Effects of Ocean Warming on Pelagic Tunas

A Review



Chapter 3.12

Effects of Ocean Warming on Pelagic Tunas, a Review

Suggested citation:

Gilman, E., Allain, V., Collette, B., Hampton, J., Lehodey, P. 2016. **Effects of Ocean Warming on Pelagic Tunas, a Review.** Pages 254-270 in: Laffole, D., Baxter, J. (Eds.). Explaining Ocean Warming: Causes, Scale, Effects and Consequences. ISBN 978-8317-1806-4. IUCN – International Union for the Conservation of Nature, Gland, Switzerland.

"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

Eric Gilman¹, Valerie Allain^{2,*}, Bruce B. Collette^{3,*}, John Hampton^{2,*}, Patrick Lehodey^{4,*}

- ¹ Hawaii Pacific University, FisheriesResearchGroup@gmail.com
- ² Pacific Community
- ³ IUCN Tuna and Billfish Specialist Group and National Marine Fisheries Service Systematics Laboratory
- ⁴ Collecte Localisation Satellites, Space Oceanography Division
- * Authors contributed equally

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.

Ocean warming effect	Consequences
Some populations may experience a range shift, moving to higher latitudes and different longitudes where they find suitable water temperatures and conditions that meet their other habitat requirements (e.g. sufficient prey, adequate dissolved O ₂ levels)	Changes the availability of market species to fisheries in that overlap with the new distributions
Some populations may occupy deeper depths where they find suitable temperatures and that meet other habitat requirements (adequate ${\rm O_2}$ concentration, ability to visually detect prey)	Reduces catchability by surface fisheries, and increases catchability by deeper fisherie
For some populations, new spawning locations may emerge in the subtropics and the timing of spawning might change	Populations that establish new spawning sites may have higher resiliency to ocean warming and other climate change outcomes Alters the distribution of young age classes which in turn would alter recruitment due to possible changes in local abundance of prey for the young tunas as well as of their predators Alters the timing of migration between foraging and spawning grounds, which would affect the availability to different fisheries
Example: Pacific Ocean skipjack tuna may shift its distribution eastward and to higher latitudes, and experience a long-term reduction in absolute biomass	Purse seine, pole-and-line and other surface fisheries in the eastern Pacific and western and central Pacific will have increased and decreased skipjack catch rates, respectively Broad changes to pelagic communities may result from the reduction in absolute biomass and range shift
Example: south Pacific Ocean albacore may shift its range south and west, a new spawning site may emerge, and total biomass may increase	Pelagic longline and other fisheries in the current range will experience reduced catch rates, while those overlapping with the new distribution will experienced higher catch rates Broad changes to pelagic communities may result from the increase in absolute biomass and range shift

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., 2005; 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, populationlevel 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 billfishes

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; Orrell 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. maccoyii) and yellowfin (T. albacares) (Majkowski, 2005). Billfishes (suborder Xiphioidei) 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 billfishes 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 billfishes 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-Jefcoats, 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).

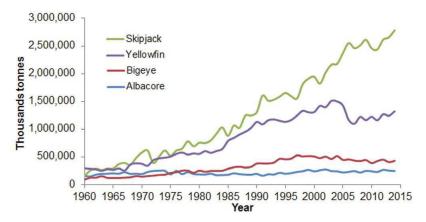


Figure 3.12.1 Global reported landings of albacore, bigeye, skipjack and yellowfin tunas, 1960-2014 (SPC, 2015).

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



Figure 3.12.2 Offloading yellowfin tuna from a Taiwanese-flagged longline vessel based in the Republic of Palau, to be exported to Japan for the sashimi market. © E. Gilman.

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) (Agorau, 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).



Figure 3.12.3 Handline caught bigeye and yellowfin Philippines. $\@$ Eleanor Pertridge Marine Photobank.

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 CO₂ and O₂ 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 sexspecific 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).

Box 3.12.1 Population-specific predicted responses of tunas to ocean warming – three examples

As conditions become more El Niño-like, including rising ocean temperatures, in the tropical Pacific, skipjack tuna may shift its distribution eastward and to higher latitudes, and experience a reduction in absolute biomass. Subtropical south Pacific albacore may shift its range south and west, a new spawning site may emerge, and total biomass may increase. Interacting effects of climate change-caused ocean warming and eddies may disrupt successful spawning of western Atlantic bluefin, resulting in a dramatic decline in abundance and possible extirpation.

