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Just a FAD? Ecosystem impacts of tuna purse-seine fishing associated with fish aggregating devices in the western Pacific Warm Pool Province

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Abstract

The western and central Pacific Ocean supports the world's largest tuna fisheries. Since the 1990s, the purse-seine fishery has increasingly fished in association with fish aggregating devices (FADs), which has increased catches of juvenile bigeye and yellowfin tunas and vulnerable bycatch species (e.g., sharks). This has raised concerns regarding the sustainability of these species' populations and the supporting ecosystem, but may provide improved food security of Pacific Island nations through utilisation of FAD-associated byproduct species (e.g., wahoo). An ecosystem model of the western Pacific Warm Pool Province was used to explore the potential ecological impacts of varying FAD fishing effort (±50% or 100%) over 30 years. The ecosystem has undergone a significant change in structure since 1980 from heavy exploitation of top predators (e.g., tunas) and "fishing up the food web" of high-trophic-level non-target species. The ecosystem appeared resistant to simulated fishing perturbations, with only modest changes (<10%) in the biomass of most groups, although some less productive shark bycatch species decreased by up to 43%, which had a subsequent positive effect on several byproduct species, the prey of sharks. Reduction of FAD effort by at least 50% was predicted to increase the biomass of tuna species and sharks and return the ecosystem structure to a pre-industrial-fishing state within 10 years. Spatial disaggregation of the model and integration of economic information are recommended to better capture ecological and economic changes that may result from fishing and/or climate impacts and to develop appropriate management measures in response.

KEYWORDS

Bycatch, Ecopath, Ecosim, ecosystem modelling, FAD, fish aggregating device, food security

1 | INTRODUCTION

A growing body of literature provides evidence of change in the structure and dynamics of marine ecosystems due to industrialised fishing (Alleway, Connell, Ward, & Gillanders, 2014; Cox et al., 2002; Myers, Baum, Shepherd, Powers, & Peterson, 2007; Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998; Polovina, Abecassis,

Howell, & Woodworth, 2009). Tuna fisheries are among the world's most important fisheries, with catches steadily rising from 0.6 million tonnes in 1950 to over 7.39 million tonnes in 2015—16% of the total global capture fisheries production (FAO, 2017). They catch large predatory species (e.g., tuna, billfish, sharks), as targets or bycatch, that occupy high trophic levels (TL > 4.0), and can play an important role in the regulation of the populations of species at

lower trophic levels (Baum & Worm, 2009; Griffiths, Olson, & Watters, 2013). As the global demand for seafood is likely to continue to increase to support a predicted global human population of 9 billion by 2050 (Msangi et al., 2013), tuna fisheries may generate a concomitant increase in their impact on marine ecosystems.

Fishing impacts on marine ecosystems have been commonly illustrated through a decline in the mean trophic level of catches, a result of fisheries progressively shifting their targeting towards smaller species as the abundance of larger predators decreases. This phenomenon, known as "fishing down the food web" (Pauly et al., 1998), or more recently "assemblage overfishing" (Pauly & Froese, 2012), can result in a regime shift in the ecosystem structure being dominated by highly productive species that often have low economic value (Carscadden, Frank, & Leggett, 2001; Christensen, 1998; Daskalov, 2002; Roux et al., 2013). A recent example of fishing down a pelagic food web by tuna fisheries was described by Polovina et al. (2009) in the North Pacific subtropical gyre ecosystem. They demonstrated that a decadal decline in the catches of apex predators—bigeye and albacore tunas, billfish and blue shark—by the Hawaiian tuna longline fishery resulted in the proliferation of smaller mid-trophic-level species (dolphinfish, sickle pomfret, escolar and snake mackerel) and a reduction in the mean trophic level of the catch from 3.85 to 3.66.

The potential negative impacts of fishing, both the direct effects on individual target and bycatch species and the indirect trophic effects that may cascade throughout an ecosystem, are now formally recognised in national and international fisheries policies in various forms of ecosystem-based fisheries management (Moffitt et al., 2016). Furthermore, concerns raised by the public and by non-governmental organisations over the sustainability of fish stocks and the impacts of fishing on non-target species have been an additional motivation for the fishing industry to address its broader ecological impacts and adopt ecologically sustainable fishing practices, which are now commonly promoted through eco-labelling (Kirby, Visser, & Hanich, 2014).

The western Pacific Warm Pool Province (Figure 1; herein termed the "Warm Pool") supports the largest and most valuable fisheries in the world (Langley et al., 2009). Using primarily purse-seine, longline and pole-and-line gears, these fisheries target a range of high-trophic-level tunas and billfish across a region of over 12 million km^2. The catches, composed mainly of skipjack, yellowfin and bigeye tunas, have increased steadily over the last decade (Williams, Terawasi, & Reid, 2017), to the point that recent stock assessments estimated that these stocks are at, or near, full exploitation (FFA, 2017).

Much of the increase in the Warm Pool tuna catch is attributable to the expansion, increased efficiency, and profitability of the purse-seine fishery associated with natural or artificial floating objects—collectively referred to as fish aggregating devices (FADs)—that exploit the behaviour of small size classes of these tunas to aggregate under these floating objects (Bromhead, Foster, Attard, Findlay, & Kalish, 2003; Dagorn, Holland, Restrepo, & Moreno, 2013). In the vast expanse of often featureless open ocean, FADs offer shelter, "meeting points" and feeding opportunities for a diverse suite of wide-ranging oceanic species (Fréon & Dagorn, 2000). FADs therefore have the potential to aggregate the biomass of several species from distances of up to several kilometres (Itano & Holland, 2000; Schaefer & Fuller, 2007) and may be seen to function as "ecological traps," whereby the accumulated assemblage biomass remains in the vicinity of the object (Hallier & Gaertner, 2008). Consequently, purse-seine fishing associated with FADs has the potential to extract a far greater biomass of these aggregated fish, and with far greater efficiency, than setting on free-swimming schools of tunas, which are more widely and heterogeneously distributed across the high seas.

Furthermore, increased FAD effort in the WCPO has increased the catch of numerous non-target bycatch species that also associate with FADs (Chan, Clarke, & Squires, 2014; Pilling, Harley, Nicol, Williams, & Hampton, 2015). These bycatch species are generally discarded, but some (herein termed "byproduct" species) are legally retained for sale or consumption. The increase in the catch of non-target species has raised concerns by scientists and fisheries managers over the long-term sustainability of more vulnerable bycatch species with less productive life history traits, such as silky and oceanic whitetip sharks (Clarke, Harley, Hoyle, & Rice, 2013; Leroy et al., 2013; Rice & Harley, 2013). However, some highly productive byproduct species, such as dolphinfish, wahoo and rainbow runner, could potentially help address growing concerns regarding food security for Pacific Island nations, whose future protein requirements may be facing a 75% shortfall under existing fishing effort regimes due to a rapidly increasing human population (Pilling et al., 2015).

To reduce the fishing mortality of small bigeye and yellowfin tunas and associated bycatch species, in 2009 the Western and Central Pacific Fisheries Commission (WCPFC) adopted a conservation and management measure (CMM 2008-01) that requires that Member Countries either cease fishing on FADs on the high seas between 20°N and 20°S during a 2-month period each year or adopt a catch limit for bigeye tuna that is 10% lower than the average catch by that Member during 2001–2004. Figure 2 summarises the change in purse-seine fishery setting behaviour through time, with a shift to setting on artificial drifting FADs, as opposed to natural FADs, in around 1995, resulting in a dramatic increase in bigeye tuna catch. The introduction of CMM 2008-01 led to a reduction in the percentage of FAD sets and the catch of bigeye tuna, but increased the catch of non-target species by around 65%, which is likely due to increased reporting of these species as they may partially offset the reduction in tuna catch.

