.15. Scatter plots for the relationship between the biological reference point ($F_{30\%}$ or $F_{40\%}$) and the instantaneous rate of natural mortality (*M*, ranging between 0.1 and 0.6 with an increment of 0.01) for North Pacific albacore (*Thunnus alalunga*). The degree 3 polynomials estimated are presented in Table 4.5. (a) $F_{30\%}$; (b) $F_{40\%}$. MS2, Model Scenario 2; MS1, Model Scenario 1.

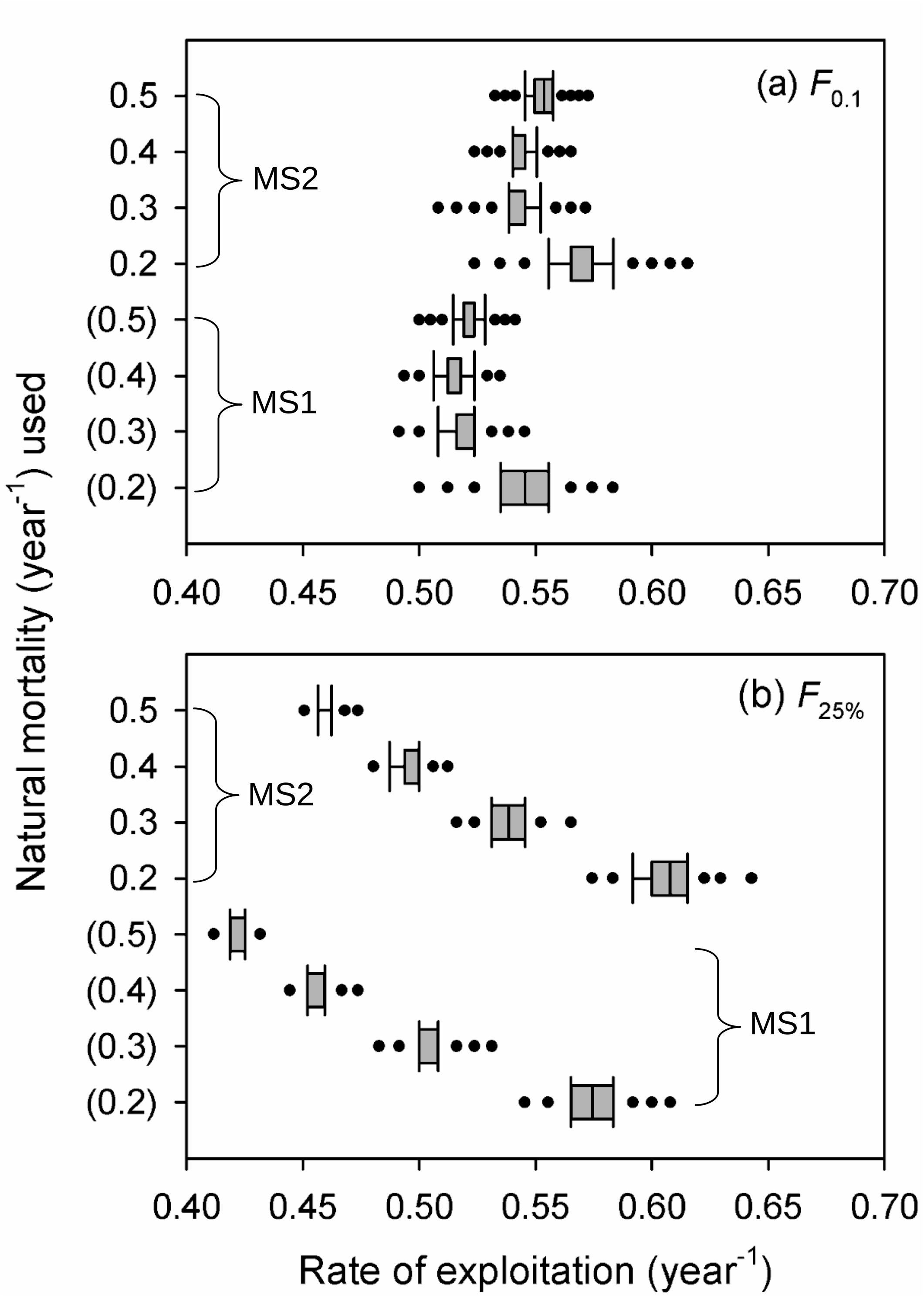

Figure 4.16. Box plots showing the rates of exploitation calculated using the $F_{0.1}$ and $F_{25\%}$ estimates obtained with bootstrap von Bertalanffy growth parameters (5 000 sets) and length-weight parameters (50 sets) for female North Pacific albacore (*Thunnus alalunga*). Each dataset has 250 000 values. Whiskers (error bars) in each box plot indicate the 10th and 90th percentiles. MS1, Model Scenario 1; MS2, Model Scenario 2.

Tables

Table 2.1. Size information for the albacore (*Thunnus alalunga*) specimens used in this study by year and sex.

Year	Sex	*n*	L_F (cm)				W (kg)			
			Mean (*SD*)	Median	Min	Max	Mean (*SD*)	Median	Min	Max
2001	F	15	86.0 (4.2)	86.0	79	94	14.3 (1.9)	14.8	11.0	18.8
	M	18	87.2 (5.4)	87.5	78	96	14.8 (2.5)	15.4	10.8	19.8
2002	F	26	81.7 (8.8)	80.0	67	100	12.4 (3.9)	11.4	7.5	23.0
	M	53	92.8 (12.3)	98.0	72	118	18.1 (6.6)	20.8	8.2	32.2
2003	F	21	92.7 (3.3)	92.0	88	99	16.5 (1.9)	16.4	13.4	20.8
	M	17	96.7 (5.7)	96.0	89	109	18.5 (3.4)	18.5	14.8	26.8
2004	F	17	93.6 (3.9)	94.0	85	101	17.9 (1.9)	17.9	13.4	20.6
	M	13	97.5 (7.3)	98.0	87	111	20.1 (4.3)	20.4	13.8	28.2
2005	F	26	94.1 (3.3)	94.5	89	101	18.3 (2.0)	18.6	15.1	22.6
	M	14	99.2 (5.8)	98.5	90	111	20.9 (3.5)	20.4	15.7	28.9
2006	F	15	58.6 (13.3)	50.0	46	88	4.9 (3.5)	2.8	2.0	14.9
	M	28	69.8 (25.0)	66.0	45	114	9.9 (10.6)	6.1	2.0	33.1
Dec. 2007–Jan. 2008	F	13	60.5 (6.0)	61.0	54	73	4.3 (1.3)	4.4	2.9	6.7
	M	17	62.5 (5.9)	63.0	53	74	4.7 (1.3)	4.9	2.6	7.7

Note. F = female; M = male; *n* = sample size; L_F = fork length; *SD* = standard deviation; Min = minimum; Max = maximum; W = body weight.