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 eastwest 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.

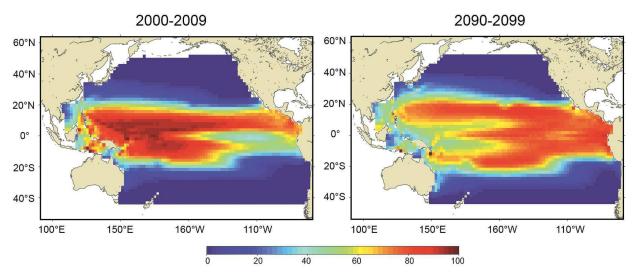
For example, eastward movement of tropical skipjack and yellowfin tunas and increased recruitment have been observed, while subtropical south Pacific albacore may exhibit reduced recruitment following El Niño phases, with opposite responses following La Niña phases (Lehodey et al., 1997; Lehodey, 2001; 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; Guilyardi, 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 (Guilyardi, 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

Mean Pacific skipjack tuna larvae distribution



Mean South Pacific albacore tuna larvae distribution

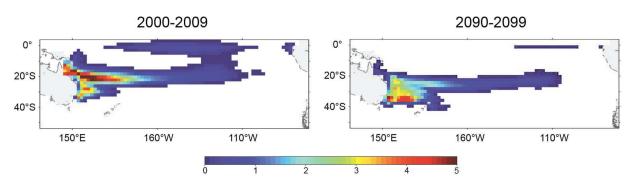


Figure 3.12.4 Model simulations of the effect of climate change on the mean spatial distributions of the density of Pacific Ocean skipjack tuna larvae (top 2 panels) and south Pacific albacore tuna larvae (bottom 2 panels) averaged over ten years at the beginning and end of the 21st Century (adapted from Lehodey *et al.*, 2013, 2015). Scales are in number of larval recruits.m⁻². For both species, the projections are based on the "business as usual" IPCC A2 scenario and using Climate model IPSL-CM4 physical forcing after correction of temperature fields and coupled to the biogeochemical model PISCES.

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).

3.12.2.3.1 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 demand increases with warmer temperatures for tuna to spawn, possible changes in ocean dissolved O₃ 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 CO₂ 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 O2 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 O₂ 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 O2 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 O2 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 O₂ 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 O2 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 O₂ concentrations (Lehodey et al., 2011; Bromhead et al., 2015).

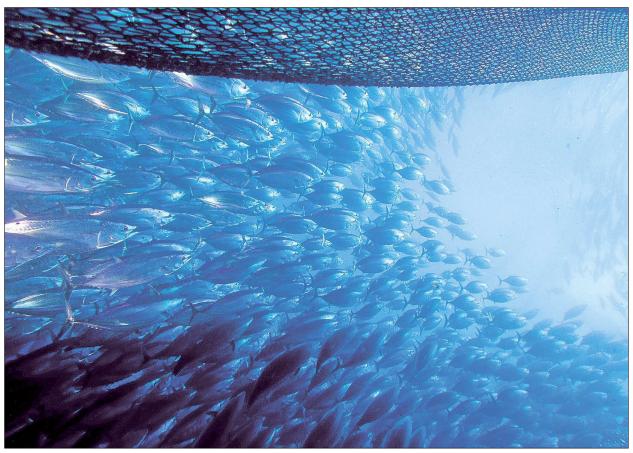


Figure 3.12.5 School of tuna in a purse seine fishing net. $\ @$ Alex Hofford

Effects on tunas and billfishes from other individual climate change outcomes include:

- 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 (O₂) 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 O₂ 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 O₂ 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 larvae survival, larvae 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 larvae 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. llyina 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 O_2 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 socioeconomically 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 O_2 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).

Acknowledgements

The authors are extremely grateful for comments provided by an anonymous reviewer and Professor John Baxter.