The objective of this study was to build an ecosystem model of the Warm Pool ecosystem to explore the potential effects of FAD fishing on ecosystem structure and the biomass of individual target, byproduct, bycatch and forage species. Fishing impacts were simulated by increasing or decreasing FAD effort by either 50% or 100% in 2016, or by transferring FAD effort to the more traditional purse-seine fishery that sets on free-swimming tuna schools not associated with FADs, and observing the ecosystem and biomass responses 30 years later in 2046.
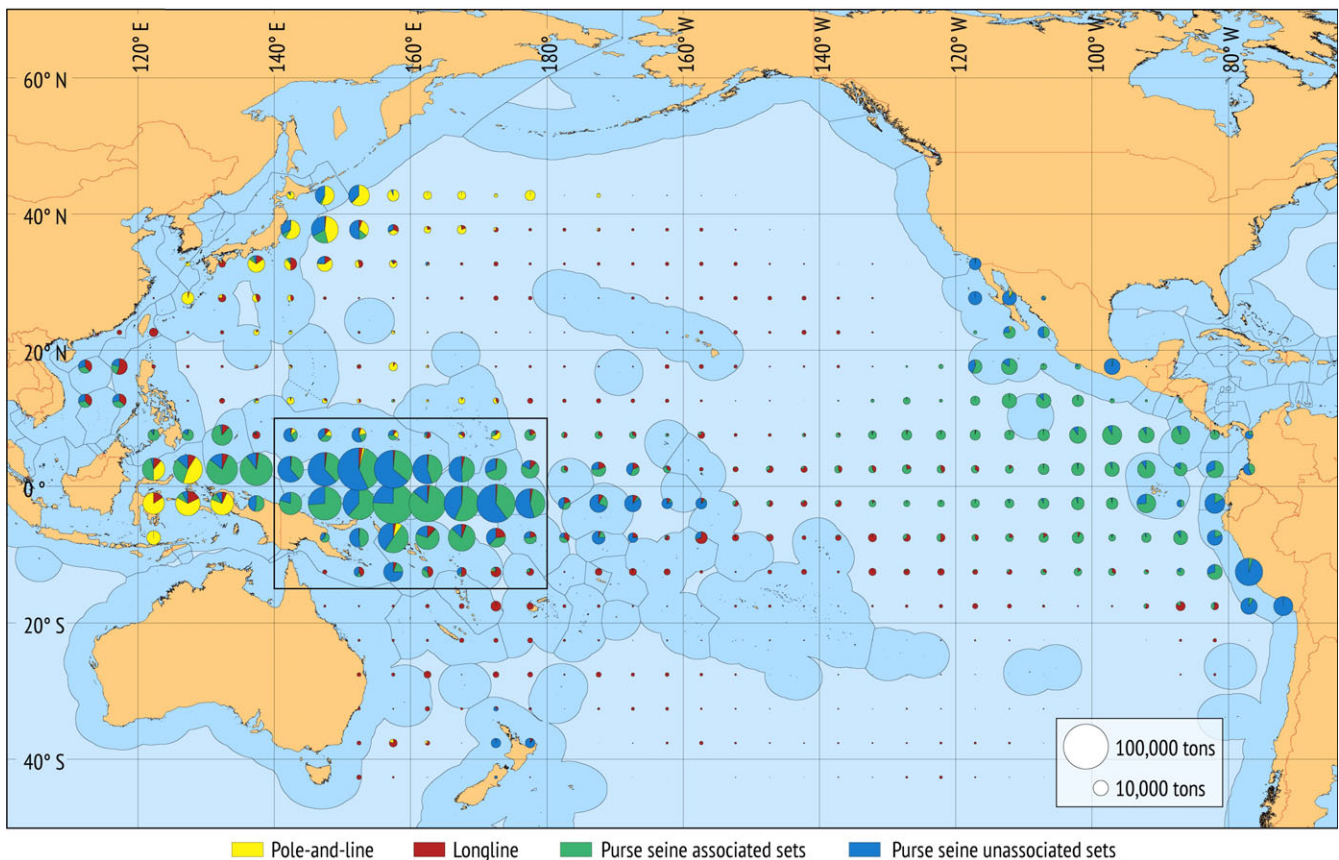
FIGURE 1 Geographic boundaries of the western Pacific Warm Pool Province ecosystem model (black rectangle) and proportions of tuna catches by pole-and-line, longline and associated (FAD) and non-associated (NOA) purse-seine sets for 2013 (unpublished SPC data) [Colour figure can be viewed at wileyonlinelibrary.com]

2 | MATERIALS AND METHODS

2.1 | Spatial extent of the model

The Warm Pool is an oceanographic province of the western Pacific Ocean characterised by surface waters with high sea surface temperature (>29°C), low salinity (due to high tropical rainfall) and low dissolved oxygen (Longhurst, 2007). The thermocline is relatively deep (~80 m), with a strong temperature gradient; in combination with a haline stratification, it restricts transfer of nutrients to the surface layer. However, during El Niño events, the thermocline is shallower (~40 m), supplying new nutrients to the euphotic zone and stimulating increased primary production. The longitude of the eastern boundary of the Warm Pool varies. It is marked by a clear front in salinity which, on average, separates the Warm Pool from the Pacific Equatorial Divergence (PEQD) at longitude 178°W (Le Borgne et al., 2011). The longitude of the front between the two provinces moves to the west during La Niña events and to the east during El Niño events. The northern boundary of the Warm Pool is the convergence between South Equatorial Current (SEC) and the North Equatorial Countercurrent (NECC), around 5°N. The southern boundary is the convergence between the SEC and the South Equatorial Countercurrent (SECC).

Although its surface layer is typically oligotrophic, the Warm Pool is the most important region in the world for skipjack and yellowfin tuna fisheries. Because the oceanography in this area is spatially dynamic, both seasonally and annually, for this study the modelled area of the Warm Pool was defined as 10°N–15°S and 140°E–180°, which covers 12,203,000 km^2, of which 11,543,000 km^2 is ocean (Figure 1).

2.2 | Ecosystem modelling approach

Ecosystem models can be structured in a variety of ways and are generally purpose-built to explore specific hypotheses. Because of the many thousands of species in the marine environment and the enormous complexities of ecological interactions among species and the influences of the environment, it is practical, from both a computer processing and conceptual visualisation point of view, to simplify an ecosystem into groups of species that play a similar ecological role (e.g., preferred habitat, diet) and have similar biological traits (e.g., maximum size, and rates of production and consumption). The taxonomic resolution of such "functional groups" needs to match the hypotheses being explored and the data available for parameterising the model for a group. Group membership can range from a representation of a specific life stage of a species (e.g., "juvenile skipjack") to a group comprising all life stages of hundreds of ecologically similar species (e.g., "micronekton"). To avoid confusion in references in the text hereafter relating to a specific functional
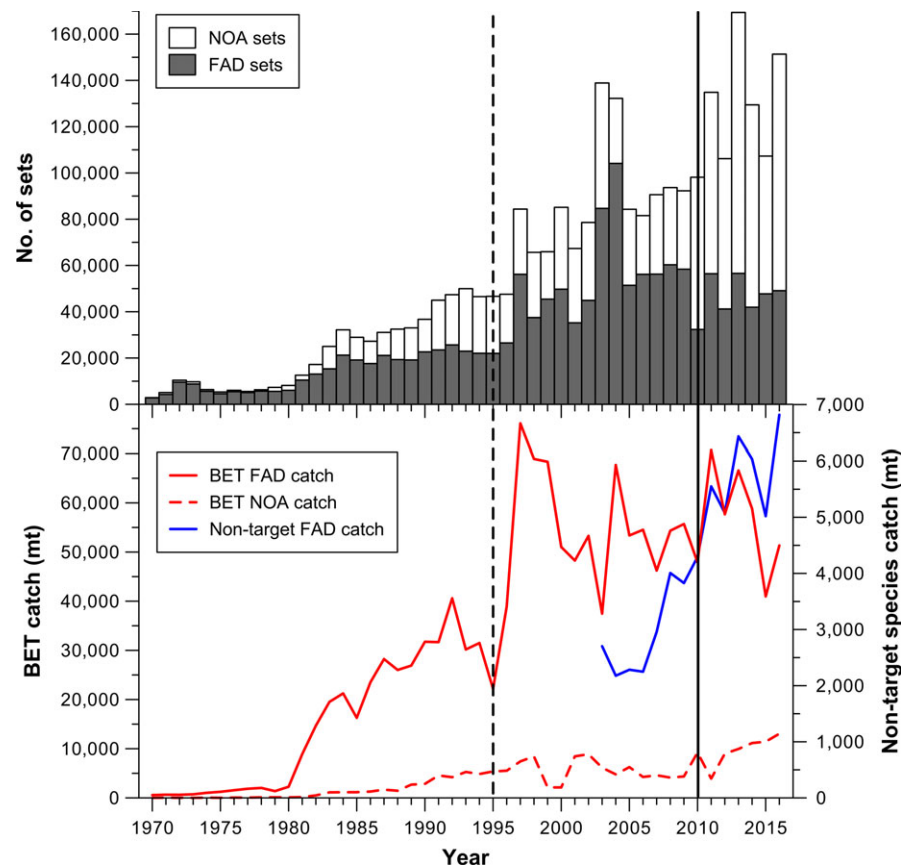
FIGURE 2 Time series of annual number of purse-seine-associated (FAD) and non-associated (NOA) sets (top panel) with the total catch of bigeye tuna (BET) from FAD and NOA sets (data from Williams et al., 2017), and the estimated total catch of six common non-target species (dolphinfish, wahoo, rainbow runner, blue marlin, silky shark and oceanic whitetip shark) from FAD sets (bottom panel; data from Peatman, Allain, Caillot, Williams, & Smith, 2012). The dashed vertical line indicates the year when the fishery began to increasingly set on artificial FADs, and the solid vertical line marks the year when WCPFC conservation and management measure CMM 2008-01 entered into force [Colour figure can be viewed at wileyonlinelibrary.com]

group of the Warm Pool model and a generic reference to a species, all functional group names are italicised.

In this case, the intended use of a Warm Pool ecosystem model was to investigate the effects of FAD fishing on the population of the primary target, byproduct (e.g., dolphinfish) and bycatch species (e.g., sharks) of tuna fisheries, and the overall structure of the ecosystem. Therefore, higher taxonomic resolutions were used for the primary target, byproduct and bycatch species (generally a single species, but even ontogenetic stages for some tuna species) to focus on the effects of hypothetical changes in FAD fishing effort. The model was also structured in this way to match stock assessment outputs and scientific observer data available for many of these species. In comparison, little empirical information was available for species, and even families, at lower trophic levels, such as mesopelagic forage species and zooplankton, and so a lower taxonomic resolution was used.

The model of the Warm Pool ecosystem was constructed using Ecopath with Ecosim software (www.ecopath.org). Detailed descriptions and discussion of Ecopath and Ecosim can be found in Polovina (1984), Walters, Christensen, and Pauly (1997), Christensen and Pauly (1992), Christensen and Walters (2004) and Coll, Bundy, and Shannon (2009). In brief, Ecopath trophic models provide a static representation of energy flows in a food web that balances a group's net production with all sources of mortality and migration. Ecosim is a dynamic extension of Ecopath that allows forecasting of ecosystem responses to specific perturbations through time by accounting for

changes in predator consumption rates and the proportion of the prey that exist in a vulnerable state.

An Ecopath model requires annual values for the following basic parameters for each functional group for the baseline year: biomass (B) and total fishery catch (Y), both expressed as tonnes km^{-2} averaged across the model region; production/biomass ratio (P/B), consumption/biomass ratio (Q/B); ecotrophic efficiency (EE; the fraction of the total production of a group utilised in the system); net migration (E), which was assumed to be zero (i.e., emigration = immigration); and the biomass accumulation rate (BA_i). The model also requires a diet matrix for all predator–prey interactions, to establish the trophic linkages between functional groups, which are represented as the proportion of the average annual diet of a predator (in terms of % wet weight) provided by each functional group. A detailed description of the methodology used to derive model parameters is provided in Supporting information Appendix S1, whereas the data sets and key references used to derive biological parameters and diet composition for each functional group are provided in Supporting information Appendix S1: Tables S1 and S2.