Table 2.2 Size information for North Pacific albacore (*Thunnus alalunga*) specimens by area, fishing gear, and sex. These specimens were collected from the central and western North Pacific Ocean from 2001 to 2008 (See also Fig. 2.1 for fishing-operation areas).

Area	Fishing gear	Sex	n	L_F (cm)				W (kg)			
				Mean (*SD*)	Median	Min	Max	Mean (*SD*)	Median	Min	Max
A1	LL	F	74	93.0 (3.9)	93.0	84	101	17.3 (2.4)	17.5	11.7	23.0
		M	62	95.5 (7.9)	97.0	76	111	18.8 (4.3)	19.0	11.0	28.9
A2	PL	F	21	55.7 (7.9)	54.0	46	73	3.5 (1.4)	2.9	2.0	6.7
		M	28	56.4 (9.1)	55.5	45	74	3.8 (1.6)	3.4	2.0	7.7
A3	LL	F	27	80.9 (9.3)	83.0	59	97	12.1 (4.0)	12.9	4.3	20.0
		M	44	83.8 (12.7)	82.5	58	111	13.6 (6.6)	11.9	3.9	31.4
A4	LL	F	11	75.2 (4.8)	75.0	67	83	9.9 (1.7)	9.6	7.5	13.5
		M	19	96.3 (11.1)	100.0	72	106	19.9 (5.4)	21.5	8.2	24.9
A5	LL	F	–	–	–	–	–	–	–	–	–
		M	6	111.8 (2.1)	112.0	109	114	29.1 (2.0)	28.4	27.7	33.1
A6	LL	F	–	–	–	–	–	–	–	–	–
		M	1	118.0	–	–	–	32.2	–	–	–

Note. LL = longline; PL = pole and line; F = female; M = male; n = sample size; L_F = fork length; *SD* = standard deviation; Min = minimum; Max = maximum; W = body weight.

Table 2.3. Age-length data of the North Pacific albacore (*Thunnus alalunga*) specimens determined by examining annuli in obliquely sectioned sagittal otoliths.

Age class (years)	Sex	n	L_F (cm) Mean (*SE*)	Median	Min	Max
1.25–1.75	F	14	52.3 (1.4)	52.0	46	63
	M	21	54.7 (1.6)	54.0	45	64
2.25–2.75	F	8	65.0 (1.6)	64.5	59	73
	M	6	67.2 (2.0)	66.5	61	74
3.25–3.75	F	15	75.7 (1.3)	75.0	67	84
	M	20	76.4 (1.4)	77.0	66	91
4.25–4.75	F	26	85.9 (1.0)	87.5	73	91
	M	21	83.7 (1.2)	83.0	72	93
5.25–5.75	F	23	90.6 (1.1)	92.0	73	96
	M	25	91.6 (1.0)	92.0	80	101
6.25–6.75	F	19	92.2 (0.9)	92.0	83	99
	M	12	98.6 (1.1)	98.5	92	104
7.25–7.75	F	14	95.7 (0.5)	95.5	92	99
	M	15	101.1 (0.9)	101.0	95	107
8.25–8.75	F	3	99.3 (0.9)	99.0	98	101
	M	4	103.0 (1.7)	104.0	98	106
9.25–9.75	F	3	99.0 (1.5)	100.0	96	101
	M	6	103.5 (0.8)	104.0	100	106
10.25–10.75	F	1	100.0 (–)	–	–	–
	M	10	107.8 (1.7)	109.0	99	114
11.25–11.75	F	–	–	–	–	–
	M	5	108.2 (1.7)	111.0	103	111
12.25–12.75	F	–	–	–	–	–
	M	–	–	–	–	–
13.25–13.75	F	–	–	–	–	–
	M	2	114.0 (4.0)	114.0	110	118
14.25–14.75	F	–	–	–	–	–
	M	1	106.0 (–)	–	–	–

Note. F = female; M = male; n = sample size; L_F = fork length; *SE* = standard error of the mean; Min = minimum length; Max = maximum length.

Table 2.4. Results for the goodness-of-fit and AICc values of growth models for North Pacific albacore (*Thunnus alalunga*).

Model	Sex	R^2	F-test for lack of fit	AICc	Δ_i
von Bertalanffy	F	.92	$F(15, 108) = 1.17, p = .31$.	368.3	4.1
	M	.93	$F(19, 126) = 1.37, p = .15$.	472.8	0
Gompertz	F	.92	$F(15, 108) = 0.94, p = .52$.	364.8	0.6
	M	.92	$F(19, 126) = 1.42, p = .13$.	473.8	1
Richards	F	.92	$F(14, 108) = 0.82, p = .65$.	364.2	0
	M	.93	$F(18, 126) = 1.44, p = .12$.	474.9	2.1

Note. R^2 = coefficient of determination; AICc = the small-sample bias-corrected form of the Akaike information criterion (AIC); $\Delta_i = \text{AICc}_i - \text{AICc}_{\text{min}}$, where AICc_{min} is the minimum value of AICc values within each sex.

Table 2.5. Estimated growth parameters of the three growth models (ordinary von Bertalanffy, Gompertz, and Richards) for North Pacific albacore (*Thunnus alalunga*). The standard error (SE) and confidence intervals (CIs) of each parameter were obtained by bootstrapping (5 000 replicates).