3.12.4 References

- Ababouch L, Catarci C. 2008. *Global Production and Marketing of Canned Tuna*. Globefish Research Programme. Food and Agriculture Organization of the United Nations, Rome.
- Aqorau T. 2009. Recent developments in Pacific tuna fisheries: The Palau Arrangement and the vessel day scheme. *The International Journal of Marine and Coastal Law* **24**: 557-581.
- Au D, Pitman R. 1986. Seabird interactions with tuna and dolphins in the eastern tropical Pacific. *Condor* **88**: 304–317.
- Bailey H, Thompson P. 2010. Effect of oceanographic features on fine-scale foraging movements of bottlenose dolphins. *Marine Ecology Progress Series* **418**: 223-233.
- Bakun A. 2012. Ocean eddies, predator pits and bluefin tuna: implications of an inferred 'low risk-limited payoff' reproductive scheme of a (former) archetypical top predator. *Fish and Fisheries* **14**: 424-438.
- Ballance L, Pitman R, Reilly S. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology* **78**: 502–518.
- Bell J, Johnson J, Hobday A. (eds). 2011. Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change. Secretariat of the Pacific Community, Noumea, New Caledonia. 927pp.
- Bell J, Reid C, Batty M, Lehodey P, Rodwell L, Hobday A, Johnson H, Demmke A. 2013a. Effects of climate change on oceanic fisheries in the tropical Pacific: Implications for economic development and food security. Climatic Change 119: 199-212.
- Bell J, Ganachaud A, Gehrke P, Griffiths S, Hobday A, Hoegh-Guldberg O, Johnson J, Le Borgne R, Lehodey P, Lough J, et al. 2013b. Mixed responses of tropical Pacific fisheries and aquaculture to climate change. *Nature Climate Change* 3: 591-599.
- Bell J, Allain V, Allison E, Andrefouet S, Andrew N, Batty M, Blanc M, Dambacher J, Hampton J, Hanich Q, et al. 2015. Diversifying the use of tuna to improve food security and public health in Pacific Island countries and territories. *Marine Policy* 51: 584-591.
- Bignami S, Enochs I, Manzello D, Sponaugle S, Cowen R. 2013. Ocean acidification alters the otoliths of a pantropical fish species with implications for sensory function. *Proceedings of the National Academy of Sciences of the United States of America* **110**: 7366-7370.
- Brander K. 2010. Impacts of climate change on fisheries. *Journal of Marine Systems* **79**: 389-402.
- Briand K, Molony B, Lehodey P. 2011. A study on the variability of albacore (*Thunnus alalunga*) longline catch rates in the southwest Pacific Ocean. *Fisheries Oceanography.* **20**: 517–529.
- Briffa M, de la Haye K, Munday P. 2012. High ${\rm CO_2}$ and marine animal behaviour: potential mechanisms and ecological consequences. *Marine Pollution Bulletin* **64**: 1519–1528.
- Brodziak J, Walsh W. 2013. Model selection and multimodel inference for standardizing catch rates of bycatch species: a case study of oceanic whitetip shark in the Hawaii-based longline fishery. Canadian Journal of Fisheries and Aquatic Sciences 1740: 1723–1740.