The year 2005 was chosen as the reference year to characterise the static description of the trophic flows in the Warm Pool in the Ecopath model, as it had high observer coverage of the purse-seine fishery and the highest quality diet information from a long-term predator sampling programme (Allain et al., 2012). Each species within the Warm Pool ecosystem was assigned to one of 46 functional groups (Table 1). Two of these (*Detritus* and *Fishery discards*)

TABLE 1 Parameters used in the Warm Pool Ecopath model

No.	Name	Trophic level	Biomass (t/km^2)	P/B (year)	Q/B (year)	EE (year)	P/Q (year)
1	Seabirds	4.42	0.000580	0.044	74.990	**0.020**	**0.001**
2	Cetaceans	4.31	0.000280	0.839	14.600	**0.113**	**0.057**
3	Sea turtles	3.83	0.001300	0.190	7.300	**0.159**	**0.026**
4	Small swordfish[T]	4.83	0.000330	0.375	5.560	**0.146**	**0.067**
5	Large swordfish[T]	4.93	0.001250	0.325	3.431	**0.431**	**0.095**
6	Blue marlin[B]	5.15	0.000300	0.429	7.300	**0.292**	**0.059**
7	Striped marlin[B]	5.12	0.000057	0.902	13.140	**0.389**	**0.069**
8	Other billfish[B]	4.91	0.000220	0.902	13.140	**0.315**	**0.069**
9	Mako shark[D]	5.38	0.000070	0.577	7.300	**0.438**	**0.079**
10	Blue shark[D]	4.76	0.000970	0.440	3.000	**0.204**	**0.147**
11	Silky shark[D]	4.49	0.000738	0.577	3.500	**0.484**	**0.165**
12	Oceanic whitetip shark[D]	5.19	0.000092	0.591	5.100	**0.648**	**0.116**
13	Other sharks[D]	4.95	0.000500	0.450	4.500	**0.310**	**0.100**
14	Small bigeye tuna[T]	4.65	0.004350	1.100	11.000	**0.712**	**0.100**
15	Large bigeye tuna[T]	4.93	0.002710	0.510	5.011	**0.519**	**0.102**
16	Small yellowfin tuna[T]	4.03	0.031101	1.500	14.600	**0.420**	**0.103**
17	Large yellowfin tuna[T]	4.78	0.004190	1.670	9.406	**0.472**	**0.178**
18	Juvenile skipjack[T]	4.01	0.020403	1.660	13.030	**0.422**	**0.127**
19	Small skipjack[T]	3.87	0.028800	1.000	7.900	**0.514**	**0.127**
20	Large skipjack[T]	4.36	0.051010	0.878	6.227	**0.706**	**0.141**
21	Albacore[T]	4.48	0.026500	0.900	11.000	**0.144**	**0.082**
22	Wahoo[B]	4.61	0.000102	1.800	17.000	**0.710**	**0.106**
23	Dolphinfish[B]	4.15	**0.002629**	3.485	20.440	0.950	**0.170**
24	Small tunas[B]	3.78	**0.034000**	1.500	7.957	0.950	**0.189**
25	Escolar & Oilfish[B]	5.02	**0.001646**	0.408	3.600	0.950	**0.113**
26	Lancetfish[D]	4.73	**0.006384**	0.470	4.000	0.950	**0.117**
27	Opah[B]	4.71	0.000107	0.392	3.900	**0.940**	**0.101**
28	Pomfret[B]	4.87	**0.000302**	0.976	8.910	0.950	**0.110**
29	Rainbow runner[B]	4.06	**0.024162**	0.868	7.957	0.950	**0.109**
30	Epipelagic crustaceans	2.36	**13.277113**	3.300	14.600	0.950	**0.226**
31	Epipelagic fish	3.36	**3.045950**	3.400	14.000	0.950	**0.243**
32	Epipelagic small fish	2.74	**7.279658**	6.000	22.000	0.950	**0.273**
33	Epipelagic molluscs	3.68	**2.831680**	4.700	14.600	0.950	**0.322**
34	Migratory mesopelagic fish & crustaceans	3.39	1.439000	4.600	13.000	**0.993**	**0.354**
35	Migratory mesopelagic molluscs	4.08	0.613000	4.500	15.000	**0.977**	**0.300**
36	Mesopelagic fish & crustaceans	3.96	0.384000	4.450	13.000	**0.988**	**0.342**
37	Mesopelagic molluscs	4.47	0.224000	4.400	15.000	**0.975**	**0.293**
38	Highly migratory bathypelagic forage	3.38	0.798000	2.200	9.000	**0.646**	**0.244**
39	Migratory bathypelagic forage	3.98	0.302000	2.000	8.000	**0.983**	**0.250**
40	Bathypelagic forage	3.74	0.221000	1.700	6.500	**0.767**	**0.262**
41	Mesozooplankton	2.16	4.358000	70.000	218.000	**0.325**	**0.321**
42	Microzooplankton	2.00	3.842000	110.000	365.000	**0.506**	**0.301**
43	Large phytoplankton	1.00	1.849000	131.000	–	**0.829**	–
44	Small phytoplankton	1.00	10.477000	152.000	–	**0.665**	–

(Continues)

TABLE 1 (Continued)

Functional group		Trophic	Biomass	P/B	Q/B	EE	P/Q
No.	Name	level	(t/km^2)	(year)	(year)	(year)	(year)
45	Detritus	1.00	53.000000	–	–	**0.772**	–
46	Fishery discards	1.00	0.001775	–	–	**0.000**	–

Notes. Biomass is expressed as tonnes (t) wet weight km^{-2}. *P/B*: production/biomass; *Q/B*: consumption/biomass; EE: ecotrophic efficiency; and *P/Q*: production/consumption, are per year. Bold values estimated by Ecopath. Superscripts denote target species ([T]), byproduct ([B]) or discarded bycatch ([D]).

are non-living detrital groups. It was necessary to create the *Fishery discards* group as a trophic pathway to make a non-living "suspended" detrital component of the system (i.e., discarded species) available to predatory species, such as sharks and seabirds; otherwise, such discards would be allocated exclusively to detritivores or be completely lost from the system (Bozzano & Sarda, 2002; Bugoni, McGill, & Furness, 2010).

Each group in Ecopath models generally acts as an independent biomass pool, despite some groups being comprised of numerous species. However, in the cases of swordfish and of bigeye, yellowfin and skipjack tunas, the availability of high-quality stock assessment data and life history parameters allowed for the construction of multi-stanza dynamic pool models within Ecopath that forced a link between different ontogenetic stages believed to have very different ecological and biological characteristics, in particular diet composition (Graham, Grubbs, Holland, & Popp, 2007).

Each multi-stanza model required input parameters of biomass, total mortality (*Z*, which approximates *P/B*) and consumption (*Q/B*) for a "leading" stanza, and the model then estimated these parameters for each remaining stanza. Because the stock assessment data were derived from non-equilibrium age-structured models, there were often minor discrepancies in the parameter estimates produced by the more simplistic dynamic pool multi-stanza models. For there to be agreement in the biomass and *Z* estimates of the two models, *Q/B* and the von Bertalanffy growth function (VBGF) curvature parameter, *K*, needed to be increased slightly in some cases.

2.3 | Fisheries

Three fisheries were included in the model: purse-seine, pelagic longline and pole-and-line. However, to facilitate changes in purse-seine effort in a modelling environment, the purse-seine fishery was divided into a fishery that set in association with natural or artificial floating objects (FAD), and a second that set on free-swimming tuna schools not associated with floating objects (NOA). These two purse-seine fisheries are the focus of this study, as they collectively accounted for 68% of the total catch in the western and central Pacific Ocean (WCPO) in 2016, most of which was taken from the Warm Pool. In 2016, the purse-seine fishery was composed of around 300 distant-water fishing nation vessels (mainly Japan, Korea, Chinese Taipei and the United States, and recently China, Ecuador, El Salvador and Spain) and Pacific Island vessels (Williams et al., 2017). In the WCPO, the fishery essentially targets skipjack, which accounted for 75% of the purse-seine catch in 2016, with smaller

proportions of yellowfin (21%) and bigeye (3%) tunas. The 2016 WCPO purse-seine catch of 1,858,198 tonnes (t) was the third highest on record. In 2016, NOA sets predominated (70% of all sets), whereas FAD sets accounted for 30% of the number of sets, but 45% of the catch. More bycatch is generally caught in FAD sets, with combined average catch rates of non-tuna species over fifteen times higher in FAD sets than NOA sets (Williams & Terawasi, 2015).

The longline and pole-and-line fisheries make comparatively minor contributions to the total catches of the WCPO tuna fishery. The longline fishery is composed of about 3,000 vessels, mainly from distant-water nations, that mainly target albacore, yellowfin and bigeye tunas. While a large fleet, the longline fishery targets larger size classes of tunas, and other species such as swordfish and sharks, resulting in lower catch volumes compared to the purse-seine fishery. The total longline catch of 231,860 t in 2016 was around 9% of the total WCPO catch (Williams et al., 2017). In contrast, the pole-and-line fishery targets mainly skipjack, and in 2016, the fleet consisted of 66 vessels and caught 224,000 t, of which only 11,000 t were caught in the Warm Pool (Williams et al., 2017).

Annual landings of each species in each fishery in 2005 were derived from vessel logbooks, which were validated using scientific observer data. Annual discards in each fishery were estimated for each species using scientific observer data and scaling up to the level of the fishing effort in the model area (Pilling, Harley, Nicol, Williams, & Hampton, 2013). The final landings and discards data included in the model are detailed in Supporting information Appendix S1: Table S1. It is important to note that although effort, catch and discards in the four fisheries are highly spatially dependent, the Warm Pool Ecopath model assumes homogeneity across the entire model area.

