Effects of Ocean Warming on Pelagic Tunas

A Review
Chapter 3.12

Effects of Ocean Warming on Pelagic Tunas, a Review

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“There remains high uncertainty of how individual populations will respond to long-term rising average ocean temperatures and synergistic effects of other climate change outcomes. Oceanic tunas and billfishes may adopt new cooler subtropical areas for spawning, either replacing or in addition to existing tropical spawning sites. They may change their migration phenology, including altering the timing of spawning and truncating the spawning season.”

Section 3.12 authors
3.12 Effects of Ocean Warming on Pelagic Tunas, A Review

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Summary
- Many marine species are undergoing rapid shifts in geospatial and depth distributions and changes in phenology in response to ocean warming and other climate change outcomes.
- Predictions of responses of pelagic (open ocean) tunas and billfishes to long-term rising average global subsurface and sea surface temperatures have been based on evidence from model simulations and observations of responses to inter-annual and decadal cyclical climate oscillations. Simulations have accounted for potential interacting effects of ocean warming with changes in dissolved O₂ concentrations, ocean circulation patterns, ocean pH, pelagic food web structure and processes, and other climate change outcomes.
- There is high uncertainty of how individual populations will respond to rising ocean temperatures and synergistic effects of other climate change outcomes. Oceanic tunas and billfishes may adopt new cooler subtropical areas for spawning, either replacing or in addition to existing tropical spawning sites. They may alter their migration phenology, including changing the timing of spawning and truncating the spawning season. These changes may alter distributions and survival rates of larvae and young age classes, reducing recruitment and biomass in existing spawning grounds, but increasing recruitment and biomass at new spawning grounds. In order to maintain species- and age class-specific preferred habitat conditions, including optimal temperature ranges, populations may alter their foraging distributions to higher latitudes and to different longitudes, and alter their vertical depth distributions.
- Long-term trends in absolute abundance in response to ocean warming will vary by individual population. Population-specific responses will be determined by whether new spawning sites emerge, how survival rates of larvae from existing and new spawning locations change, where suitable foraging habitat occurs, the local abundance of forage species at foraging areas, and how changes in distribution affect catchability and fishing mortality rates.
- Selection for phenotypes tolerant of higher ocean temperatures at spawning and foraging habitats could occur for some populations. Warmer water temperatures, however, might increase susceptibility to overheating, reducing spawning success and recruitment. This might also reduce the likelihood of establishing new spawning and foraging areas meeting all optimal habitat conditions.
- Changes in horizontal and vertical distributions would redistribute benefits derived from tuna fisheries due to changes in the locations of fishing grounds and due to species- and stock-specific changes in catchability by surface and subsurface fishing gears.
### 3. The significance of warming seas for species and ecosystems

<table>
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<tr>
<th>Ocean warming effect</th>
<th>Consequences</th>
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<td>Some populations may experience a range shift, moving to higher latitudes and</td>
<td>Changes the availability of market species to fisheries in that overlap with</td>
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<td>different longitudes where they find suitable water temperatures and conditions</td>
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<td>O$_2$ levels)</td>
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<td>Some populations may occupy deeper depths where they find suitable</td>
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<td>temperatures and that meet other habitat requirements (adequate O$_2$</td>
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<td>concentration, ability to visually detect prey)</td>
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<td>For some populations, new spawning locations may emerge in the subtropics and the</td>
<td>Populations that establish new spawning sites may have higher resiliency to</td>
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<td>timing of spawning might change</td>
<td>ocean warming and other climate change outcomes</td>
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<td>Example: Pacific Ocean skipjack tuna may shift its distribution eastward and to</td>
<td>Alters the distribution of young age classes which in turn would alter</td>
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<td>higher latitudes, and experience a long-term reduction in absolute biomass</td>
<td>recruitment due to possible changes in local abundance of prey for the young</td>
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<td>tunas as well as of their predators</td>
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<td>Alters the timing of migration between foraging and spawning grounds, which</td>
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<td>would affect the availability to different fisheries</td>
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<td>Example: south Pacific Ocean albacore may shift its range south and west, a new</td>
<td>Purse seine, pole-and-line and other surface fisheries in the eastern Pacific</td>
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<td>spawning site may emerge, and total biomass may increase</td>
<td>and western and central Pacific will have increased and decreased skipjack</td>
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<td>Broad changes to pelagic communities may result from the reduction in absolute</td>
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<td>Pelagic longline and other fisheries in the current range will experience</td>
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<td>reduced catch rates, while those overlapping with the new distribution will</td>
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#### 3.12.1 Introduction