- Bromhead D, Scholey V, Nicol S, Margulies D, Wexler J, Stein M, Hoyle S, Lennert-Cody C, Williamson J, Havenhand J, et al. 2015. The potential impact of ocean acidification upon eggs and larvae of yellowfin tuna (*Thunnus albacares*). Deep-Sea Research // 113: 268-279.
- Cai W, Borlace S, Lengaigne M, vanRensch P, Collins M, Vecchi G, Timmermann A, Santoso A, McPhaden M, Wu L, et al. 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. Nature Climate Change http://dx.doi.org/10.1038/NCLIMATE2100.
- Cinner E, Folke C, Daw T, Hicks C. 2011. Responding to change: using scenarios to understand how socioeconomic factors may influence amplifying or dampening exploitation feedbacks among Tanzanian fishers. Global Environmental Change-Human and Policy Dimensions 21: 7-12.
- Collette B, Reeb C, Block B. 2001. Systematics of the tunas and mackerels (Scombridae). In: Tuna: Physiology, Ecology, and Evolution. Block B, Stevens E. (eds). Academic Press, San Diego. pp. 1-33
- Collette B, McDowell J, Graves J. 2006. Phylogeny of Recent billfishes (Xiphioidei). *Bulletin of Marine Science* **79**: 455-468.
- Collette B, Carpenter K, Polidoro B, Juan-Jorda M, Boustany A, Die D, Elfes C, Fox W, Graves J, Harrison L, et al. 2011. High value and long life Double jeopardy for tunas and billfishes. Science 333: 291-292.
- Collette B, Fox W, Juan Jorda M, Nelson R, Pollard D, Suzuki N, Teo S. 2014. *Thunnus orientalis*. The IUCN Red List of Threatened Species. http://dx.doi.org/10.2305/IUCN.UK.2014-3.RLTS.T170341A65166749.en).
- Cox S, Essington T, Kitchell J, Martell S, Walters C, Boggs C, Kaplan I. 2002. Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. II. A preliminary assessment of the trophic impacts of fishing and effects on tuna dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1736–1747.
- Croll D, Dewar H, Dulvy N, Fernando D, Francis M, Galván-Magaña F, Hall M, Heinrichs S, Marshall A, Mccauley D, et al., 2016. Vulnerabilities and fisheries impacts: the uncertain future of manta and devil rays. Aquatic Conservation: Marine and Freshwater Ecosystems 26: 562-575.
- Davies N, Harley S, Hampton J, McKechnie S. 2014. Stock Assessment of Yellowfin Tuna in the Western and Central Pacific Ocean. WCPFC-SC10-2014/SA-WP- 04. Western and Central Pacific Fisheries Commission, Kolonia, Federated States of Micronesia.
- Dueri S, Bopp L, Maury O. 2014. Projecting the impacts of climate change on skipjack tuna abundance and spatial distribution. *Global Change Biology* **20**: 742-753.
- Dufour F, Arrizabalaga H, Irigoien X, Santiago J. 2010. Climate impacts on albacore and bluefin tunas migrations phenology and spatial distribution. *Progress in Oceanography* **86**: 283–290.
- Edwards M, Richardson A. 2004. Impact of climate change on marine pelagic phenology and troiphic mismatch. *Nature* **430**: 881-884.
- Essington T. 2010. Trophic cascades in open ocean ecosystems In: Trophic Cascades. Predators, Prey and the Changing Dynamics of Nature. Terborgh J, Estes JA. (eds). Island Press, Washington, D.C. pp. 91-106.

- Fabry V, Seibel B, Feely R, Orr J. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science* **65**: 414–432.
- FAO. 2014. The State of World Fisheries and Aquaculture. Opportunities and Challenges. Food and Agriculture Organization of the United Nations, Rome.
- FAO. 2015a. Global Tuna Catches by Stock 1950-2010. Available online, http://www.fao.org/fishery/statistics/tuna-catches/ query/en, accessed 28 Sept. 2015. Food and Agriculture Organization of the United Nations, Rome.
- FAO. 2015b. Global Tuna Catches by Stock. Fishery statistical Collections. Available online, http://www.fao.org/fishery/statistics/tuna-catches/en, accessed 28 Sept. 2015. Food and Agriculture Organization of the United Nations, Rome.
- FFA. 2015 Economic Indicators Report. Pacific Islands Forum Fisheries Agency, Honiara, Solomon Islands.
- Fonteneau A, Gaertner D, Nordstrom V. 1999. An overview of problems in the catch per unit of effort and abundance relationship for the tropical purse seine fisheries. *Collective Volume of Scientific Papers, ICCAT* **49**: 258-278.
- Gaertner D, Dreyfus-Leon M. 2004. Analysis of non-linear relationships between catch per unit effort and abundance in a tuna purseseine fishery simulated with artificial neural networks. *ICES Journal of Marine Science* **61**: 812-820.
- Ganachaud A, Gupta A, Orr J, Wijffels S, Ridway K, Hemer M, Maes C, Steinberg C, Tribollet A, Qiu B, et al. 2011. Chapter 3. Observed and expected changes to the tropical Pacific Ocean. In: Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change. Bell J, Johnson J, Hobday A. (eds). Secretariat of the Pacific Community, Noumea, New Caledonia. pp. 101-188.
- Gillett R. 2009. Fisheries in the Economies of Pacific Island Countries and Territories. Pacific Studies Series, Asian Development Bank, Manila.
- Gilman E. 2011. Bycatch governance and best practice mitigation technology in global tuna fisheries. *Marine Policy* **35**: 590-609.
- Gilman E, Chaloupka M, Read A, Dalzell P, Holetschek J, Curtice C. 2012. Hawaii longline tuna fishery temporal trends in standardized catch rates and length distributions and effects on pelagic and seamount ecosystems. Aquatic Conservation: Marine and Freshwater Ecosystems 22: 446-488.
- Gilman E, Owens M, Kraft T. 2014a. Ecological risk assessment of the Marshall Islands longline tuna fishery. Marine Policy 44: 239-255.
- Gilman E, Passfield K, Nakamura K. 2014b. Performance of regional fisheries management organizations: ecosystem-based governance of bycatch and discards. *Fish and Fisheries* **15**: 327-351.
- Gilman E, Hall M. 2015. Potentially Significant Variables Explaining Bycatch and Survival Rates and Alternative Data Collection Protocols to Harmonize Tuna RFMOs' Pelagic Longline Observer Programmes. Appendix 1 to WCPFC-SC11-2015/EB-IP-05. Western and Central Pacific Fisheries Commission, Kolonia, Pohnpei, Federated States of Micronesia.
- Griffiths S, Young J, Lansdell M, Campbell R, Hampton J, Hoyle S, Langley A, Bromhead D, Hinton M. 2010. Ecological effects of longline fishing and climate change on the pelagic ecosystem off eastern Australia. *Reviews in Fish Biology and Fisheries* **20**: 239-272.