2.4 | Balancing, calibrations and diagnostic tests

Once all model parameters were estimated for 2005, the Ecopath model was balanced. Before the balanced Ecopath model was finalised as the 2005 representation of the Warm Pool ecosystem, diagnostic tests were undertaken to confirm that it was thermodynamically stable and produced ecologically and biologically realistic results. The balancing procedure and diagnostic tests followed the recommendations of Link (2010) and Heymans et al. (2016), described in Supporting information Appendix S2.

To increase the reliability of predictions from the Ecosim scenarios, the model was calibrated using 111 time series of data, consisting of biomass and/or fishing mortality and/or catch for 37 of the 44

living functional groups. The data types used, and their sources, are shown in Supporting information Appendix S1: Table S4 whereas a detailed description of the Ecosim calibration to time series data is provided in Supporting information Appendix S3.

2.5 | Ecological indicators

In addition to examining the changes in biomass of individual ecological functional groups and species, ecological indicators were used to quantify any structural changes that may have occurred in the Warm Pool ecosystem during the history of the fishery, and after implementing hypothetical changes in FAD effort. Following the recommendations of Fulton, Smith, and Punt (2005), the mean trophic level of the catch (MTL_c), fishing-in-balance (FIB) index and Kempton's Q index adapted for ecosystem models (Ainsworth & Pitcher, 2006) were used. In brief, MTL_c is the average trophic level of animals caught by all fisheries combined; FIB relates catches and the mean trophic level of the catch in a given year to a reference year, to determine whether the change is compatible with the transfer efficiency (TE) between trophic levels, whereas Kempton's Q is a diversity measure. A description of each indicator is provided in Supporting information Appendix S4.

2.6 | Modelling changes in FAD fishing effort

Using the balanced and calibrated Ecopath ecosystem model, three hypothetical scenarios were implemented that focused on examining the changes in (a) biomass of target and byproduct species in the purse-seine fishery and (b) ecosystem structure. Each model simulation was run by importing a separate time series into Ecosim. This included complete time series used in the calibration procedure, supplemented with hypothetical data relevant to the scenario (e.g., a 50% increase in FAD effort) that extended to the end of 2046. All hypothetical changes to fishing practices or fishery management strategies were introduced at the beginning of 2016.

Scenario 1 explored the desire of fishery stakeholders to increase the catch of FAD-associated byproduct species for improved food security of Pacific Island nations by increasing FAD effort from the 2016 level by 50% and 100% and maintaining these levels to 2046. NOA effort was maintained at the 2016 level until the end of 2046.

Scenario 2 simulated a management measure aiming to decrease the fishing mortality of small size classes of target tuna species, which was simulated by the reduction of FAD effort by 50% and 100% in 2016 and maintained to 2046. NOA effort was maintained at the 2016 level until the end of 2046.

Scenario 3 also simulated a management measure aiming to decrease the fishing mortality of small size classes of target tuna species by reducing the FAD effort by 50% and 100% in 2016, but simultaneously increasing NOA effort by 50% and 100%, respectively, and maintaining these effort levels to 2046.

Results are expressed as the percentage change in biomass of each group in 2046 relative to 2016. Only biomass changes larger than 5% are described in the results.

3 | RESULTS

3.1 | Ecopath model outputs

The balanced Ecopath model parameters for the 46 functional groups are shown in Table 1. The group with the highest TL was *Mako shark* (5.38), followed by *Oceanic whitetip shark* (5.19) and *Blue marlin* (5.15). The mean trophic level of the catch (MTL_c) in 2005 was 4.26, due to the large predatory fish targeted by the pelagic fisheries (i.e., tunas and swordfish), as well as the high trophic level of the incidentally caught species (e.g., sharks, billfish and tuna-like species).

Summary statistics for the overall flows in the Warm Pool model are shown in Table 2. Total system throughput was 11,231 t km^{-2} year^{-1}. Total consumption accounted for 18% of this total, less than the flows to detritus (41%) or exports from the system (33%). Together with the very low gross efficiency of the system, measured as catch/primary production, of <0.001, these results indicate that very little of the production in the system was harvested.

The Connectance Index was 0.293, indicating that the ratio of actual trophic links between functional groups relative to the maximum number of possible links was high. The System Omnivory Index of 0.416 indicates that the prey base of predators was diverse, and transcended trophic levels (Table 2) and complemented the results of the Connectance Index.

The Warm Pool ecosystem comprised six trophic levels, but the majority of the system's biomass (74%) was in TLs 1 and 2, whereas 89% of the catch was in TLs 3–5 (Table 3). About 55% of the total flows occurred in the first two TLs (Table 3). Flows originating from

TABLE 2 Summary of basic flows, biomass and indices in the Warm Pool Ecopath model

Parameter	Value	Units
Sum of all consumption	2,046.225	t km^{-2} year^{-1}
Sum of all exports	3,725.478	t km^{-2} year^{-1}
Sum of all respiratory flows	810.493	t km^{-2} year^{-1}
Sum of all flows into detritus	4,649.377	t km^{-2} year^{-1}
Total system throughput	11,231.570	t km^{-2} year^{-1}
Sum of all production	5,362.455	t km^{-2} year^{-1}
Mean trophic level of the catch (MTL_c)	4.260	
Gross efficiency (catch/net p.p.)	<0.001	
Calculated total net primary production	4,535.968	t km^{-2} year^{-1}
Total primary production/total respiration	5.597	
Net system production	3,725.475	t km^{-2} year^{-1}
Total primary production/total biomass	106.353	
Total biomass/total throughput	0.004	
Total biomass (excluding detritus)	42.650	t km^{-2} year^{-1}
Total catch	0.059	t km^{-2} year^{-1}
Connectance index	0.293	
System Omnivory Index	0.416	

TABLE 3 Biomass and catch, by trophic level (TL), and annual trophic flows (t/km²) from primary production and detritus in the Warm Pool Ecopath model

TL	Biomass	Catch	From primary production					From detritus				
			Consumed	Export	To detritus	Respiration	Throughput	Consumed	Export	To detritus	Respiration	Throughput
VI	0.242	0.00459	0.344	0.00208	0.322	0.731	1.399	0.374	0.00251	0.352	0.801	1.530
V	0.927	0.0133	1.381	0.00550	1.287	2.973	5.646	1.514	0.00784	1.411	3.218	6.151
IV	3.347	0.0237	5.531	0.00809	5.150	12.43	23.12	6.050	0.0156	5.642	13.31	25.01
III	9.545	0.0156	22.90	0.00633	62.05	83.51	168.5	24.55	0.00932	35.80	66.28	126.6
II	16.18	0.000098	168.5	0.000005	355.8	230.5	754.9	126.6	0.000093	401.0	396.2	923.9
I	24.33	0.000	755.7	0.000	3,780	0.000	4,536	924.0	3,725	0.000	0.000	4,649
Sum	54.655	0.0573	954.4	0.0220	4,205	330.1	5,490	1,083	3,725	444.2	479.8	5,732

primary producers and detritus showed that the transfer efficiency between TLs was extremely low (<0.25%), but generally increased with increasing TL (Table 3). The mean transfer efficiency for TLs 2–5 was 13.8%.

3.2 | Mixed trophic impact

A mixed trophic impact (MTI) sensitivity analysis revealed that the strongest trophic interactions were *Small yellowfin tuna* on *Rainbow runner* and *Dolphinfish* (Figure 3), even though the percentage of these two species in the diet of *Small yellowfin tuna* is small (3.6% and 1%, respectively). However, this predator has a large biomass, and high *P/B* and very high *Q/B* ratios. Many of the strongest trophic interactions occurred within the mid-trophic-level forage species, such as *Epipelagic molluscs* on *Highly migratory bathypelagic pelagic forage*, and *Mesopelagic fish* on *Bathypelagic forage* (Figure 3). These interactions were due to the high standing biomasses (>1 t/km²) and very high *P/B* values (>3.0/year) of these groups.

The strongest species interactions with fisheries were *Oceanic whitetip shark*, *Silky shark*, *Cetaceans*, *Blue marlin*, *Striped marlin*, *Small bigeye tuna* and *Small yellowfin tuna* with the FAD fishery (Figure 3), as the catches were high relative to the biomass of these species. The strongest species interactions with the NOA fishery was *Large yellowfin tuna* and *Large skipjack* (Figure 3), as these species are targets of this fishery. Ironically, the largest positive interactions were the FAD fishery on the bycatch species *Wahoo*, *Dolphinfish* and *Rainbow runner*.

3.3 | Keystone groups

The keystone index and relative total impact values for each functional group are shown in Supporting information Appendix S4: Table S7. The most important keystone species in the Warm Pool model were *Mesopelagic fish* and *crustaceans* (relative total impact = 1.0), *Epipelagic molluscs* (0.87), *Epipelagic small fish* (0.83) and *Small yellowfin tuna* (0.81), due to their high *P/B* and *Q/B* values and their diverse diets, but also because they are important prey for a range of predators.

3.4 | Ecosim model time series fitting

The Ecosim model fitted standardised biomass, catch and fishing mortality (*F*) well for most species (Figure 4). The model fits to *F* were excellent for the 14 species for which a time series of *F* was available. In the case of biomass, all species with long time series showed a consistent pattern of generally poor fits to the data until about 1970, owing to logbook data reliability issues, after which the fits improved greatly (Figure 4).