Model	Sex	Parameter	Parameter estimate (*SE*)	95% CIs [2.5%, 97.5%]
von Bertalanffy	F	L_∞ (cm)	103.540 (1.308)	[101.109, 106.230]
		K (year^{-1})	0.340 (0.022)	[0.298, 0.384]
		t_0 (years)	−0.531 (0.115)	[−0.787, −0.331]
	M	L_∞ (cm)	113.997 (1.820)	[110.773, 117.871]
		K (year^{-1})	0.253 (0.017)	[0.218, 0.287]
		t_0 (years)	−1.014 (0.159)	[−1.374, −0.752]
Gompertz	F	L_G (cm)	101.041 (0.991)	[99.107, 102.950]
		K_2 (year^{-1})	0.453 (0.024)	[0.406, 0.501]
		t_2 (years)	0.624 (0.060)	[0.478, 0.724]
	M	L_G (cm)	111.417 (1.461)	[108.904, 114.745]
		K_2 (year^{-1})	0.336 (0.020)	[0.296, 0.374]
		t_2 (years)	0.543 (0.089)	[0.339, 0.694]
Richards	F	L_R (cm)	97.933 (1.592)	[95.168, 101.604]
		K_3 (year^{-1})	0.730 (0.279)	[0.405, 1.345]
		t_3 (years)	2.009 (0.693)	[0.297, 3.112]
		r	2.317 (2.009)	[−0.278, 6.809]
	M	L_R (cm)	114.386 (11.050)	[108.090, 135.608]
		K_3 (year^{-1})	0.243 (0.119)	[0.066, 0.509]
		t_3 (years)	−1.254 (56.262)	[−16.345, 2.268]
		r	−1.116 (1.408)	[−3.271, 2.040]

Note. F = female; M = male.

Table 2.6. Predicted mean values for the fork length (L_F) and body weight (W) of North Pacific albacore (1- to 10-year-old fish; at the beginning of May) based on the growth and length-weight parameters obtained in this study. The three growth models used were the ordinary von Bertalanffy, Gompertz, and Richards models. The growth parameters used for the predictions are presented in Table 2.5. Only the rounded-off data for L_F (cm) and W (kg) are presented.

Growth model	von Bertalanffy				Gompertz				Richards			
Age (years)	Female		Male		Female		Male		Female		Male	
	L_F	W	L_F	W	L_F	W	L_F	W	L_F	W	L_F	W
1	42	1.7	45	2.1	43	1.9	47	2.4	46	2.2	45	2.1
2	60	4.7	61	4.9	59	4.6	60	4.9	58	4.4	61	5.0
3	72	8.2	73	8.4	72	8.1	72	8.1	71	7.7	73	8.4
4	81	11.6	82	11.9	81	11.6	81	11.7	81	11.6	82	11.9
5	88	14.5	89	15.2	88	14.7	89	15.2	89	14.9	89	15.1
6	92	16.8	95	18.1	93	17.0	95	18.3	93	17.2	95	18.1
7	96	18.6	99	20.6	96	18.6	99	20.9	95	18.6	99	20.6
8	98	19.9	102	22.8	98	19.8	103	23.0	97	19.3	102	22.7
9	99	20.9	105	24.5	99	20.5	105	24.6	97	19.7	105	24.5
10	101	21.7	107	25.9	100	21.0	107	25.9	98	19.8	107	25.9

Table 2.7. A list of previous studies that reported von Bertalanffy growth parameters for North Pacific albacore (*Thunnus alalunga*).

Reference	Material	Size range (cm)	n	L_∞ (cm)	K (year^{-1})	t_0 (years)
Uno (1936)	Vertebrae	69–90[‡]	688	104.8	0.431	1.504
Nose et al. (1957)[a]	Scales	83–102[‡]	44	114.4	0.308	0.818
Nose et al. (1957)[b]	Scales	57–97[‡]	48	145.3	0.159	−0.056
Otsu (1960)[c]	Tagging data	60–91[*]	12	118.8	0.250	1.999
Clemens (1961)	Tagging data	54–77[*]	21	135.6	0.17	−1.87
Bell (1962)	Scales	51–94[‡]	324	108.8	0.225	−2.273
Yabuta & Yukinawa (1963)[c]	Scales	48–95[†]	–	146.3	0.150	−0.396
Yang (1970)	Scales	–	74	126.0	0.240	–
Wetherall et al. (1987)[d]	Otoliths	30–90	98	94.1	0.61	0.21
Wetherall et al. (1987)[d]	Tagging data	–	257	136.0	0.18	−0.7
Wetherall et al. (1987)[e]	Otoliths	36–93	127	136.7	0.28	−0.12
Wetherall et al. (1987)[e]	Tagging data	–	264	122.9	0.27	−0.37
Present study (females)[f]	Otoliths	45–101	126	103.5	0.340	−0.53
Present study (males)[f]	Otoliths	46–118	148	114.0	0.253	−1.01

[a] Parameters calculated by Shomura (1966) using 1952–1953 samples.

[b] Parameters calculated by Shomura (1966) using 1953–1954 samples.

[c] Parameters calculated by Shomura (1966).

[d] For north albacore in the authors' paper.

[e] For south albacore in the authors' paper.

[f] The first annulus adjusted to represent 0.75 years.

[‡] Mean observed lengths.

[*] Lengths at release.

[†] Size at the time of ring formation.

Table 2.8. A list of previous studies that reported von Bertalanffy growth parameters for albacore (*Thunnus alalunga*).