- Guilyardi E. 2006. 2006: El Niño-mean state-seasonal cycle interactions in a multi-model ensemble. *Climate Dynamics* **26**: 329–348.
- Gulland J. 1964. Catch per unit effort as a measure of abundance. Rapports et Procès-verbaux des Réunions Conseil International pour l'Exploitation de la Mer 155: 8–14.
- Hall M, Alverson D, Metuzal K. 2000. By-catch: problems and solutions. *Marine Pollution Bulletin* **41**: 204–219.
- Hinke J, Kaplan I, Avdin K, Watters G, Olson R, Kitchell J. 2004. Visualizing the food-web effects of fishing for tunas in the Pacific Ocean. *Ecology and Society* 9: 10, http://www.ecologyandsociety.org/vol9/iss1/art10.
- Hobday A, Arrizabalaga H, Evans K, Nicol S, Young J, Weng K. 2015. Impacts of climate change on marine top predators: advances and future challenges. *Deep Sea Research II* 113: 1-8.
- Hobday A, Young J, Abe O, Costa D, Cowen R, Evans K, Gasalla M, Kloser R, Maury O, Weng K. 2013. Climate Impacts and Oceanic Top Predators: Moving from impacts to adaptation in oceanic systems. *Reviews in Fish Biology and Fisheries* **23**: 537-546.
- Hyrenbach K, Forney K, Dayton P. 2000. Marine protected areas and ocean basin management. *Aquatic Conservation: Marine and Freshwater Ecosystems* **10**: 437–458.
- Hyrenbach K, Veit R, Weimerskirch H, Hunt Jr. GL. 2006. Seabird associations with mesoscale eddies: the subtropical Indian Ocean. *Marine Ecology Progress Series* **324**: 271–279.
- Ilyina T, Zeebe R, Brewer P. 2010. Future ocean increasingly transparent to low frequency sound owing to carbon dioxide emissions. *Nature Geoscience* **3**: 18–22.
- IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Stocker T, Qin D, Plattner G, Tignor M, Allen S, Boschung J, Nauels A, Xia Y, Bex V, Midgley P. (eds). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- ISC. 2010. Report of the Tenth Meeting of the International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific Ocean. Plenary Session. 21-26 July 2010. Victoria, B.C., Canada. International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific Ocean, Takamatsu, Japan.
- ISSF. 2016. *Tuna Stock Status Update 2016*. ISSF Technical Report 2016-05. International Seafood Sustainability Foundation, Washington, D.C., USA.
- Kitchell J, Essington T, Boggs C, Schindler D, Walters C. 2002. The role of sharks and longline fisheries in a pelagic ecosystem of the central Pacific. *Ecosystems* **5**: 202–216.
- Last P, White W, Gledhill D, Hobday A, Brown R, Edgar G, Pecl G. 2011. Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. *Global Ecology and Biogeography* **20**: 58–72.
- Le Borgne R, Allain V, Griffiths S, Matear R, McKinnon A, Richardson A, Young J. 2011. Chapter 4. Vulnerability of open ocean food webs in the tropical Pacific to climate change. In: *Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change*. Bell J, Johnson J, Hobday A. (eds). Secretariat of the Pacific Community, Noumea, New Caledonia. pp. 189-249.