With respect to catch, the Ecosim model produced good fits for most groups (Figure 4), although for *Small* and *Large yellowfin tuna* and *Striped marlin*, the agreement between the model and the observed data decreased from around 1995, which coincided with the major historic increase in FAD effort (Leroy et al., 2013) and probably a change in fishing power.
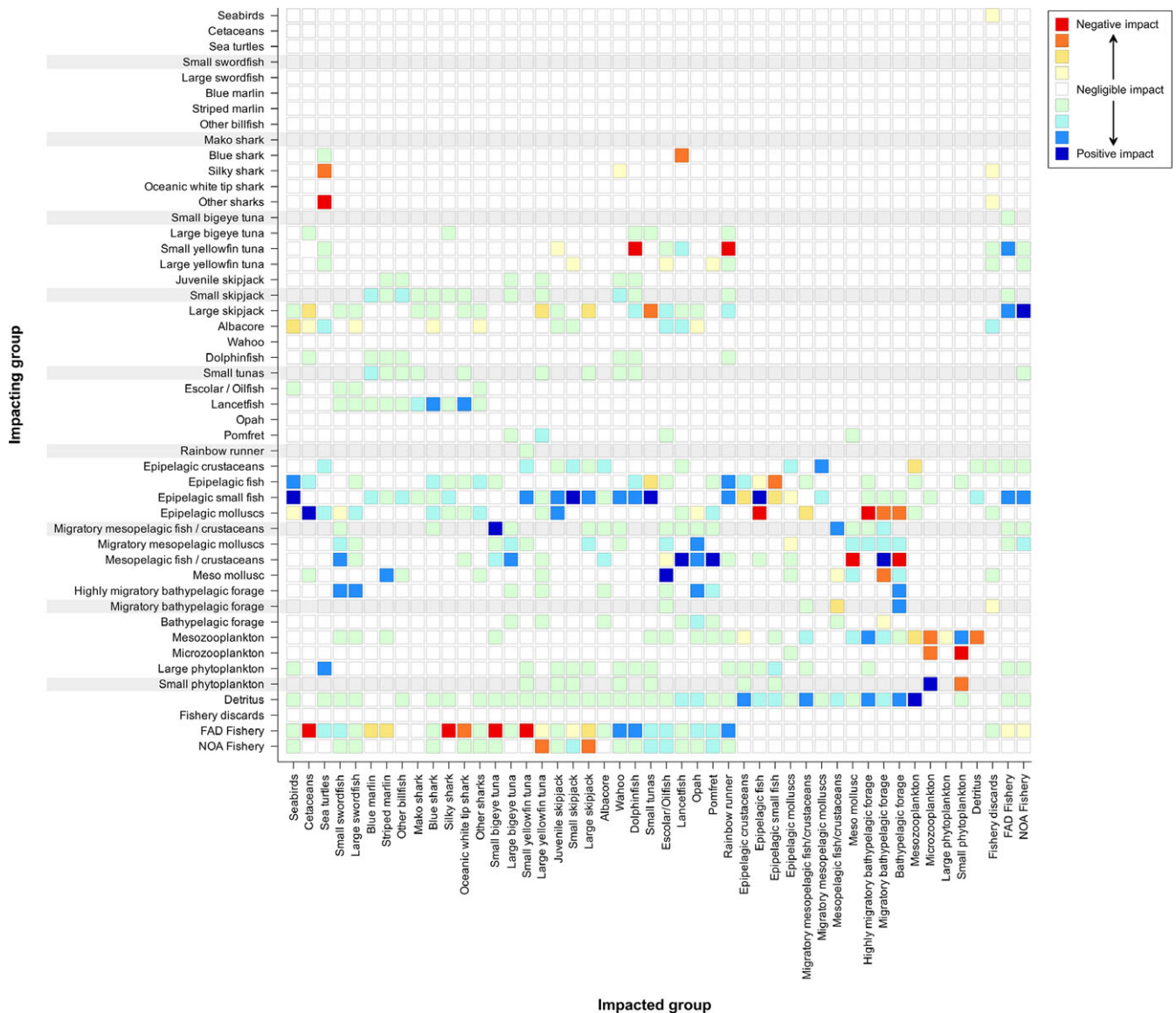
FIGURE 3 Results of the mixed trophic impact analysis. The relative trophic interaction strength from red (most negative) to blue (most positive) between functional groups and the purse-seine fisheries (FAD, purse-seine sets associated with floating objects; NOA, purse-seine sets not associated with floating objects) in the Warm Pool model [Colour figure can be viewed at wileyonlinelibrary.com]

The poorest fits were for biomass and catch of *Juvenile skipjack*, due to this age class (0–3 months of age) not being estimated by the stock assessment model. Therefore, the results from Ecosim simulations for this group need to be viewed with caution.

3.5 | Historic changes in ecosystem structure

The three ecosystem indices produced by Ecosim revealed substantial changes in the ecosystem from 1980 through 2010, the last year for which data were available (Figure 5). MTL_c steadily increased from 4.21 in 1980 to 4.28 in 2010, whereas the FIB index increased over the same period from -0.4×10^{-6} to 1.2×10^{-6}, with the most marked increase occurring after 2002 (Figure 5). Kempton's Q index decreased from 3.77 in 1980 to 3.65 in 2010. Together, these

indicators signal an expansion of the fishery and an increase in the diversity and magnitude of the catch, but a decrease in the standing biomass of higher level predators (TL > 3).

3.6 | Scenario 1—increase FAD effort to increase catches of byproduct species

The groups showing the largest negative change in biomass between 2016 and 2046 after 50% and 100% increases in FAD effort were *Silky shark* (−22.7% and −43.3%, respectively), *Large yellowfin tuna* (−16.4% and −33.8%), *Small yellowfin tuna* (−12.2% and −27.3%), *Oceanic whitetip shark* (−12.9% and −26.1%) and *Mako shark* (−13.6% and −24.1%; Figure 6). The largest positive changes in biomass were for *Escolar* and *Oilfish* (7.7% and
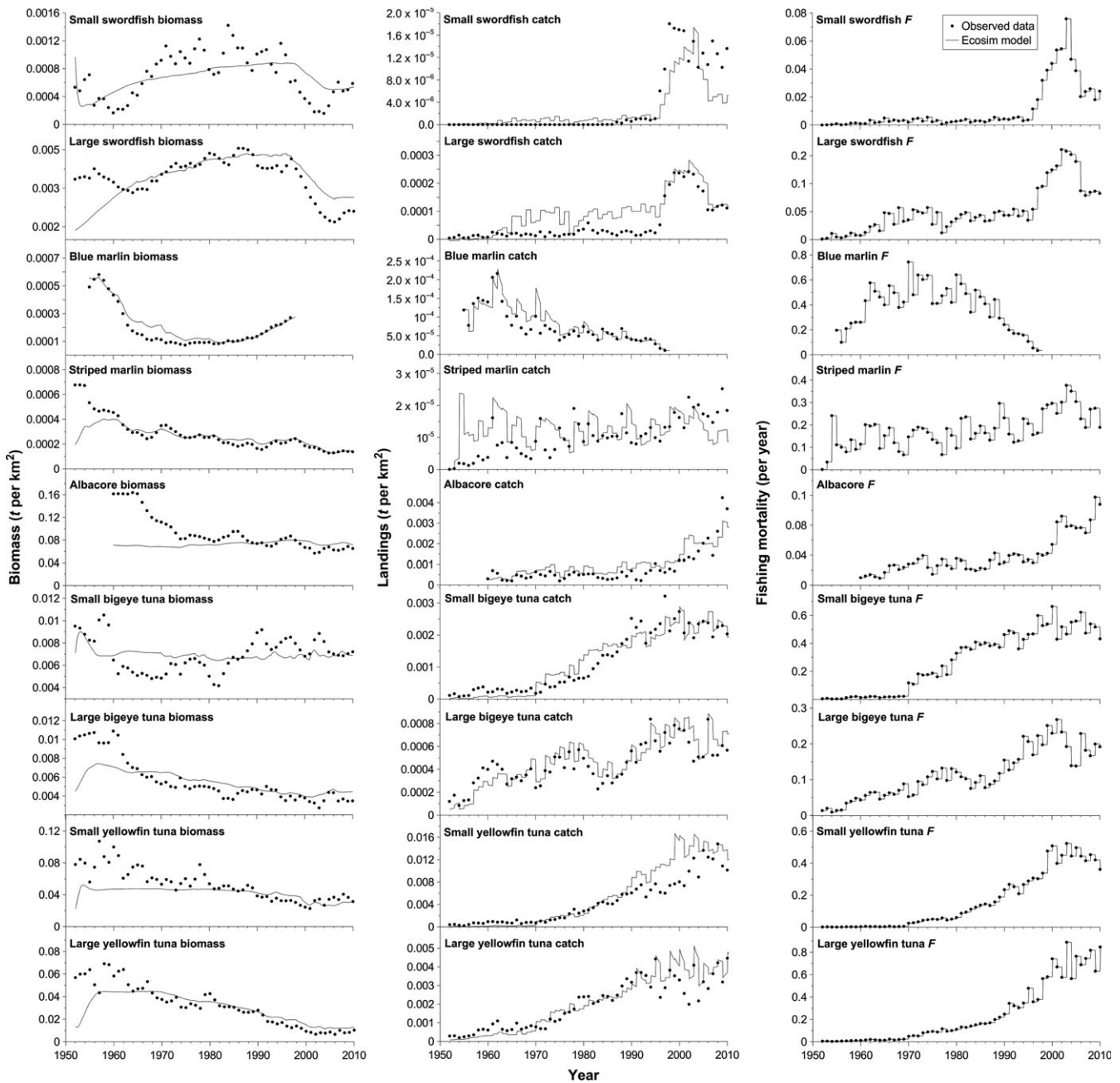
FIGURE 4 Ecosim model fits (solid lines) to observed annual time series data (black dots) for biomass (t/km²), catches (t/km²) and fishing mortality (*F*) for 26 functional groups in the Warm Pool ecosystem model. Only biomass data were available for the 11 forage groups and phytoplankton

16.7%), *Wahoo* (6.4% and 15.2%) and *Dolphinfish* (5.2% and 12.5%).