Many marine species have been observed to have undergone rapid shifts in distributions to higher latitudes, deeper depths or both, as well as changes in phenology (e.g. timing of migrations and spawning) modelled or inferred to be a response to increases in global average ocean temperatures (e.g. Edwards and Richardson, 2004; Perry et al., 2006; Dufour et al., 2010; Last et al., 2011; Poloczanska et al., 2013), which are projected to warm at a faster rate in the future (IPCC, 2013). Tuna resources supply the fourth most valuable globally traded fishery products and provide substantial economic revenue, employment and food security to fishing and coastal states (Gillett, 2009; Bell et al., 2011; FAO, 2014). There is increasing concern over projected effects of ocean warming and other outcomes of climate change on pelagic (oceanic) ecosystems, the recruitment, biomass, distributions, and resistance and resilience to other stressors of pelagic tunas and billfishes, and concomitant effects on benefits derived from tuna fisheries (Lehodey et al., 2011; Bell et al., 2013a; Hobday et al., 2015). This section reviews the likely effects of ocean warming on principal market species of tunas for globally traded products. First, we describe the principal market tunas, their ecology and socio-economic importance. We review the broad community- and ecosystem-level effects of selective fishery removals of pelagic apex predators, population-level responses to declining abundance, and stock status and IUCN species conservation status of the seven principal market tunas. We also review how stressors from fisheries affect tunas’ resistance and resilience to ocean warming and other climate change outcomes (Brander, 2010). We conclude by describing
the degree of certainty of predicted responses of market tunas to ocean warming and other climate change outcomes and identifying research priorities.

### 3.12.1.1 Ecological significance of tuna and tuna-like species and billishes

The term ‘tuna and tuna-like species’ refers to species of the suborder Scombroidei, which is composed of the ‘true’ tunas and other tuna-like species (Collette et al., 2001, 2006; Omell et al., 2006). There are 15 genera with 51 species currently recognized in the Scombridae (Collette et al., 2001). There are seven principal market species of tunas for globally traded products: albacore (**Thunnus alalunga**), Atlantic bluefin (**T. thynnus**), bigeye (**T. obesus**), Pacific bluefin (**T. orientalis**), skipjack (**Katsuwonus pelamis**), southern bluefin (**T. maccocyii**) and yellowfin (**T. albacares**) (Majkowski, 2005). Billishes (suborder Xiphioidae) contain four species of marlins in three genera (**Makaira**, **Istiompax**, and **Kajikia**), the sailfish (**Istiophorus platypterus**), and four species of spearfishes (**Tetrapturus**) in the Istiophoridae plus the swordfish (**Xiphias gladius**) in the family Xiphiidae (Collette et al., 2006). The seven species of market tunas and billishes are all pelagic. Other tunas and some tuna-like species are primarily neritic, meaning that they are found in waters primarily over continental shelves (Majkowski, 2005, 2007).

Large tunas, other Scombroidei and billishes are at the top of the pelagic foodweb and contribute to pelagic ecosystem structure, functioning and stability (discussed in more detail in para. 3.12.1.3) (Cox et al., 2002; Kitchell et al., 2002; Hinke et al., 2004; Ward and Myers, 2005; Polovina et al., 2009; Gilman et al., 2012; Polovina and Woodworth-Jelcoats, 2013; Hobday et al., 2015).

Market tunas are some of the largest and fastest marine fishes. They have extremely efficient metabolic systems, including a circulatory system that permits them to retain or disperse heat to achieve optimal performance, as well as tolerate a broad range of water temperatures, enabling these highly migratory species to make use of a range of oceanic habitats (Majkowski, 2005; Trenkel et al., 2014). As they get larger, tunas produce more heat, enabling some species to inhabit higher latitudes and deeper waters. Tunas have strong schooling behaviour and often associate with floating objects and large marine organisms. They are highly fecund and mature at a relatively young age (Majkowski, 2005).

Skipjack and yellowfin tunas are largely tropical in distribution. Albacore and bluefin occur in temperate waters. Bigeye tuna are tropical in distribution but feed in cooler waters by feeding deeper than other tropical tunas (Collette et al., 2001; Majkowski, 2007). All of the principal market tunas spawn in warm tropical waters. The three bluefin tuna species spawn in limited areas, such as Pacific bluefin tuna, which spawn in an area off Taiwan, and Atlantic bluefin which spawn in the Gulf of Mexico and western Mediterranean (Muhling et al., 2011). The bluefins also have relatively short spawning periods of 1-2 months (Collette et al., 2011; Muhling et al., 2011). Bigeye, yellowfin, skipjack and albacore tunas, on the other hand, have extensive spawning grounds in tropical waters and long spawning seasons relative to bluefin species. Bluefin and albacore tunas make seasonal migrations between foraging grounds at higher latitudes and spawning grounds in tropical waters (Nishikawa et al., 1985; Schaefer, 2001; Muhling et al., 2011; Lehodey et al., 2015).