Reference	Area	Material	Age range	L_∞ (cm)	K (year^{-1})	t_0 (years)
Yang (1970)	North Atlantic	Scales	1–7	135.0	0.190	0.15[*]
Beardsley (1971)	North Atlantic	Length data	1–10	140.0	0.141	−1.63
Bard & Compean-Jimenez (1980)	North Atlantic	Spines	1–5	124.7	0.228	−0.99
Huang et al. (1990)	Indian Ocean	Scales	1–8	128.1	0.162	−0.90
Lee & Liu (1992)	Indian Ocean	Vertebrae	1–10	163.7	0.102	−2.07
Lee & Yeh (1993)	South Atlantic	Spines	2–13	142.3	0.145	−0.67
Chang et al. (1993)	Indian Ocean	Length data	1–12	147.2	0.133	–
Labelle et al. (1993)	South Pacific	Vertebrae	2–11	121.0	0.134	−1.92
Ortiz de Zárate & C-Parrack (1996)	North Atlantic	Tagging data	0^+–5	108.2	0.306	−1.25
Megalofonou (2000)	Mediterranean	Spines	1–9	94.7	0.258	−1.35
Santiago & Arrizabalaga (2005)	North Atlantic	Spines & tagging data	1–9	122.2	0.209	−1.34
Shih (2008)	Indian Ocean	Length data	1–9	144.0	0.157	–
Present study (females)	North Pacific	Otoliths	1–10	103.5	0.340	−0.53
Present study (males)	North Pacific	Otoliths	1–14	114.0	0.253	−1.01

Note. [*] Parameter calculated by the mean-length-at-age data reported in the author’s paper.

Table 2.9. Parameters of the length-weight functions reported for North Pacific albacore (*Thunnus alalunga*). Other than Uchiyama & Kazama (2003), the length (L_F)-weight (W) relationships presented are expressed as a power function (i.e., $W = a \times L_F{}^{b}$).

Study	North Pacific	Size range (cm)	n	a	b
Partlo (1955a)	Eastern	50–85	–	1.225×10^{-5}	3.13
Clemens (1961)[a]	Eastern	38–100	1073	4.936×10^{-8}	2.99
Suda & Warashina (1961)[b]	Western	–	–	8×10^{-6}	3.2
Suda & Warashina (1961)[c]	Western	–	–	8.2×10^{-6}	3.2
Suda & Warashina (1961)[d]	Western	–	–	9.35×10^{-6}	3.2
Nakamura & Uchiyama (1966)	Central	50–128	200	2.596×10^{-5}	2.9495
Lee et al. (1978)	Western	45–85	344	1.781×10^{-5}	3.053
Uchiyama & Kazama (2003)[e]	Central & Eastern	56–127	143	$W = 6.164 - 0.324 L_F + 0.006 L_F{}^{1.946}$	
Present study	Western & Central	45–118	293	2.964×10^{-5}	2.928

Note. L_F = fork length (cm); W = body weight (kg).

[a] L_F (mm) and W (lbs).

[b] Parameters calculated for January and February samples.

[c] Parameters calculated for April samples.

[d] Parameters calculated for June samples.

[e] Fitted by a degree 2 polynomial.

Table 2.10. The maximum age estimates reported for *Thunnus* species based on analyses of sagittal otolith annuli.

Species	Reference	Maximum age estimate (years)
T. alalunga (Bonnaterre)	This study	14
T. obesus (Lowe)	Farley et al. (2006)	16
T. tonggol (Bleeker)	Griffiths et al. (2010)	18
T. orientalis (Temminck & Schlegel)	Shimose et al. (2009)	26
T. thynnus (Linnaeus)	Secor et al. (2009)	33
T. maccoyii (Castelnau)	Gunn et al. (2008)	41

Table 3.1. Examination of a sex ratio of 1:1 for each length class of the North Pacific albacore (*Thunnus alalunga*) specimens collected in this study using the normal approximation to the binomial test.

Fork length (cm)	Total	Females	Males	Percent (females/total)	Binomial test (Z)
< 81	96	41	55	42.7	−1.43
81–85	24	12	12	50.0	0
86–90	34	21	13	61.8	1.37
91–95	56	40	16	71.4	3.21**
96–100	41	17	24	41.5	−1.09
> 100	42	2	40	4.8	−5.86***

Note. **p < .01. ***p < .001.

Table 4.1. Data used in the sex-specific yield-per-recruit analyses for North Pacific albacore (*Thunnus alalunga*). Predicted mean fork length (L_F) and weight (W) are based on the von Bertalanffy and length-weight parameters presented in Chapter 2, and only the rounded-off data for L_F and W are presented.

Age	Female		Male		S		P
(years)	L_F (cm)	W (kg)	L_F (cm)	W (kg)	MS1	MS2	
1.5	52	3.1	54	3.4	.2	.1	0
2.5	67	6.5	67	6.6	1	.6	0
3.5	77	10.0	78	10.1	1	1	0
4.5	85	13.1	86	13.5	1	1	.5
5.5	90	15.7	92	16.7	1	1	1
6.5	94	17.8	97	19.4	1	1	1
7.5	97	19.3	101	21.8	1	1	1
8.5	99	20.5	104	23.7	1	1	1
9.5	100	21.3	106	25.2	1	1	1
10.5	101	21.9	108	26.5	1	1	1
11.5	102	22.4	109	27.5	1	1	1
12.5	102	22.7	110	28.3	1	1	1
13.5	103	23.0	111	29.0	1	1	1
14.5	–	–	112	29.5	1	1	1
15.5	–	–	112	29.8	1	1	1
16.5	–	–	113	30.1	1	1	1
17.5	–	–	113	30.4	1	1	1

Note. S = selectivity probability for fishing mortality; MS1 = Model Scenario 1; MS2 = Model Scenario 2; P = the proportion of mature fish.

Table 4.2. Parameter estimates for the Pauly equation (Pauly, 1980) and a modified Pauly equation.

Model	Regression equation $[\log_{10}(M) = \beta_0 + \beta_1 \log_{10}(L_\infty) + \beta_2 \log_{10}(K) + \beta_3 \log_{10}(T)]$				
	β_0	β_1	β_2	β_3	R^2
Pauly's equation	−0.0066	−0.279	0.6543	0.4634	.72
A modified Pauly equation[a]	0	−0.2802 (*SE* = 0.0525)	0.6553 (*SE* = 0.0626)	0.4597 (*SE* = 0.0536)	.72

Note. L_∞ = the asymptotic length of the von Bertalanffy growth model; K = the growth coefficient of the von Bertalanffy growth model; T = seawater temperature (°C); R^2 = multiple coefficient of determination; *SE* = standard error of measurement (obtained by bootstrapping with 1 000 replicates).