With respect to ecosystem indices, both the 50% and 100% increases in FAD effort resulted in a decrease in MTL$_c$ of <1%, whereas the FIB index increased by 49.9% and 35.3%, respectively, indicating that the functionality of the ecosystem is being increasingly impaired with increasing effort. Kempton's *Q* index decreased only slightly when FAD effort was increased by 50% (−2.9%) and 100% (−3.8%; Figure 5), indicating a slight decrease in the diversity and evenness of the higher trophic level (TL > 3) assemblages of functional groups.

3.7 | Scenario 2—decrease FAD effort to reduce the catch of small-sized target tunas

The primary beneficiaries of 50% and 100% decreases in FAD effort were *Mako shark* (20.9% and 37.0%), *Silky shark* (16.8% and 28.9%), *Oceanic whitetip shark* (12.1% and 22.0%), *Other sharks* (10.3% and 19.7%) and *Large bigeye tuna* (9.2% and 14.7%; Figure 6). Interestingly, the biomass of *Small bigeye tuna* decreased slightly (−4.0% and −7.7%), due to the increase in biomass of sharks and *Blue marlin*, some of their main predators. The largest negative changes in biomass (>5%) were for *Opah* (−12.7% and −18.7%) and *Wahoo* (−7.7% and −13.2%; Figure 6).
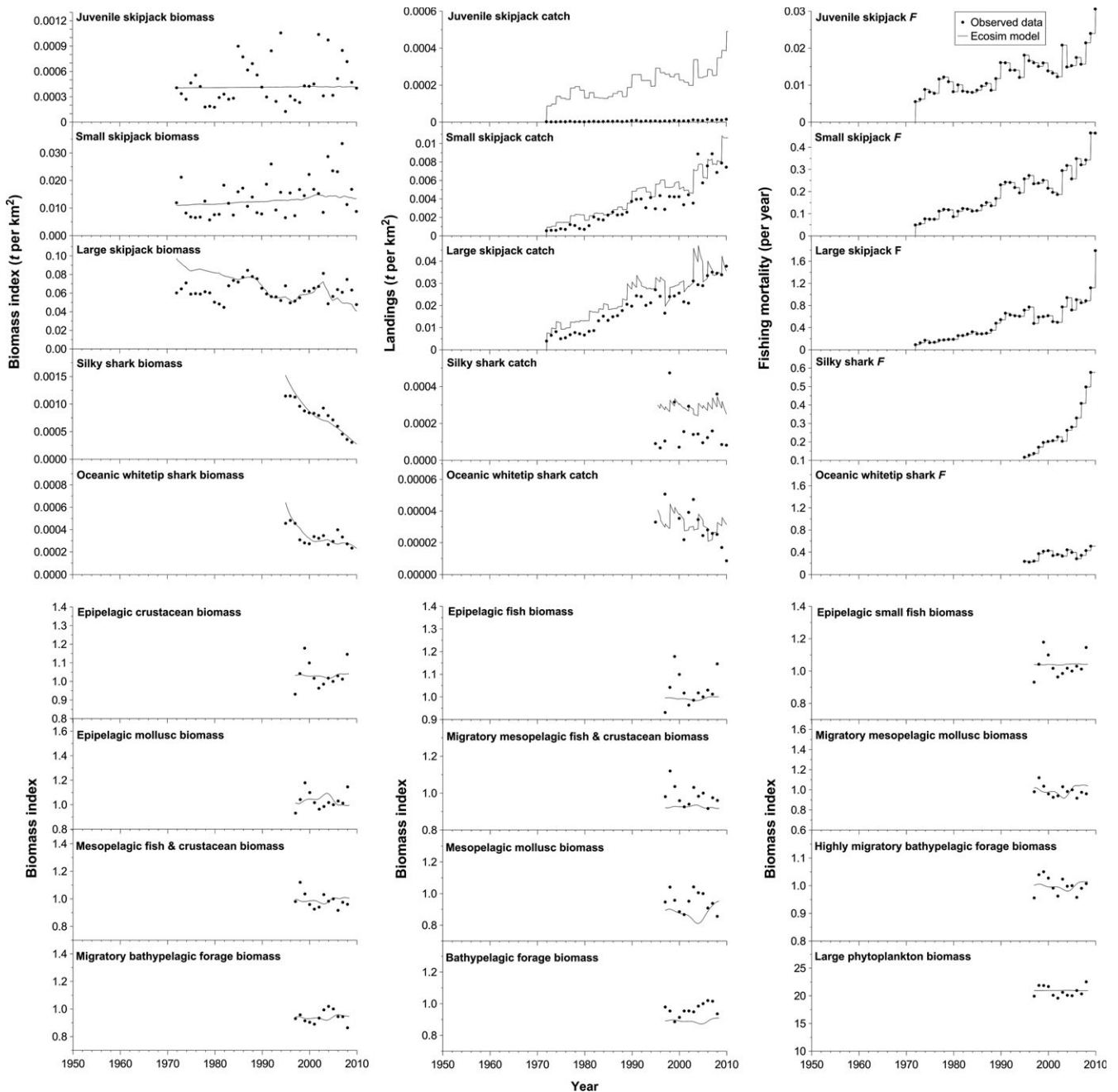
FIGURE 4 Continued

In these two scenarios, the MTL_c increased from 4.27 to 4.29 and 4.31, respectively (Figure 5). The FIB index decreased by 36.4% and 81.8%, to values approaching zero, indicating optimal functionality of the ecosystem. Kempton's Q index increased slightly when FAD effort was decreased by 50% (1.1%) and 100% (4.1%; Figure 5), indicating an increase in the diversity and evenness of the higher trophic level (TL > 3) assemblages of functional groups.

3.8 | Scenario 3—effort transfer from FAD to NOA sets to reduce catch of small-sized target tunas

The scenario involving 50% and 100% decreases in FAD effort and simultaneous 50% and 100% increases in NOA effort resulted in biomass increases for *Large bigeye tuna* (11.0% and 17.9%), *Mako shark* (9.5% and 14.6%), *Oceanic whitetip shark* (6.5% and 11.1%) and *Other sharks* (5.2% and 9.0%; Figure 6). Again, the biomass of *Small bigeye tuna* decreased slightly (−3.4% and −6.1%). The largest negative changes in biomass were for *Blue marlin* (−14.0% and −21.8%), *Large skipjack* (−6.1% and −8.9%) and *Opah* (−6.7% and −7.7%; Figure 6).

MTL_c increased from 4.28 to 4.31 and 4.34, respectively, for the 50% and 100% effort scenarios, whereas the FIB index increased abruptly but stabilised around the 2016 value for both scenarios (Figure 5). Kempton's Q index decreased by 3.8% for both scenarios, indicating a decrease in the diversity and evenness of the higher trophic level (TL > 3) assemblages of functional groups.
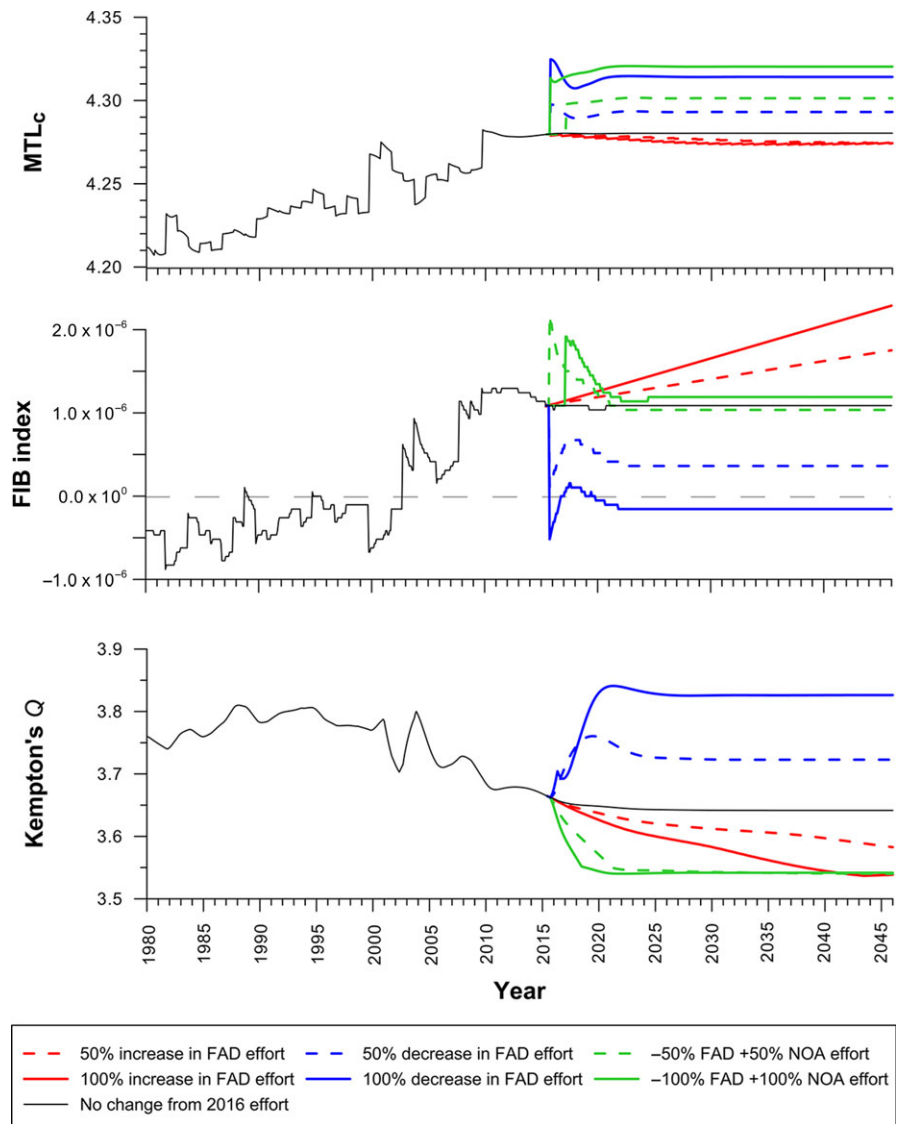
FIGURE 5 Estimates of three ecosystem indicators—mean trophic level of the catch (MTL$_c$), fishing-in-balance (FIB) index and Kempton's Q index—calculated by Ecosim for the Warm Pool model, 1980–2046, for the three scenarios in which FAD effort was manipulated during 2016–2046. The horizontal grey dashed line in the centre graph shows a FIB index of zero, which indicates that fishing is in balance with the available primary productivity in the ecosystem [Colour figure can be viewed at wileyonlinelibrary.com]