### 3.12.1.2 Socio-economic significance

Tuna and tuna-like species have been an important food source since ancient times, and are target species of fisheries worldwide (Majkowski, 2007; Miyake et al., 2010). In the 19th Century, most tuna fisheries were coastal, conducted by locally-based fleets (Majkowski, 2005, 2007). Industrial tuna fisheries began in the 1940s. Over the next few decades, fishing grounds quickly expanded as did the number of countries with large-scale coastal and distant-water tuna fleets. Demand for both canned and fresh tuna has increased rapidly, with reported landings of principal market tunas increasing from about 700,000 t in 1960 to almost 4.8 million t in 2014 (Figure 3.12.1) (SPC, 2015).

Principal market tunas and several tuna-like species are used for globally traded canned, fresh and frozen products (Figures 3.12.2, 3.12.3). The reported landings of skipjack, yellowfin, bigeye and albacore tunas is about 66% of all landed tuna and tuna-like species (FAO, 2015b). Of the principal market tunas, the three bluefin species each make up less than 1% of total global reported landings by weight (FAO, 2015b). About 82% of world tuna is consumed as canned product, and 18% as fresh product (including as sashimi) (Miyake, 2008). Japan consumes an estimated 78% of the fresh tuna (Miyake, 2008). By 2010, purse seine fisheries accounted for 66.5% of global reported landings, followed by longline (12.4%), pole-and-line (7.9%), troll (1.6%) and other gears (11.6%, e.g. drift gillnet, handline, traps) (FAO, 2015a).
3. The significance of warming seas for species and ecosystems

Tuna is the fourth most valuable globally traded fishery product, accounting for ca. 8% of the $129 billion value of internationally traded fishery products (FAO, 2014). Since 2006, over half of principal market tunas have come from the western and central Pacific Ocean (SPC, 2015). Several Pacific Island Countries and territories obtain a large proportion of their gross domestic product from revenue from tuna fisheries, including fees from licensing and from granting access to foreign purse seine and longline tuna fisheries to fish in their exclusive economic zones, representing as high as 63% of total government revenue (Kiribati) (Aqorau, 2009; Gillett, 2009; Bell et al., 2015; FFA, 2015). Capture and processing sectors generate additional revenue and substantial employment in the Pacific islands region (Gillett, 2009; Bell et al., 2015; FFA, 2015). In 2014 the Pacific Islands Forum Fisheries Agency members (15 Pacific small islands developing states, Australia and New Zealand) obtained an estimated US$ 556 million of their combined gross domestic product from the tuna fisheries catch sector, and employed over 22,000 people in processing and various other tuna-sector related positions (FFA, 2015). Some locally-based tuna fisheries supply largely low-value fishes (smaller tunas, incidental tuna-like species) to local markets in Pacific Island Countries and territories, contributing to local food security and tourism industries (Gillett, 2009; Bell et al., 2015).

3.12.1.3 Trends and impacts

Of the 23 stocks of the seven principal market tuna species, nine are over-exploited. Over-exploited stocks are either over-fished (biomass is below a level estimated to produce maximum sustainable yields [MSY] or similar threshold), or over-fishing is occurring (the fishing mortality rate exceeds an MSY-based or similar reference point, indicating that the stock is not rebuilding its biomass), or both (ISSF, 2016). Most tuna stocks are under or fully exploited, dominated by skipjack, albacore and yellowfin tunas.

Of 61 Scombroidei species assessed against the IUCN Red List criteria, 13% were listed as Threatened and 7% as Near Threatened (Collette et al., 2011, 2014). Pacific bluefin, southern bluefin, Atlantic bluefin, and bigeye tuna were four of the Scombroidei categorized as Threatened. The characteristics that these Threatened tunas have in common are long generational lengths, longer lived and later maturity, which when combined, results in longer time to recover from population declines (Collette et al., 2011). These Threatened tuna species also have higher economic values per unit of weight relative to the other market tunas (Miyake et al., 2010).
3.12 Pelagic tunas and billishes

Except for bluefin species, which have relatively restricted spawning grounds and short spawning periods, other market tunas likely have low risks of extirpation (permanent loss of a population, local extinction) from fishery removals. This is because, for these highly fecund broadcast spawning marine fishes, there is no relationship between recruits and the abundance, biomass and egg production by adult age classes, and only at extremely low population sizes is egg production likely to be a limiting factor for recruitment (Myers et al., 1999; Essington, 2010). When the biomass of a market tuna falls below the level that is estimated to produce MSY for a sufficiently long period, this could trigger decreases in supply, and increases in both value and demand, which in turn would create a larger incentive to increase fishing effort (Cinner et al., 2011). Thus, market forces may drive the biomass of an over-exploited stock to a critical level if the governance system is ineffective (Gilman et al., 2014a).