[a] Parameter estimates obtained in this chapter based on the data reported in Pauly's paper (Pauly, 1980).

Table 4.3. A summary of the formulae used in the yield-per-recruit equation. The number of fish at recruitment is R (for 1-year-old fish).

Age class	Number of fish (R_t)	Number of fish caught by fishing	Survival
1	$R_1 = R$	$R\times(1-e^{-Z_1})\times\frac{F_1}{Z_1}$	$R\times e^{-Z_1}$
2	$R_2 = R\times e^{-Z_1}$	$(R\times e^{-Z_1})\times(1-e^{-Z_2})\times\frac{F_2}{Z_2}$	$R\times e^{-Z_1}\times e^{-Z_2}$
3	$R_3 = R\times e^{-Z_1}\times e^{-Z_2}$	$(R\times e^{-Z_1}\times e^{-Z_2})\times(1-e^{-Z_3})\times\frac{F_3}{Z_3}$	$R\times e^{-Z_1}\times e^{-Z_2}\times e^{-Z_3}$
$\vdots$	$\vdots$	$\vdots$	$\vdots$
t_λ	$R_{t_\lambda} = R\times e^{-\sum_{j=0}^{t_\lambda-1} Z_j}$	$(R\times e^{-\sum_{j=0}^{t_\lambda-1} Z_j})\times(1-e^{-Z_{t_\lambda}})\times\frac{F_{t_\lambda}}{Z_{t_\lambda}}$	not calculated

Note. t_λ = maximum fish age (years); R_t (t = 1, 2, 3, …, t_λ) = the number of fish at age t; F_t (t = 1, 2, 3, …, t_λ) = the instantaneous rate of fishing mortality at age t; Z_t (t = 1, 2, 3, …, t_λ) = the instantaneous rate of total mortality at age t ($Z_t = F_t + M$, where M is the instantaneous rate of total mortality for all age classes); Z_j (j = 0, 1, 2, 3, …, $t_\lambda-1$) = the instantaneous rate of total mortality at age j ($Z_0 = 0$).

Table 4.4. The biological reference points (F_{max} and $F_{0.1}$) estimated in the sex-specific yield-per-recruit analyses for North Pacific albacore (*Thunnus alalunga*). The number in parentheses is the corresponding yield-per-recruit value (kg).

Reference point (year^{-1})	Model Scenario	Sex	Natural mortality (year^{-1})							
			0.2	0.25	0.3	0.35	0.4	0.45	0.5	0.55
F_{max}	1	F	0.45 (5.3)	0.58 (4.6)	0.75 (4.1)	0.96 (3.7)	1.24 (3.4)	1.61 (3.2)	2.08 (3.0)	2.62 (2.9)
		M	0.40 (5.5)	0.54 (4.8)	0.73 (4.3)	0.99 (3.9)	1.37 (3.6)	1.93 (3.3)	2.65 (3.2)	3.51 (3.0)
	2	F	0.54 (5.6)	0.72 (4.8)	0.95 (4.3)	1.25 (3.9)	1.69 (3.5)	2.32 (3.3)	3.26 (3.1)	*
		M	0.48 (5.8)	0.66 (5.0)	0.91 (4.4)	1.28 (4.0)	1.86 (3.6)	2.88 (3.4)	*	*
$F_{0.1}$	1	F	0.24 (4.9)	0.28 (4.3)	0.32 (3.7)	0.37 (3.3)	0.43 (3.1)	0.48 (2.8)	0.55 (2.6)	0.61 (2.4)
		M	0.21 (5.1)	0.25 (4.4)	0.30 (3.8)	0.35 (3.4)	0.41 (3.1)	0.47 (2.9)	0.54 (2.7)	0.61 (2.5)
	2	F	0.26 (5.1)	0.31 (4.4)	0.36 (3.8)	0.41 (3.4)	0.48 (3.1)	0.55 (2.8)	0.62 (2.6)	0.70 (2.4)
		M	0.23 (5.3)	0.27 (4.5)	0.33 (3.9)	0.39 (3.5)	0.45 (3.1)	0.52 (2.8)	0.60 (2.6)	0.68 (2.4)

Note. F = female; M = male. *$F_{\text{max}} > 4$.

Table 4.5. The degree 3 polynomials obtained for the relationship between the biological reference point ($F_{0.1}$, $F_{\max}$, $F_{20\%}$, $F_{25\%}$, $F_{30\%}$, or $F_{40\%}$) and instantaneous rate of natural mortality (x, in year^{-1}) for North Pacific albacore (*Thunnus alalunga*).

Reference point (year^{-1})	MS	Sex	The degree 3 polynomial estimated $a_1x^3 + b_1x^2 + c_1x + d_1$ $(a_1; b_1; c_1; d_1)$	R^2	Data range $[x_{\text{lo}}, x_{\text{up}}]$
$F_{0.1}$	1	F	(−0.639; 1.656; 0.113; 0.155)	.999	[0.1, 0.6]
		M	(−0.176; 1.186; 0.324; 0.099)	.999	[0.1, 0.6]
	2	F	(−0.165; 1.370; 0.285; 0.154)	.999	[0.1, 0.6]
		M	(−0.369; 1.593; 0.270; 0.112)	.999	[0.1, 0.6]
$F_{\max}$	1	F	(14.841; −2.563; 1.400; 0.152)	.999	[0.1, 0.6]
		M	(36.401; −15.251; 3.881; −0.053)	.999	[0.1, 0.57]
	2	F	(58.643; −31.871; 8.368; −0.303)	.999	[0.1, 0.53]
		M	(110.586; −65.077; 15.077; −0.786)	.998	[0.1, 0.48]
$F_{20\%}$	1	F	(−0.180; 0.064; 0.387; 0.244)	.997	[0.1, 0.6]
		M	(−0.355; 0.122; 0.494; 0.186)	.998	[0.1, 0.6]
	2	F	(−0.217; 0.108; 0.484; 0.268)	.998	[0.1, 0.6]
		M	(−0.316; 0.066; 0.644; 0.195)	.998	[0.1, 0.6]
$F_{25\%}$	1	F	(−0.301; 0.254; 0.252; 0.212)	.996	[0.1, 0.6]
		M	(−0.241; 0.061; 0.428; 0.154)	.997	[0.1, 0.6]
	2	F	(−0.519; 0.464; 0.288; 0.234)	.997	[0.1, 0.6]
		M	(−0.393; 0.206; 0.494; 0.165)	.998	[0.1, 0.6]
$F_{30\%}$	1	F	(−0.163; 0.096; 0.263; 0.176)	.994	[0.1, 0.6]
		M	(−0.219; 0.103; 0.341; 0.133)	.996	[0.1, 0.6]
	2	F	(−0.253; 0.246; 0.273; 0.197)	.996	[0.1, 0.6]
		M	(−0.339; 0.220; 0.399; 0.140)	.997	[0.1, 0.6]
$F_{40\%}$	1	F	(−0.001; −0.040; 0.231; 0.126)	.990	[0.1, 0.6]
		M	(−0.227; 0.143; 0.235; 0.098)	.993	[0.1, 0.6]
	2	F	(−0.296; 0.311; 0.158; 0.149)	.994	[0.1, 0.6]
		M	(−0.523; 0.462; 0.197; 0.109)	.996	[0.1, 0.6]