Legend:
- - - - 50% increase in FAD effort
——— 100% increase in FAD effort
——— No change from 2016 effort
- - - - 50% decrease in FAD effort
——— 100% decrease in FAD effort
- - - - −50% FAD +50% NOA effort
——— −100% FAD +100% NOA effort

4 | DISCUSSION

The impetus for this study was the conundrum faced by WCPO fisheries managers, who seek a balance between optimising the sustainable and profitable harvest of commercially important tuna target species, improving food security for the rapidly growing human population of the Pacific Island nations through utilisation of byproduct species, and maintaining the integrity of the supporting ecosystem to ensure it can continue to provide services to WCPO stakeholders. The study sought to provide potential solutions to these complex issues by building a model that would quantify the potential ecosystem impacts and changes in the biomass of target and byproduct species under a variety of alternative effort scenarios in the purse-seine fishery.

4.1 | Historical changes in the Warm Pool ecosystem structure

The ecological indices produced by the model showed that the Warm Pool ecosystem has undergone a substantial change in

structure since reliable catch and effort data on pelagic fisheries in the region began to be collected around 1980. The most obvious indicator of this change was the gradual increase in the MTL$_c$ as these fisheries continued to target high-trophic-level species, such as tunas and billfish. There are several examples from fisheries worldwide in which MTL$_c$ has decreased over time by "fishing down the food web" (Alleway et al., 2014; Christensen, 1998; Milessi, Arancibia, Neira, & Defeo, 2005; Polovina et al., 2009), contributing to the overall estimated decline of around 0.1 per decade of the MTL of global reported fisheries landings (Pauly et al.,1998). In the Pacific Ocean, for example, Sibert, Hampton, Kleiber, and Maunder (2006), using a series of single-species stock assessment models for eight target and bycatch species caught in tuna fisheries, estimated that the MTL$_c$ decreased from 4.1 to 4.0 in the past 50 years, due to the increasing catches of smaller size classes of target species of tunas.

In contrast, the model in this study indicated that the MTL$_c$ in the Warm Pool has increased by about 0.025 per decade, from 4.21 in 1980 to 4.28 in 2010. This result was initially surprising, given the precipitous reduction in biomass in several high-trophic-level target
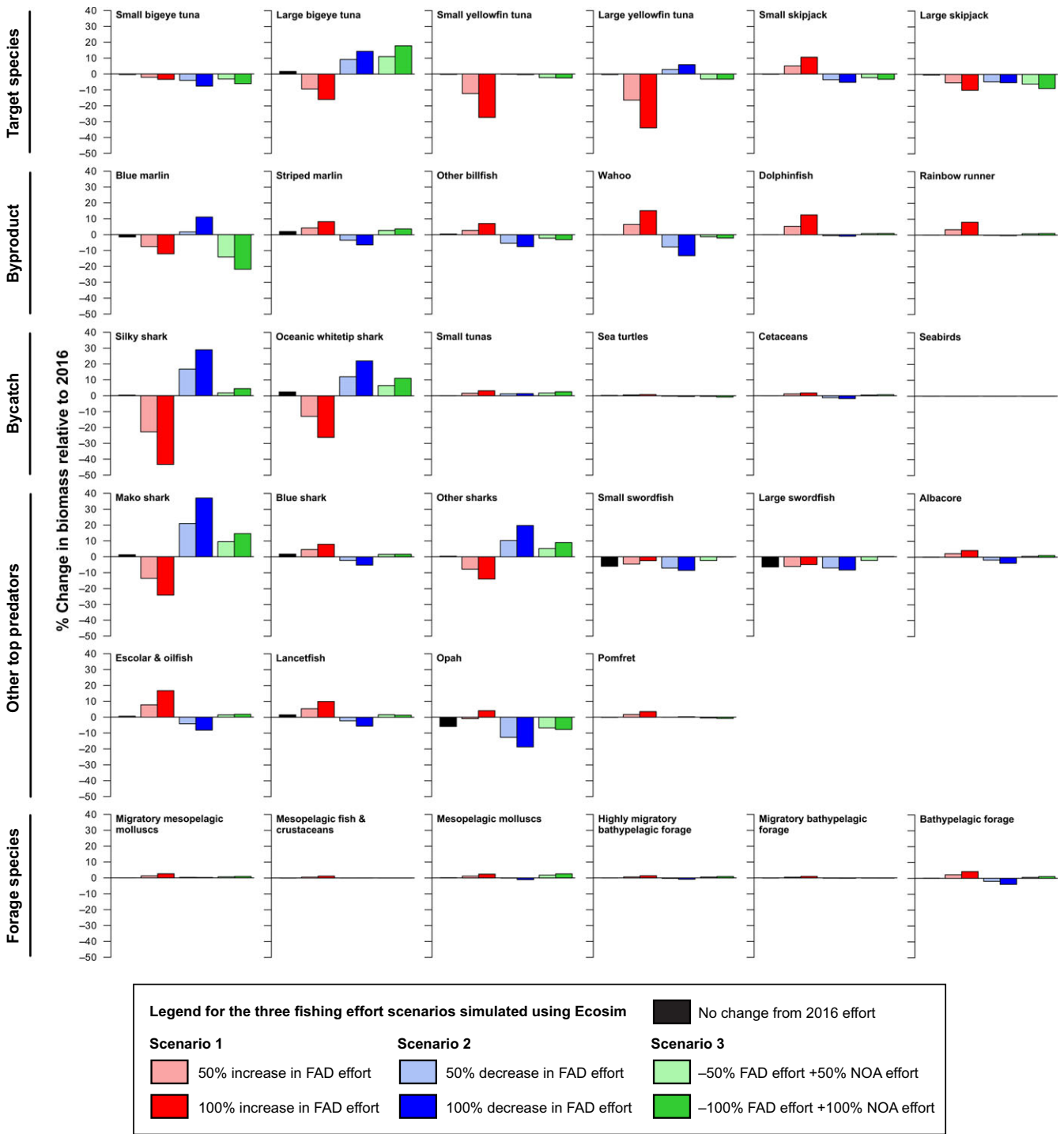
FIGURE 6 Predicted relative percentage change in the biomass of functional groups in the Warm Pool province representing primary target species of the purse-seine fishery, byproduct, bycatch, other top predators (either target or non-target species in other pelagic fisheries in the region) and forage species for the three scenarios in which FAD effort was manipulated during 2016–2046 [Colour figure can be viewed at wileyonlinelibrary.com]

and bycatch species caught in WCPO pelagic fisheries, such as yellowfin and bigeye tunas (McKechnie, Pilling, & Hampton, 2017; Tremblay-Boyer, McKechnie, Pilling, & Hampton, 2017), swordfish (Takeuchi, Pilling, & Hampton, 2017) and striped marlin (Davies, Hoyle, & Hampton, 2012) since the 1950s, and since the mid-1990s for silky and oceanic whitetip sharks (Rice & Harley, 2012, 2013) as

a result of increasing effort and fishing power of purse-seine and longline fisheries. The FIB index indicated an expansion of the fishery since the mid-1990s (FIB > 0), which coincides with the major historic increase in FAD effort in the WCPO (Leroy et al., 2013). However, there is evidence (FIB < 0) to suggest that the collective WCPO fisheries had fully exploited the available biomass in the

ecosystem prior to this period, as the rate at which biomass was extracted was greater than the rate at which it could be expected to be replenished, given the available biomass of primary producers.

Complementing the MTL_c and FIB results, Kempton's Q index has declined since the mid-1990s, and particularly since the early 2000s, indicating that the evenness of the upper-trophic-level (TL > 3.0) groups was altered. Together, the results from the three indicators show the declining catches of high-trophic-level target species being increasingly augmented by catches of FAD-associated byproduct species that occupy similar high trophic levels (TL > 4.0) as the depleted target species. The increase in MTL_c, especially since the early 2000s, is likely to have been further exacerbated by significant improvements in logbook reporting of byproduct species and in the observer coverage of the purse-seine fleet, with catches and discards generally recorded at high taxonomic resolution, usually by species.

These results serve as a warning against using a single ecosystem indicator for detecting major fishery-induced ecosystem changes such as "fishing down the food web." They reflect a potentially more worrisome situation for the Warm Pool, where there is "fishing up the food web" (Branch et al., 2010), indicated by an increase in the MTL_c caused by bias resulting from changes in the quality or type of catch data available and/or changes in fishing behaviour and efficiency (Stergiou & Tsikliras, 2011). Without using multiple ecosystem indicators in concert, the extent of the impacts of fishing on the Warm Pool ecosystem cannot be known until the biomasses of the majority of the species in trophic levels 4 and 5 are so severely depleted that the change is reflected in ecosystem indicators such as MTL_c.