Some fisheries, including pelagic longline, purse seine and drift gillnet fisheries that target relatively fecund species with r-selected life history characteristics like tunas can have large impacts on incidentally caught species with K-selected life-history strategies (i.e. low fecundity, slow growth, etc.), including seabirds, sea turtles, marine mammals, elasmobranchs (sharks and rays) and some bony fishes (Hall et al., 2000; Stevens et al., 2000; Gilman, 2011; Croll et al., 2016). There has been substantial progress in identifying effective and economically viable mitigation methods for some of these bycatch problems. However, there has been limited uptake in most fisheries in part due to management deficiencies (Gilman et al., 2014b). Responses of these marine predator populations to ocean warming and other climate change outcomes are additional compounding stressors (e.g. Willis-Norton et al., 2015).

Reductions in populations of scombrids and billfishes may also cause broad protracted or permanent changes to pelagic communities and ecosystems (Myers et al., 1999; Essington, 2010). There is increasing understanding of these broad effects from selective fishery removals of pelagic apex predators, largely from species- and more recently size-based ecosystem trophic interaction models, and some empirical studies (Cox et al., 2002; Kitchell et al., 2002; Hinke et al., 2004; Ward and Myers, 2005; Polovina et al., 2009; Gilman et al., 2012; Polovina and Woodworth-Jefcoats, 2013). Broad effects of tuna fisheries that remove large Scombroidei, which are the top of the pelagic foodweb (e.g. Collette et al., 2011), include, for example, altered pelagic trophic structure and processes, where the selective removal of older age classes of a subset of species of a pelagic ecosystem apex predator guild could have cascading effects down the pelagic ecosystem food web. For example, pelagic longline selective removal of apex predators has resulted in a top-down trophic effect by releasing pressure and increasing abundance of mid-trophic level species, altering the ecosystem size structure with a decline in abundance of large-sized species of fish and increase in abundance of smaller-sized species, and possibly altering the length frequency distribution of populations subject to fishing mortality (Cox et al., 2002; Kitchell et al., 2002; Hinke et al., 2004; Ward and Myers, 2005; Polovina et al., 2009; Gilman et al., 2012; Polovina and Woodworth-Jefcoats, 2013).

However, in systems with high diversity and ecological redundancy of top predators, when fishing mortality reduces a pelagic top predator species’ biomass, other marine predators, including sympatric competitors that are less susceptible to capture in tuna fisheries, may functionally replace them, so that trophic cascades do...
not occur, with small effect on ecosystem regulation (Cox et al., 2002; Kitchell et al., 2002; Hinke et al., 2004; Ward and Myers, 2005; Young et al., 2009; Griffiths et al., 2010). Instead of being controlled by top-down processes, these pelagic systems may be ‘wasp-waist’ systems, where high biomass mid-trophic level organisms (micronekton) exert the greatest influence on the system due to their importance as both prey (including by tunas) and predators (Olson and Watters, 2003; Griffiths et al., 2010).

The selective removal of large individuals could be a driver favouring genotypes for maturation at an earlier age, smaller-size and slower-growth, potentially altering the size structure and evolutionary characteristics of affected populations (Stevens et al., 2000; Ward and Myers, 2005; Zhou et al., 2010).

Because tunas and possibly other pelagic apex predators drive baitfish to the surface, reducing the abundance of tunas and other subsurface predators indirectly reduces the availability of prey to seabirds (Au and Pitman, 1986; Ballance et al., 1997).

As their population abundance declines, the distributions of tuna populations are predicted to respond by contracting towards the centre of their ranges, where they would maintain a stable density (Pitcher, 1995). There also could be hyperstability of relative abundance at aggregating features such as at shallow seamounts and at artificial fish aggregating devices (Gulland, 1964; Pitcher, 1995, Fonteneau et al., 1999; Gaertner and Dreyfus-Leon, 2004; Morato et al., 2010; Gilman et al., 2012). While possible, to date, there has been no direct evidence of this occurring for tunas. For example, for western and central Pacific yellowfin tuna, greater reductions in local abundance have been observed in the tropics, the core area for this stock, where most catch and effort occurs, than at higher latitudes, the periphery of the stock’s distribution (Davies et al., 2014).

3.12.2 Effects and responses to ocean warming and other stressors from climate change outcomes

Several outcomes of human-induced changes to the Earth’s climate resulting from modifications in the atmosphere’s composition and alterations to land surfaces are likely to affect market tunas and other pelagic fishes. The atmosphere’s composition is altered, for example, from the production of greenhouse gases and aerosols through the combustion of fossil fuels, biomass burning and deforestation. Alterations to the Earth’s land surfaces, such as through deforestation, damming rivers, urbanization and soot covering snow alter climate, for example, by altering the surface’s albedo, changing the amount of dust blown from the surface to the atmosphere, and altering the amount of water that evaporates from leaves and the soil. Human-induced climate changes include decadal and longer-term trends in ocean surface and subsurface temperature, dissolved CO$_2$ and O$_2$ concentrations, pH, ocean circulation patterns, vertical mixing, eddies, and indirect effects such as from changes in functionally linked ecosystems (Brander, 2010; Le Borgne et al., 2011; Lehodey et al., 2011). These outcomes of changes in climate may affect the survival of tuna larvae and subsequent recruitment and biomass, the productivity and survival of organisms in lower trophic levels that are part of tunas’ food webs, larval dispersal, migration patterns, distribution, and resistance and resilience to other stressors such as fishing mortality (Brander, 2010; Le Borgne et al., 2011; Lehodey et al., 2011).