Note. MS = Model Scenario; a_1, b_1, c_1, and d_1 = the parameters for a degree 3 polynomial; R^2 = multiple coefficient of determination; x_{lo} = the lower limit of x; x_{up} = the upper limit of x.

Table 4.6. The biological reference points ($F_{20\%}$, $F_{25\%}$, $F_{30\%}$, and $F_{40\%}$) estimated in the analyses of spawning potential ratios for North Pacific albacore (*Thunnus alalunga*).

Reference point (year^{-1})	Model Scenario	Sex	Natural mortality (year^{-1})							
			0.2	0.25	0.3	0.35	0.4	0.45	0.5	0.55
$F_{20\%}$	1	F	0.32	0.34	0.36	0.38	0.40	0.42	0.43	0.45
		M	0.29	0.31	0.34	0.36	0.38	0.40	0.42	0.44
	2	F	0.37	0.39	0.42	0.44	0.47	0.49	0.51	0.53
		M	0.32	0.36	0.39	0.42	0.44	0.47	0.49	0.52
$F_{25\%}$	1	F	0.27	0.29	0.30	0.32	0.34	0.35	0.36	0.38
		M	0.24	0.26	0.28	0.30	0.32	0.34	0.35	0.37
	2	F	0.31	0.33	0.35	0.37	0.39	0.41	0.43	0.45
		M	0.27	0.30	0.32	0.35	0.37	0.39	0.41	0.43
$F_{30\%}$	1	F	0.23	0.25	0.26	0.27	0.29	0.30	0.31	0.32
		M	0.20	0.22	0.24	0.26	0.27	0.29	0.30	0.32
	2	F	0.26	0.28	0.30	0.31	0.33	0.35	0.36	0.38
		M	0.23	0.25	0.27	0.29	0.31	0.33	0.35	0.37
$F_{40\%}$	1	F	0.17	0.18	0.19	0.20	0.21	0.22	0.23	0.24
		M	0.15	0.16	0.18	0.19	0.20	0.21	0.22	0.23
	2	F	0.19	0.20	0.22	0.23	0.24	0.26	0.27	0.28
		M	0.16	0.18	0.20	0.21	0.23	0.24	0.26	0.27

Note. F = female; M = male.

Appendix A

This appendix presents the bootstrapping procedure used in the construction of bias-corrected and accelerated (BCa) confidence intervals (CIs) of a parameter estimate in Chapter 2. The equations presented below are based on the book *An Introduction to the Bootstrap* (Efron & Tibshirani, 1993). In computing the BCa CIs of a parameter estimate, the bias correction $\hat{z}_0$ can be obtained from the proportion of bootstrap replicates (B) that are less than the original estimate $\hat{\theta}$ as follows:

$$\hat{z}_0 = \Phi^{-1}\left(\frac{\#\left\{\hat{\theta}^*(b) < \hat{\theta}\right\}}{B}\right),$$

where $\Phi^{-1}(\cdot)$ is the inverse function for a standard normal cumulative distribution function. The acceleration $(\hat{a})$ can be obtained by jackknifing as shown below:

$$\hat{a} = \frac{\sum_{j=1}^{n}\left(\hat{\theta}_{(\bullet)} - \hat{\theta}_{(j)}\right)^3}{6 \times \left[\sum_{j=1}^{n}\left(\hat{\theta}_{(\bullet)} - \hat{\theta}_{(j)}\right)^2\right]^{3/2}},$$

where $\hat{\theta}_{(j)}$ is the *j*th jackknife replication of $\hat{\theta}$;

$\hat{\theta}$ is an estimator of the sample, that is, $\hat{\theta} = s(x)$;

$x_{(j)}$ is the original sample without the *j*th point x_j;

let $\hat{\theta}_{(j)} = s(x_{(j)})$; and we define $\hat{\theta}_{(\bullet)} = \sum_{j=1}^{n}\hat{\theta}_{(j)}/n$.

The BCa CIs that cover $1-2\alpha$ (the coverage probability) can be calculated as

$$\text{BCa}: \left(\hat{\theta}_{\text{lo}}, \hat{\theta}_{\text{up}}\right) = \left(\hat{\theta}^{*(\alpha 1)}, \hat{\theta}^{*(\alpha 2)}\right),$$

where $\hat{\theta}^{*(\alpha)}$ is the $100 \cdot \alpha\text{th}$ percentile of B bootstrap replicates,

$$\alpha_1 = \Phi\left(\hat{z}_0 + \frac{\hat{z}_0 + z^{(\alpha)}}{1 - \hat{a}\left(\hat{z}_0 + z^{(\alpha)}\right)}\right), \quad \text{and} \quad \alpha_2 = \Phi\left(\hat{z}_0 + \frac{\hat{z}_0 + z^{(1-\alpha)}}{1 - \hat{a}\left(\hat{z}_0 + z^{(1-\alpha)}\right)}\right).$$

In the above variables (α_1 and α_2), $\Phi^{-1}(\cdot)$ is the standard normal cumulative distribution function, and $z^{(\alpha)}$ is the $100 \cdot \alpha\text{th}$ percentile point of a standard normal distribution (e.g., $z^{(0.95)}$=1.645).