- Lehodey P. 2000. Impacts of the El Niño Southern Oscillation on tuna populations and fisheries in the tropical Pacific Ocean. Working Paper SCTB13-RG-1. 13th Standing Committee on Tuna and Billfish, Noumea, 5-12 July 2000, Secretariat of the Pacific Community, Noumea.
- Lehodey P. 2001. The pelagic ecosystem of the tropical Pacific Ocean: Dynamic spatial modelling and biological consequences of ENSO. *Progress in Oceanography* **49**: 439–468.
- Lehodey P. 2004. Chapter 11: Climate and fisheries: an insight from the Pacific Ocean. In *Ecological Effects of Climate Variations in the North Atlantic*. Stenseth N, Ottersen G, Hurrel J, Belgrano A. (eds). Oxford University Press; pp.137-146.
- Lehodey P, Bertignac M, Hampton J, Lewis A, Picaut J. 1997. El Niño Southern Oscillation and tuna in the western Pacific. *Nature* **389**: 715-718.
- Lehodey P, Alheit J, Barange M, Baumgartner T, Beaugrand G, Drinkwater K, Fromentin J, Hare S, Ottersen G, Perry R, et al. 2006. Climate variability, fish and fisheries. *Journal of Climate* **19**: 5009–5030.
- Lehodey P, Senina I, Sibert J, Hampton J. 2008. A spatial ecosystem and populations dynamics model (SEAPODYM) modelling of tuna and tuna-like populations. *Progress in Oceanography* **78**: 304–318.
- Lehodey P, Senina I, Sibert J, Bopp L, Calmettes B, Hampton J, Murtugudde R. 2010. Preliminary forecasts of population trends for Pacific bigeye tuna under the A2 IPCC scenario. *Progress in Oceanography* **86**: 302–315.
- Lehodey P, Hampton J, Brill R, Nicol S, Senina I, Calmettes B, Portner H, Bopp L, Ilyina T, Bell J, Sibert J. 2011. Chapter 8. Vulnerability of oceanic fisheries in the tropical Pacific to climate change. In: Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change. Bell J, Johnson J, Hobday A. (eds). Secretariat of the Pacific Community, Noumea, New Caledonia. pp. 433-492.
- Lehodey P, Senina I, Calmettes B, Hampton J, Nicol S. 2013. Modelling the impact of climate change on Pacific skipjack tuna population and fisheries. *Climatic Change* **119**: 95-109.
- Lehodey P, Senina I, Nicol S, Hampton J. 2015. Modelling the impact of climate change on South Pacific albacore tuna. *Deep-Sea Research II* **113**: 246-259.
- Lough J, Meehl G, Salinger M. 2011. Chapter 2. Observed and projected changes in surface climate of the tropical Pacific. In: Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change. Bell J, Johnson J, Hobday A. (eds). Secretariat of the Pacific Community, Noumea, New Caledonia. pp. 49-100.
- Lu H, Lee K, Liao H. 1998. On the relationship between El Niño-Southern Oscillation and South Pacific albacore. *Fisheries Research* **39**: 1–7.
- Majkowski J. 2005. Tuna and tuna-like species. In: Review of the State of World Marine Fishery Resources. FAO Fisheries Technical Paper 457. Food and Agriculture Organization of the United Nations, Rome, pp. 163-174.
- Majkowski J. 2007. Global Fishery Resources of Tuna and Tunalike Species. FAO Fisheries Technical Paper 483. Food and Agriculture Organization of the United Nations, Rome.