3.12.2.1 Ocean temperature and Scombroidei preferred habitat

Ocean surface and subsurface temperatures strongly affect the distributions and local abundance of principal market tunas and other Scombroidei. Pelagic apex predators, and in some cases sizes and sexes within species, have different pelagic habitat preferences for foraging and breeding (Hyrenbach et al., 2000, 2006; Polovina et al., 2004; Bailey and Thompson, 2010; Muhling et al., 2011; Mitchell et al., 2014; Vandeperre et al., 2014). Various environmental parameters have been used to define these static and dynamic pelagic habitats. Sea surface temperature (SST), one of several dynamic environmental variables frequently used to standardize catch rates, has been observed to significantly explain species- and sex-specific catch rates of pelagic species (see review by Gilman and Hall, 2015). Individual pelagic predators, including tuna species, have disparate temperature preferences and tolerances (e.g. Lehodey et al., 2011; Muhling et al., 2011; Brodziak and Walsh, 2013). Larval and juvenile tunas have a narrower range of water temperatures and other environmental variables in which they can live than adults, while optimal temperatures are narrowest and warmest for spawning tunas (Lehodey et al., 2011, 2015; Bromhead et al., 2015).
3.12.2.2 Using responses to ENSO phases to predict responses to ocean warming

Evidence of the effect of natural climate variability on tunas provides one basis for predicting responses to ocean warming from anthropogenic-caused climate change. The distribution, recruitment and biomass of tropical and temperate tunas have been observed to respond to variability resulting from natural large scale climate cycles such as inter-annual El Niño-Southern Oscillation (ENSO) (see Chapter 1 and Section 4.1) phases and longer-scale Pacific Decadal Oscillation (PDO) phases (Lehodey, 2000; Lehodey et al., 1997, 2006). In the western and central Pacific Ocean, ENSO phases are associated with large scale east-west shifts in the Warm Pool and the highly productive convergence zone between the Warm Pool and ‘cold tongue’, altering upwelling intensity and the depth of the thermocline in different regions of the Pacific. This variability in the spatial and temporal occurrence of areas of high ocean productivity and variability in thermocline depth result in variability in the horizontal and vertical distributions (and hence variability in their availability to fisheries) and recruitment of pelagic apex predators.

For example, eastward movement of tropical skipjack and yellowfin tunas and increased recruitment have been observed, while subtropical south Pacific albacore may exhibit reduced recruitment following El Niño phases, with opposite responses following La Niña phases (Lehodey et al., 1997; Lehodey, 2001; ISC, 2010). ENSO phases also affect tuna catch rates in purse seine, pole-and-line and other surface fisheries (Lehodey et al., 2011). In the western Pacific Warm Pool, a shallower thermocline during El Niño phases increases the concentration of fish in the upper layer, while a deeper thermocline during La Niña phases has the opposite effect. The effect of ENSO phase on the thermocline is the opposite in the eastern equatorial Pacific. Similar effects of ENSO spatial and temporal variability in sea surface temperature, degree of vertical stratification, depth of the mixed layer, and degree of spatial concentration of preferred water temperature habitat on longline catch rates of bigeye, yellowfin and albacore tunas occur (Lu et al., 1998; Briand et al., 2011). There is a lag in these recruitment, biomass, and distribution responses to ENSO phases. For example, the change in skipjack average abundance occurs about eight months following an ENSO phase, and in subsequent years for adult albacore (Lehodey et al., 1997, 2004; Senina et al., 2008). The frequency and amplitude of ENSO varies on a multi-decadal scale due to the influence of the Pacific basin-wide Interdecadal Pacific Oscillation (IDO) and PDO, the component of the IDO in the north Pacific (e.g. Power et al., 1999).

Most Earth climate model projections predict greater average warming in the eastern than the western equatorial Pacific, referred to as an ‘El Niño-like’ response, with continued El Niño and La Niña events (Meehl and Washington, 1996; Gilyardi, 2006; Ganachaud et al., 2011). There is, however, high uncertainty in whether the frequency and strength of future El Niño and La Niña phases will change in response to climate change (Gilyardi, 2006; Lough et al., 2011; Cai et al., 2014; Risbey et al., 2014).