Appendix B

This appendix presents the maximum likelihood method for the logistic regression (Kutner et al., 2004) used in Chapter 3. The binomially distributed maturity data are of the form:

$$Y_i \sim B(1, P_i), \quad \text{for } i = 1, \ldots, n.$$

The logistic function is

$$P_i = \{1 + \exp[-(\beta_0 + \beta_1 X_i)]\}^{(-1)}.$$

The logit function is

$$\log\text{it}(P_i) = \ln[P_i/(1 - P_i)] = \beta_0 + \beta_1 X_i.$$

The maximum likelihood estimates, $\hat{\beta}$, maximize the log-likelihood:

$$\sum_{i=1}^{n} \{Y_i \ln(P_i) + (1 - Y_i)\ln(1 - P_i)\},$$

where

$$P_i = \{1 + \exp[-(\beta_0 + \beta_1 X_i)]\}^{(-1)} = \frac{\exp(\beta_0 + \beta_1 X_i)}{1 + \exp(\beta_0 + \beta_1 X_i)}.$$

Moreover, the log-likelihood function can be rewritten as

$$L(\beta) = \sum_{i=1}^{n} \{Y_i(\beta_0 + \beta_1 X_i) - \ln[1 + \exp(\beta_0 + \beta_1 X_i)]\}.$$

To find the critical points of the log-likelihood function, we can let the first derivative with respect to each β equal zero. We then have

$$\frac{\partial}{\partial \beta_k}(\beta_0 + \beta_1 X_i) = X_i \qquad \text{and}$$

$$\frac{\partial L(\beta)}{\partial \beta_k} = \sum_{i=1}^{n} \left\{ Y_i X_i - \frac{1}{1 + \exp(\beta_0 + \beta_1 X_i)} \times \frac{\partial}{\partial \beta_k}[1 + \exp(\beta_0 + \beta_1 X_i)] \right\}.$$

Accordingly, it can be expressed that

$$\frac{\partial L(\beta)}{\partial \beta_k} = \sum_{i=1}^{n} \left\{ Y_i X_i - \frac{1}{1 + \exp(\beta_0 + \beta_1 X_i)} \times \exp(\beta_0 + \beta_1 X_i) \times \frac{\partial}{\partial \beta_k}(\beta_0 + \beta_1 X_i) \right\}.$$

$$= \sum_{i=1}^{n} \{Y_i X_i - P_i X_i\}.$$

Moreover, the general form of the second partial derivatives can be written as

$$\frac{\partial^2 L(\beta)}{\partial\beta_k \partial\beta_{k'}} = \frac{\partial}{\partial\beta_{k'}}\sum_{i=1}^{n} Y_i X_i - P_i X_i$$

$$= \frac{\partial}{\partial\beta_{k'}}\sum_{i=1}^{n} - P_i X_i$$

$$= -\sum_{i=1}^{n} X_i \frac{\partial}{\partial\beta_{k'}}\left(\frac{\exp(\beta_0 + \beta_1 X_i)}{1+\exp(\beta_0 + \beta_1 X_i)}\right)$$

$$= -\sum_{i=1}^{n}\{X_i \cdot P_i \cdot (1-P_i)\cdot X_i\}.$$

After verifying that the second partial derivatives are negative, we can use the Newton-Raphson method to solve the nonlinear equation. To solve for x, it can be written that

$$x = x_0 - \frac{f'(x_0)}{f''(x_0)}.$$

In applying this method to the above formula in logistic regression, let $\beta^{(0)}$ represent the vector of the initial approximations of each β_k ; then, the first step of the Newton-Raphson method can be expressed as

$$\beta^{(1)} = \beta^{(0)} + \left[-L''(\beta^{(0)})\right]^{-1} \times L'(\beta^{(0)}).$$

Using matrix multiplication, it can be further written as

$$\beta^{(1)} = \beta^{(0)} + \left[X^T W X\right]^{-1} \cdot X^T \times (Y_i - P_i),$$

where

$$X = \begin{bmatrix} 1 & X_1 \\ 1 & X_2 \\ \vdots & \vdots \\ 1 & X_n \end{bmatrix}$$

and W is a square matrix of order n, with elements $P_i \times (1-P_i)$ on the diagonal and zeros everywhere else.

Appendix C

List of Abbreviations

AIC	Akaike information criterion
AICc	The small-sample bias-corrected of the Akaike information criterion
BCa	Bias-corrected and accelerated
BRP	Biological reference point
CI	Confidence interval
ISC	The International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean
MS1	Model Scenario 1 (denote a set of gear selectivity)
MS2	Model Scenario 2 (denote a set of gear selectivity)
SPR	Spawning potential ratio
SSBPR	Spawning stock biomass per recruit
VBGM	Von Bertalanffy growth model
YPR	Yield per recruit

List of Symbols

a	A parameter of a power function for expressing length-weight relationship
a_1	A parameter of a degree 3 polynomial ($a_1x^3 + b_1x^2 + c_1x + d_1$)
a_2	A parameter of an exponential growth function ($W_\mathrm{O} = a_2 \times e^{b_2 \times L_\mathrm{F}}$)
A_F	Fish age (measured in years)
b	The exponent of a power function for expressing length-weight relationship
b_1	A parameter of a degree 3 polynomial ($a_1x^3 + b_1x^2 + c_1x + d_1$)
b_2	A parameter of an exponential growth function ($W_\mathrm{O} = a_2 \times e^{b_2 \times L_\mathrm{F}}$)
c_1	A parameter of a degree 3 polynomial ($a_1x^3 + b_1x^2 + c_1x + d_1$)
d_1	A parameter of a degree 3 polynomial ($a_1x^3 + b_1x^2 + c_1x + d_1$)
C_t	The catch (kg) of fish at age t from a recruit in yield-per-recruit analysis
df	Degrees of freedom
D_t	The number of fish that die (by both M and F) at age t
E	Rate of exploitation (i.e., $E = F / Z$); exploitation fraction
F	Instantaneous rate of fishing mortality (year^{-1})
$F_{0.1}$	The instantaneous rate of fishing mortality (year^{-1}) corresponding to the point on a yield-per-recruit curve where the slope is 10% of that at the origin
$F_{20\%}$	The instantaneous rate of fishing mortality (year^{-1}) to theoretically maintain a 20% of spawning stock biomass from a recruit in the analysis of spawning potential ratios
$F_{25\%}$	The instantaneous rate of fishing mortality (year^{-1}) to theoretically maintain a 25% of spawning stock biomass from a recruit in the analysis of spawning potential ratios