- Matear R, Chamberlain M, Sun C, Feng M. 2015. Climate change projection for the western tropical Pacific Ocean using a high-resolution ocean model: Implications for tuna fisheries. *Deep-Sea Research II* 113: 22–46.
- Meehl G, Washington W. 1996. El Niño-like climate change in a model with increased atmospheric ${\rm CO_2}$ concentrations. *Nature* **382**: 56–60.
- Michael P, Tuck G, Strutton P, Hobday A. 2015. Environmental associations with broad-scale Japanese and Taiwanese pelagic longline effort in the southern Indian and Atlantic Oceans. *Fisheries Oceanography* **24**: 478-493.
- Mitchell J, Collins K, Miller P, Suberg L. 2014. Quantifying the impact of environmental variables upon catch per unit effort of the blue shark *Prionace glauca* in the western English Channel. *Journal of Fish Biology* **85** (3): 657-670.
- Miyake M. 2008. Overview of the world tuna fisheries industry and its managements. IN *Proceedings of the Fourth International Fishers Forum, November 12-14 2007, Puntarenas, Costa Rica*. Western Pacific Regional Fishery Management Council, Honolulu.
- Miyake M, Guillotreau P, Sun C, Ishimura G. 2010. Recent Developments in the Tuna Industry. Stocks, Fisheries, Management, Processing, Trade and Markets. FAO Fisheries and Aquaculture Technical Paper 543. Food and Agriculture Organization of the United Nations, Rome.
- Morato T, Hoyle S, Allain V, Nicol S. 2010. Tuna longline fishing around West and Central Pacific seamounts. *PLoS ONE* **5**: e14453. doi:10.1371/journal.pone.0014453.
- Muhling B, Lee S, Lamkin J, Liu Y. 2011. Predicting the effects of climate change on bluefin tuna (*Thunnus thynnus*) spawning habitat in the Gulf of Mexico. *ICES Journal of Marine Science* **68**: 1051-1062.
- Munday P, Mccormick MI, Meekan M, Dixson DL, Watson S, Chivers DP, Ferrari MCO. 2012. Selective mortality associated with variation in CO₂ tolerance in a marine fish. *Ocean Acidification*. 1: 1–6.
- Musick J. 1999. Ecology and conservation of long-lived marine animals. In: Life in the Slow Lane: Ecology and Conservation of Long-lived Marine Animals. Musick H. (ed.). American Fisheries Society Symposium 23, Bethesda, Maryland, USA. pp. 1-10.
- Myers R, Bowen K, Barrowman N. 1999. Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences* **56**: 2404-2419.
- Nicol S, Menkes C, Jurado-Molina J, Lehodey P, Usu T, Kumasi B, Muller B, Bell J, Tremblay-Boyer L, Briand K. 2014. Oceanographic characterization of the Pacific Ocean and the potential impact of climate variability on tuna stocks and tuna fisheries. SPC Fisheries Newsletter 145: 37-48.
- Nilsson G, Dixson D, Domenici P, McCormick M, Sorensen C, Watson S, Munday P. 2012. Near-future carbon dioxide levels alter fish behaviour by interfering with neurotransmitter function. *Nature Climate Change* 2: 201–204.
- Nishikawa Y, Honma M, Ueyenagi S, Kikawa S. 1985. Average distribution of larvae of oceanic species of scombrid fishes, 1951–1981. Contribution of the Far Seas Fisheries Research Laboratory, Fishery Agency of Japan 236: 1–99.