3.12.2.3 Model-based predicted and observed responses

Findings from models simulating responses of some populations of Pacific tunas to climate change indicate there will be shifts in distributions and changes in absolute biomass (some increasing, others decreasing) (Box 3.12.1) (Figure 3.12.4) (Lehodey et al., 2010, 2013, 2015; Nicol et al., 2014). For example, model simulations of the effect of climate change scenarios predict the distribution of larvae of Pacific Ocean skipjack tuna will shift towards the eastern Pacific and to higher latitudes (Figure 3.12.4), with total biomass starting to decline after 2060 (Lehodey et al., 2013). And, for comparison, model simulations for south Pacific albacore tuna
predict the distribution of larvae and juveniles will shift to the south closer to the Tasman Sea, while the density of individuals of these early life stages in their current core area in the Coral Sea decreases (Figure 3.12.4). Total adult biomass of south Pacific albacore is predicted to decrease and stabilize after 2035, but after 2080 when the new spawning ground in the north Tasman Sea emerges, the trend in absolute abundance is predicted to reverse (Lehodey et al., 2015).

Model results also indicate there might be a decrease from the current habitat area supporting larvae and truncated spawning season for western Atlantic bluefin (Muhling et al., 2011). Changes in the timing of migration from spawning to foraging grounds and in the spatial distribution of north Atlantic albacore and eastern Atlantic bluefin tunas have also been observed, possibly a response to climate change (Dufour et al., 2010).

3.12.3.1 Effects on spawning
With rising average global subsurface and sea surface temperatures, tunas may change their spawning location and timing, which would affect the success of recruitment. Some models predict increased recruitment and biomass as a result of the formation of new spawning grounds (e.g. Lehodey et al., 2015). Tunas may alter their locations for spawning from tropical to cooler subtropical areas, which in turn would alter the distribution of young age classes, altering recruitment due to possible changes in foraging success and predation of larvae and juvenile tunas (Lehodey et al., 2011, 2015; Muhling et al., 2011; Nicol et al., 2014). Or, if tunas continue to spawn in the tropics, where warmer water temperatures might result in higher susceptibility to overheating, spawning success and thus recruitment may decline (Lehodey et al., 2011, 2015).
For western Atlantic bluefin, which are already stressed by warm water temperatures at their spawning grounds in the Gulf of Mexico, ocean warming, and global climate change effects on eddies, might cause a substantial reduction or even cessation of successful spawning (Bakun, 2012). Because the dissolved \(O_2\) demand increases with warmer temperatures for tuna to spawn, possible changes in ocean dissolved \(O_2\) concentrations in response to climate change may narrow the temperature range of habitat suitable for spawning (Portner and Farrell, 2008; Lehodey et al., 2011). Another phenological adaptation in response to ocean warming, tunas may alter their timing of spawning, and hence timing of migration between foraging and spawning grounds (Muhling et al., 2011), as has been observed for young Atlantic bluefin and albacore tunas (Dufour et al., 2010). Altering the season and duration of spawning could reduce larval survival due to changes in local abundance of predators and prey (Muhling et al., 2011). Based on observations of variability in sensitivity to \(CO_2\) concentrations in coral reef fishes, which might be heritable (Munday et al., 2012), selection for phenotypes tolerant of higher ocean temperatures at spawning grounds could occur for some tunas, which might maintain current spawning locations but possibly at a reduced level of spawning success. This would reduce the likelihood of the phenological adaptation to new spawning areas at higher latitudes of becoming established, reducing recruitment and biomass, as predicted by one simulation run of a model for south Pacific albacore (Lehodey et al., 2015).

### 3.12.2.3.2 Effects on foraging habitat for non-spawning tunas

Tunas, when not spawning, may respond to ocean warming by occupying new areas with suitable water temperatures and that also meet other requirements such as \(O_2\) concentration and local abundance of prey. Tunas might alter their vertical distribution by occupying deeper depths and might alter their horizontal distribution by moving to higher latitudes and to longitudes where preferred temperatures and \(O_2\) concentrations occur, as takes place during current El Niño phases (Lehodey et al., 2011, 2015; Bell et al., 2013b; Nicol et al., 2014). Increased vertical structure of the water column (stratification) may restrict the depth distributions of skipjack and yellowfin tunas and billfishes that are sensitive to temperature stratification, constraining them to surface layers where SST is within tolerance ranges, affecting their access to forage species in deep water, and affecting their catchability in surface fisheries (Lehodey et al., 2011; Nicol et al., 2014). There is limited understanding of how prey species of oceanic tunas and billfishes will respond to ocean warming and other climate change outcomes, which in turn limits the certainty of predictions of where new tuna and billfish foraging habitat might emerge (e.g. Muhling et al., 2011). For example, the micronekton that are prey for tunas may be less resilient to changes in dissolved \(O_2\) concentrations and other physical effects of ocean warming than tunas, which might make a subset of habitat within tunas’ thermal tolerance range unsuitable for foraging (LeBorgne et al., 2011). Reduced \(O_2\) concentration at depth and lower ability to visually detect prey in low light environments may reduce the suitability of deeper water habitats and prevent expanding vertical distributions by some tuna and tuna-like species, similar to the effect of increased stratification (Poisson et al., 2010; Lehodey et al., 2011). Subsurface changes in temperature and \(O_2\) concentration are expected to have a larger effect on yellowfin, albacore and bigeye tunas, which have relatively wide depth distributions, than skipjack, which largely occupies surface waters (Lehodey et al., 2011, 2014; Nicol et al., 2014). As with the ocean warming effect on the location of spawning grounds, selection for phenotypes tolerant to higher ocean temperatures at foraging grounds could also occur for some tunas.