$F_{30\%}$	The instantaneous rate of fishing mortality (year^{-1}) to theoretically maintain a 30% of spawning stock biomass from a recruit in the analysis of spawning potential ratios
$F_{40\%}$	The instantaneous rate of fishing mortality (year^{-1}) to theoretically maintain a 40% of spawning stock biomass from a recruit in the analysis of spawning potential ratios
$F_{\max}$	The instantaneous rate of fishing mortality (year^{-1}) corresponding to the point on a yield-per-recruit curve where the maximum yield-per-recruit value is obtained
F_t	The instantaneous rate of fishing mortality (year^{-1}) for fish at age t (incorporate gear selectivity)
I_A	Index of the average percent error
k	The number of parameters for the growth model for calculating AICc
K	A parameter of the von Bertalanffy growth model (a growth coefficient)
K_2	A parameter of the Gomperz model (the instantaneous rate of growth at age t_2)
K_3	A parameter of the Richards model
L_1	The length (mm) from the primordium to the outer-ventral margin of the first annulus (for measuring L_P)
L_2	The length (mm) from the outer-ventral margin of the first annulus to the posterior-ventral otolith edge (for measuring L_P)
L_∞	A parameter of the von Bertalanffy growth model (an asymptotic mean length theoretically)
L_F	Fork length (cm)
L_G	A parameter of the Gompertz growth model
L_P	The length (mm) calculated from the primordium to the posterior-ventral otolith edge
L_R	A parameter of the Richards growth model
L_t	The fork length for fish at age t
m	The number of age classes in the F-test for lack of fit

M	Instantaneous rate of natural mortality (year^{-1})
n	Number of samples
N	Total number of samples
N_t	The number of fish at age t from a recruit in yield-per-recruit analysis
p	The p value for a statistical test
p_1	The number of parameters fitted by regression in the F-test for lack of fit
P	Proportion of mature fish
P_i	The proportion of mature fish at age i
P_L	The proportion of the von Bertalanffy growth parameter L_∞ for calculating t_λ
r	A parameter of the Richard model
r^2	Coefficient of determination for simple linear regression
R	The number of fish at recruitment in yield-per-recruit analysis
R^2	Coefficient of determination; multiple coefficient of determination
R_A	The number of age readings in calculating the I_A value
$R_S{}^2$	Coefficient of determination for logistic regression in SAS (Equation 3.4)
$R_{sas}{}^2$	Coefficient of determination for logistic regression in SAS (Equation 3.5)
SD	Standard deviation
SE	Standard error of measurement; standard error of the mean
SS_{con}	Total sum of squares obtained by fitting a growth model using the hypothesized constraints of parameters
SS_{err}	Residual sum of squares
SS_{lof}	Sum of squared residuals caused by lack of fit

$\boldsymbol{SS_{\text{pur}}}$	Sum of squared residuals caused by pure error
$\boldsymbol{SS_{\text{sep}}}$	Total sum of squares obtained from fitting the growth model by setting all parameters different between sexes
$\boldsymbol{SS_{\text{tot}}}$	Total sum of squares
$\boldsymbol{S_t}$	The selectivity proportion at age t
$\boldsymbol{t}$	The fish age (in years) or the statistic for t-test
$\boldsymbol{t_0}$	A parameter of the von Bertalanffy growth model (the age at zero fish length)
$\boldsymbol{t_2}$	A parameter of the Gompertz model
$\boldsymbol{t_3}$	A parameter of the Richards model
$\boldsymbol{t_{\text{c}}}$	The fish age at first capture (here $t_{\text{c}} = t_{\text{r}}$)
$\boldsymbol{t_{\text{r}}}$	The fish age at recruitment in yield-per-recruit analysis (here $t_{\text{r}} = t_{\text{c}}$)
$\boldsymbol{t_\lambda}$	Maximum fish age
$\boldsymbol{T}$	The sea water temperature (°C) used in Pauly's equation
$\boldsymbol{W}$	Body weight (kg); body mass
$\boldsymbol{W_{\text{O}}}$	Left otolith weight (mg); left otolith mass
$\boldsymbol{W_t}$	The mean body weight (kg) of fish at age t calculated by growth and length-weight parameters
$\boldsymbol{X_{ij}}$	The ith age estimate of the jth fish in calculating I_{A}
$\boldsymbol{X_j}$	The mean age estimate calculated for the jth fish
$\boldsymbol{Z}$	Instantaneous rate of total mortality (year^{-1}); that is, $Z = F + M$
$\boldsymbol{Z_t}$	The instantaneous rate of total mortality (year^{-1}) for fish at age t (incorporating gear selectivity)
$\boldsymbol{\beta_0}$	A parameter of a logistic function; a parameter for linear regression
$\boldsymbol{\beta_1}$	A parameter of a logistic function; a parameter for linear regression

ε_t	Independent and normally distributed random errors with zero mean and unknown finite variance ($\sigma^2 > 0$) in the growth model
λ	The degrees of freedom of the assumed chi-square distribution in the likelihood ratio test
σ^2	variance
χ^2	The sample value of the chi-square test statistic
Δ_i	The difference of two AICc values ($\Delta_i = \mathrm{AICc}_i - \mathrm{AICc}_{\min}$, where $\mathrm{AICc}_{\min}$ is the minimum value of AICc values within each sex)