- Olson R, Watters G. 2003. A Model of the Pelagic Ecosystem in the Eastern Tropical Pacific Ocean. IATTC Bulletin Vol. 22 No. 3. ISSN 0074-0993. Inter-American Tropical Tuna Commission, La Jolla. USA.
- Orrell T, Collette B, Johnson G. 2006. Molecular data support separate scombroid and xiphioid clades. *Bulletin of Marine Science* **79**: 505-519.
- Perry A, Low P, Ellis J, Reynolds J. 2005. Climate change and distribution shifts in marine fishes. *Science* **308**: 1912-1915.
- Pitcher T. 1995. The impact of pelagic fish behaviour on fisheries. Scientia Marina 59: 295-306.
- Poisson F, Gaertner J, Taquet M, Durbec J, Bigelow K. 2010. Effects of lunar cycle and fishing operations on longline-caught pelagic fish: fishing performance, capture time, and survival of fish. *Fishery Bulletin* **108**: 268-281.
- Poloczanska E, Brown C, Sydeman W, Kiessling W, Schoeman D, Moore P, Brander K, Bruno J, Buckley L, Burrows M, et al. 2013. Global imprint of climate change on marine life. Nature Climate Change 3: 919–925.
- Polovina J, Balazs G, Howell E, Parker D, Seki M, Dutton P. 2004. Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fisheries Oceanography* **13**: 36-51.
- Polovina J, Abecassis M, Howell E, Woodworth P. 2009. Increases in the relative abundance of mid-trophic level fishes concurrent with declines in apex predators in the subtropical North Pacific, 1996-2006. Fishery Bulletin 107: 523-531.
- Polovina J, Woodworth-Jefcoats P. 2013. Fishery-induced changes in the subtropical Pacific pelagic ecosystem size structure: Observations and theory. *PLoS ONE* 8: doi:10.1371/journal.pone.0062341.
- Portner H, Langenbuch M, Reipschlager A. 2004. Biological impact of elevated ocean CO₂ concentrations: Lessons from animal physiology and earth history. *Journal of Oceanography* **60**: 705–718.
- Portner H, Storch D, Heilmayer O. 2005. Constraints and trade-offs in climate dependent adaptation: Energy budgets and growth in a latitudinal cline. *Scientia Marina* **69**: 271–285.
- Portner H, Farrell A. 2008. Physiology and climate change. *Science* **322**: 690-692.
- Power S, Casey T, Folland C, Colman A, Mehta V. 1999. Interdecadal modulation of the impact of ENSO on Australia. *Climate Dynamics* **15**: 319–324.
- Risbey J, Lewandowsky S, Langlais C, Moneselesan D, O'Kane T, Oreskes N. 2014. Well-estimated global surface warming in climate projections selected for ENSO phase. *Nature Climate Change* **4** (9): 835-840.
- Schaefer K. 2001. Assessment of skipjack tuna (*Katsuwonus pelamis*) spawning activity in the eastern Pacific Ocean. *Fishery Bulletin US* **99**: 343–350.
- Senina I, Sibert J, Lehodey P. 2008. Parameter estimation for basin-scale ecosystem-linked population models of large pelagic predators: Application to skipjack tuna. *Progress in Oceanography* **78**: 319–335.

- SPC. 2014. Stock Assessment of Bigeye Tuna in the Western and Central Pacific Ocean. WCPFC-SC10-2014/SA-WP-01. Rev1. Secretariat of the Pacific Community, Noumea, New Caledonia.
- SPC. 2015. Western and Central Pacific Fisheries Commission Tuna Fishery Yearbook 2014. Oceanic Fisheries Programme, Secretariat of the Pacific Community, Noumea, New Caledonia.
- Stevens J, Bonfil R, Dulvy N, Walker P. 2000. The effects of fishing on sharks, rays and chimaeras (chondrichthyans) and implications for marine ecosystems. *ICES Journal of Marine Science* **57**: 476–949.
- Stock CA, Alexander MA, Bond, NA, Brander K, Cheung WWL, Curchitser EN, Delworth TL, Dunne JP, Griffies SM, Haltuch MA, et al. 2011. On the use of IPCC-class models to assess the impact of climate on living marine resources. Progress in Oceanography 88: 1-27.
- Trenkel V, Huse G, MacKenzie B, Alvarez P, Arrizabalaga H, Castonguay M, Goni N, Gregoire F, Hatun H, et al. 2014. Comparative ecology of widely distributed pelagic fish species in the North Atlantic: Implications for modelling climate and fisheries impacts. Progress in Oceanography 129: 219-243.
- Vandeperre F, Aires-da-Silva A, Santos M, Ferreira R, Bolten A, Serrao Santos R, Afonso P. 2014. Demography and ecology of blue shark (*Prionace glauca*) in the central North Atlantic. *Fisheries Research* **153**: 89–102.
- Ward P, Myers R. 2005. Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology* **86**: 835–847.
- Willis-Norton E, Hazen E, Fossette S, Shillinger G, Rykaczewski R, Foley D, Dunne J, Bograd S. 2015. Climate change impacts on leatherback turtle pelagic habitat in the Southeast Pacific. *Deep Sea Research II* 113: 260-267.
- Young J, Lansdell M, Hobday A, Dambacher J, Griffiths S, Cooper S, Kloser R, Nichols P, Revell A. 2009. *Determining Ecological Effects of Longline Fishing in the Eastern Tuna and Billfish Fishery*. CSIRO Marine and Atmospheric Research, Hobart, Australia.
- Zhou S, Smith A, Punt A, Richardson A, Gibbs M, Fulton E, Pasco S, Bulman C, Bayliss P, Sainsbury K. 2010. Ecosystem-based fisheries management requires a change to the selective fishing philosophy. Proceedings of the National Academy of Sciences of the United States of America 107: 9485-9489.