### 3.12.2.4 Individual and interacting effects of climate change outcomes on tunas

Synergistic effects of the predicted outcomes of climate change on market tunas are not well understood (Hobday et al., 2015). For instance, the interacting effects of ocean warming and changes in \(O_2\) concentrations might have a much different and larger effect on the success of tuna spawning than predicted effects from these factors individually (Portner and Farrell, 2008; Lehodey et al., 2011). There may be interacting effects between ocean warming and ocean acidification, where for example, acidosis could narrow the range of optimal temperatures, narrowing new locations of optimal spawning habitat in response to ocean warming. And, possible reductions in larvae survival rates from changes in the location of suitable spawning habitat due to ocean warming may be exacerbated if reduced pH also causes a reduction in tuna larvae survival rates at low dissolved \(O_2\) concentrations (Lehodey et al., 2011; Bromhead et al., 2015).
The direction and speed of currents influence the locations of suitable foraging and spawning habitat for pelagic organisms, including the locations and strength of eddies, upwelling and vertical stratification and mixing of the water column. Currents in the tropics are expected to weaken, causing a decrease in the formation of eddies and increased stability of water masses (Nicol et al., 2014). These changes resulting from altered ocean circulation patterns affect pelagic organisms’ horizontal and vertical distributions for foraging and spawning, which in turn affects foraging success, predation and survival rates, recruitment, growth and abundance (Ganachaud et al., 2011).

Vertical mixing of the water column, including through eddies, wind-driven upwelling and turbulence in the mixed layer, affects the availability of nutrients for primary production at the base of tuna food webs.

Eddies, in addition to affecting vertical mixing, also influence the distribution and survival rates of larvae and juveniles. Eddies retain larvae and juvenile tunas in suitable habitat that increases the probability of successful recruitment, and create suitable foraging habitat for tunas and other pelagic apex predators by concentrating their prey (Ganachaud et al., 2011; Lehodey et al., 2011). Bluefin tunas in particular may heavily depend on eddies to support spawning schools above a density threshold for successful reproduction (Bakun, 2012).

Dissolved oxygen (O$_2$) concentration can affect the spawning success, growth, survival and vertical and horizontal distributions of tunas and organisms in their food webs. Organisms will not survive in areas with dissolved O$_2$ levels that are insufficient to meet their energy and oxidation physiological requirements, which are affected by ocean temperature (Ganachaud et al., 2011; Lehodey et al., 2011). Due to their broad distribution of spawning grounds, changes in O$_2$ concentration is not likely to affect the reproduction of albacore, bigeye, skipjack and yellowfin tunas (Lehodey et al., 2011).

Ocean acidification may cause tuna species and age classes with high metabolic demands to
experience physiological costs, including a reduced range of optimal temperatures, compounding adverse effects of ocean warming, and energy costs to compensate for acidosis (increased carbonic acid in body fluids) (Portner et al., 2004, 2005; Lehodey et al., 2011). There is evidence from one laboratory study on yellowfin tuna eggs and larvae that increased oceanic CO₂ concentrations and lower pH caused significantly reduced larval survival, larval size and growth, and increased time required for egg hatching (Bromhead et al., 2015). Decreasing pH may affect tuna otolith formation, important for orientation, acceleration and detecting sound, particularly by tuna larvae, and thus might affect larval survival (Fabry et al., 2008; Lehodey et al., 2011; Bignami et al., 2013). Decreasing pH is expected to reduce sound absorption and increase sound propagation, which might affect tuna and organisms in their food webs, such as their ability to detect prey and predators (e.g. Ilyina et al., 2010). Ocean acidification affects the availability of carbonate ions, affecting the abundance of some species of calcifying phytoplankton and zooplankton that are small components of lower trophic levels of tuna food webs (Ganachaud et al., 2011). Based on observations in other species, tunas may also experience sub-lethal effects from reduced pH, such as reduced growth and size at age, neurological and behavioral changes and altered evolutionary characteristics of populations (Briffa et al., 2012; Munday et al., 2012; Nilsson et al., 2012; Bromhead et al., 2015).

3.12.3 Conclusions and recommendations

There remains high uncertainty of how individual populations will respond to long-term rising average ocean temperatures and synergistic effects of other climate change outcomes. Oceanic tunas and billfishes may adopt new cooler subtropical areas for spawning, either replacing or in addition to existing tropical spawning sites. They may change their migration phenology, including altering the timing of spawning and truncating the spawning season. These changes may alter distributions and reduce survival rates of larvae and young age classes, reducing recruitment and biomass in existing spawning grounds, but possibly increasing recruitment and biomass at new spawning grounds. Some populations may alter their foraging distributions to higher latitudes and to different longitudes, and alter their vertical depth distributions, in order to maintain preferred species- and age class-specific habitat conditions, including optimal temperature ranges.

Long-term trends in absolute abundance in response to ocean warming will vary by individual population. Whether a population increases or decreases in total abundance will depend, in part, on whether new spawning sites emerge, how survival rates of larvae change at existing and new spawning locations and season of spawning, where suitable foraging habitat emerges and the local abundance of forage species at foraging sites. Furthermore, changes in geospatial and depth distributions might affect fishing mortality rates due to changes in susceptibility to capture in purse seine, longline and other fishing gears. Changes in horizontal and vertical distributions will redistribute benefits derived from tuna fisheries due to changes in the locations of fishing grounds and due to species- and stock-specific changes in catchability by surface and subsurface fishing gears.

There is also high uncertainty of how the effects of ocean warming and other climate change outcomes on oceanic tunas and billfishes will affect pelagic ecosystem structure, processes and stability, and in turn how these broad changes will directly and indirectly affect the population dynamics of tunas and billfishes (Le Borgne et al., 2011; Lehodey et al., 2011; Nicol et al., 2014). For example, effects of climate change outcomes on the productivity of lower- and mid-trophic levels in tuna food chains, as well as changes in vertical and horizontal distributions, and changes in tuna access to prey at depth due to increased stratification and decreased O₂ concentrations (Lehodey et al., 2011) may test the resistance and resilience of tunas to climate change.

Improvements in the certainty of predicted responses to climate change are needed, in part, to inform decisions for achieving long-term ecologically and socio-economically sustainable tuna fisheries. Addressing large uncertainties with basin-, meso- and finer-scale climate change projections, pelagic ecosystem modelling and fundamental aspects of tuna biology and ecology will contribute to improved models of response of tunas to ocean warming and other climate change outcomes (Lehodey et al., 2008, 2011; Senina et al., 2008; Stock et al., 2011; Dueri et al., 2014; Trenkel et al., 2014). For example, Lehodey et al. (2011) identified research on species- and life stage-specific temperature and dissolved O₂ thresholds as a priority. Recent simulations of projected climate change on primary production using
a new generation Earth climate model at high resolution suggest that primary production may decrease less than previously simulated in the western warm pool (Matear et al., 2015). Additionally, there is a need for improved understanding of how individual species and age classes within species are affected by and will respond to ocean warming and other climate change outcomes. Improving the understanding of potential synergistic effects of predicted climate change outcomes is a large research priority, where interacting effects may have substantially different and potentially larger effect on tunas than from the individual factors. There is a need to expand research on climate change effects on oceanic tunas and billfishes to underrepresented areas while continuing to invest in research in the Pacific Ocean, where most research has been conducted to date.

Furthermore, stressors from fisheries affect tunas’ and pelagic ecosystems’ resistance and resilience to ocean warming and other climate change outcomes (Brander, 2010). Tuna fleets may adjust the spatial distribution and magnitude of effort in response to changes in the abundance and distributions of different tuna stocks, as has been observed to occur in some regions in response to large scale climate cycles (Michael et al., 2015). Responses of the fishing industry to changes in the abundance and distributions of market tunas resulting from climate change need to be accounted for in predicted responses of tunas to climate change. Thus, improving the certainty of predictions of ocean warming effects on tunas will require, in part, improved certainty of catch and effort data as well as predictions of the distribution of future catch and effort by the fishing industry (Lehodey et al., 2011) (Figure 3.12.5).

Improvements in the certainty of predicted changes in geospatial and depth distributions and abundance of market oceanic tunas and billfishes in response to climate change will augment the capacity for making long-term management and investment decisions to achieve ecologically sustainable and commercially viable tuna fisheries and supply chains that depend on tuna products (Bell et al., 2011, 2013; Lehodey et al., 2011). Improved predictions will also support the identification of adaption options (Bell et al., 2011; Hobday et al., 2013).

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3.12.4 References
Briffa M, de la Haye K, Munday P. 2012. High CO
2 levels and ocean warming effects on tunas will require, in part, improved certainty of catch and effort data as well as predictions of the distribution of future catch and effort by the fishing industry (Lehodey et al., 2011) (Figure 3.12.5).

3. The significance of warming seas for species and ecosystems


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