4.2 | Simulated ecological impacts of alternative FAD effort regimes

The results of this study indicate that increasing FAD effort is unlikely to be a viable management measure, as it decreases the sustainability of the populations of directly impacted target tuna species, and particularly of vulnerable long-lived bycatch species (*Silky*, *Mako* and *Oceanic whitetip sharks* and *Blue marlin*), whose biomass were predicted to decline by up to 43%. Recent stock assessments of silky and oceanic whitetip sharks in the western Pacific Ocean indicated that these species are already overfished (Rice & Harley, 2012, 2013), and although less is known about the impacts of increased FAD effort on the blue marlin population, the species can live for at least 20 years in the Pacific Ocean (Andrews, Humphreys, & Sampaga, 2017), and so it may be as vulnerable to overfishing as pelagic sharks.

One major benefit of increasing FAD effort was a predicted increase of up to 30% in the biomass of byproduct species (mainly *Wahoo*, *Dolphinfish* and *Rainbow runner*), which might reduce the estimated 75% shortfall in future protein requirements for Pacific Island nations under existing fishing effort regimes (Pilling et al., 2015) to around 40% or less. Although this increase seems counterintuitive, given the increase in fishing mortality, this type of result is common in ecological systems, where "the predator of my predator is my friend." The increase in FAD effort caused a substantial decrease in

the biomass of the primary predators of these species, like sharks and tunas. The predation pressure was so high (*Wahoo* 0.765/year, *Dolphinfish* 3.262/year, *Rainbow runner* 0.781/year) that the increase in fishing mortality from 2010 to 2046 (*Wahoo* 0.868/year to 0.9/year, *Dolphinfish* 0.039 to 0.065/year, *Rainbow runner* 0.023 to 0.041/year) was negligible by comparison, thus allowing the biomasses of these species to increase.

From an ecosystem perspective, the substantial decrease in the biomasses of high-level predators following increased FAD effort is predicted to change the structure of the ecosystem further from its likely already altered state caused by decades of industrial fishing (FIB index; Figure 4). Although substantial trophic cascades are not predicted to occur within the 30-year simulation period, perpetual increases in purse-seine fishing effort, coupled with the impacts of the longline and pole-and-line fisheries and a changing climate, may eventually drive the ecosystem to a tipping point from which its altered internal dynamics can no longer be reversed by any level of fisheries management intervention.

In contrast, decreasing FAD effort is predicted to be a far more conservative strategy for alleviating the primary concern of WCPO fisheries managers: reducing the fishing mortality of bigeye tuna. This also benefits the populations of several other economically important target and byproduct species, but comes at the cost of a decrease of about 25% in the total catch. This management strategy may therefore be less favourable for WCPFC Member Countries from an economic viewpoint, but has several other significant conservation and ecological benefits that may help the WCPFC meet its conservation objectives (*Conservation and Management Measure for Sharks*—CMM 2010-07) and other adopted international instruments, such as the *FAO International Plan of Action for the Conservation and Management of Sharks*. For example, even a 50% reduction in FAD effort was predicted to result in an increase of up to 21% in the biomass of vulnerable shark bycatch groups such as *Silky*, *Mako* and *Oceanic whitetip* sharks. This is a particularly important consideration for managers, given the "vulnerable" classification of silky and oceanic whitetip sharks by the International Union for Conservation of Nature (IUCN), due to their high susceptibility to capture in industrial tuna fisheries and their low productivity (Baum, Medina, Musick, & Smale, 2015; Rigby, Sherman, Chin, & Simpfendorfer, 2017). For example, in parts of the eastern Pacific, the populations of these two species declined by 92% and 99%, respectively, over a 40-year period, primarily due to industrial longline fishing (Baum & Myers, 2004). Furthermore, this was the only simulated management measure that predicted a return of the ecosystem to its pre-industrial-fishing structure, which may be achieved in as little as 10 years.

The scenario involving the transfer of 50% or 100% FAD effort to NOA effort resulted in little change in biomass for most target and byproduct species, but slightly improved the recovery of shark bycatch populations. However, this strategy did little to reduce the fishing mortality of economically important species, as it essentially transferred the fishing mortality from FAD to NOA sets. As a result of the continued removal of biomass of top predators under this scenario, the structure of the ecosystem was

predicted to be compromised to an extent similar to that predicted under the increased FAD effort scenario, primarily with respect to the upper component of the ecosystem (TL > 3; see Kempton's Q index; Figure 5).

4.3 | Ecological drivers of the Warm Pool ecosystem structure

The Warm Pool model is not only useful for exploring the consequences of alternative fishing effort regimes on economically important species, but it also allows a better understanding of how fishing impacts may propagate through pelagic ecosystems. The modelling showed that the Warm Pool ecosystem structure was resistant to the substantial changes in biomass of many high-trophic-level target and bycatch species that would result from changes in FAD fishing effort. Over the 30-year simulation, the biomass of only eight of the 44 living groups varied by more than 10% under the largest simulated FAD effort changes (±100%). It is possible that these reasonably modest impacts are a result of the analyses being based upon a "shifting baseline" (Pauly, 1995) of the ecosystem state after decades of industrial fishing. However, such inertia appears to be a common characteristic of pelagic ecosystems in the eastern Pacific (Watters et al., 2003), northern and central Pacific (Kitchell, Boggs, He, & Walters, 1999; Kitchell, Essington, Boggs, Schindler, & Walters, 2002) and the Coral Sea (Griffiths et al., 2010).

In the case of the Warm Pool ecosystem, this inertia appears to be attributable to the upper trophic levels consisting of a high diversity of highly productive groups that are generally opportunistic predators and consume a wide variety of prey. Therefore, the effects on the biomass of directly impacted groups of perturbations caused by these hypothetical fishing effort scenarios can be tempered by small changes in the biomass of a wide range of opportunistic and biologically productive predators. As a result, there were no trophic cascades that reached lower trophic levels (TL < 3), with only a <3% change in the biomass of any of these lower functional groups over 30 years.

This also indicates that the majority of high-level predators in the Warm Pool appear to be exerting only weak top-down regulation of the tropical Warm Pool ecosystem. This runs contrary to widespread beliefs about the importance of top-down regulation, which appear to be based on less complex temperate ecosystems that contain only a few predominant apex predators (Baum & Worm, 2009; Heithaus, Frid, Wirsing, & Worm, 2008). On the other hand, in the nutrient-poor waters of the Warm Pool (Le Borgne et al., 2011), it is also unlikely that bottom-up drivers from primary producers completely regulate the system.

Alternatively, the mixed trophic impact and "keystoneness" analyses both demonstrated that the ecosystem structure was most sensitive to changes in the biomass of mid-trophic-level forage groups (e.g., *Mesopelagic fish and crustaceans*). This is because the species composing these groups not only have a very high standing biomass, are highly productive (P/B = 2.0–4.5/year) and exert high top-down predation pressure on lower trophic levels, but also exert strong bottom-up pressure by being key prey for high-level predators. This type of ecosystem regulation is known as "wasp-waist" control, because the energy flow from primary producers is largely constricted through a narrow "waist" created by a few highly productive species occupying intermediate trophic levels that are both important prey and predators (Rice, 1995).

Wasp-waist regulation is considered one of the likely drivers for maintaining the structure and function of pelagic ecosystems in the eastern and western Pacific (Griffiths et al., 2013), but apparently less so in the northern Pacific (Choy, Wabnitz, Weijerman, Woodworth-Jefcoats, & Polovina, 2016). A key characteristic of wasp-waist systems is that disruption of the biomass of the "waist" groups by natural or anthropogenic impacts can create cascading effects, unpredictable in direction and magnitude, both upward and downward through the trophic levels of an ecosystem (Cury et al., 2000). In the context of the present study, this means that if increased catches by the FAD fishery affect, directly or indirectly, the biomass of mid-trophic-level forage groups (TL 3.4–4.0), this may compromise the structure and function of the Warm Pool ecosystem and have major implications for its dependent fisheries.

Although the values used in the study were the best available estimates of biomass for forage groups from the forage submodel of SEAPODYM (Lehodey, Murtugudde, & Senina, 2010), they were found during the Ecopath model balancing process to be too small to sustain the prey biomasses required by higher order predators, for which reliable estimates of biomass, P/B and Q/B were available. This discrepancy may result from Ecopath and SEAPODYM using very different model structures and assumptions. SEAPODYM is a two-dimensional ocean-basin-scale physical–biological–fisheries model that includes a nutrient–phytoplankton–zooplankton model, a forage submodel and a tuna age-structured model, all of which are driven by an ocean physical–biogeochemical model in monthly time steps. Although SEAPODYM is considered an ecosystem model, it describes more a food chain, from primary producers to a single tuna predator, rather than a food web, with multiple apex predator groups. Therefore, it is plausible that SEAPODYM underestimated the biomass of forage groups that is required to support the consumptive demands of a suite of apex predators.

By contrast, Ecopath represents the ecosystem as a single biomass pool and assumes that the biomass of each functional group is homogenously distributed across the Warm Pool during the entire 2005 reference year. This is obviously an oversimplification of the ecosystem, as pelagic fish abundance is highly influenced by physical and oceanographic features (Musyl et al., 2003; Royer, Fromentin, & Gaspar, 2004), and may have resulted in Ecopath overestimating the biomass of forage groups for which little reliable biomass and biological information was available. In future, spatially disaggregating the model into oceanographic habitats, and even Exclusive Economic Zones of Pacific Island nations, using Ecospace (Walters, Pauly, & Christensen, 1999), may allow the assumption of a closed ecosystem (i.e., immigration = emigration) to be relaxed. This may permit the exploration of different import and export rates for forage biomass in an attempt to resolve the discrepancies in the standing biomass

estimates for forage groups between Ecopath and the SEAPODYM model constructed for the same region (Lehodey et al., 2010). This may also allow the production of region-specific results that are more relevant to the fishery managers of the numerous island nations within the Warm Pool region.

4.4 | Improving ecosystem model reliability by fitting to time series of observed data

Ecosystem models can be powerful tools for representing the structure of marine ecosystems and quantifying the ecological impacts of fishing. However, they require a large number of biological, ecological and fishery parameters to be estimated. A common shortcoming of ecosystem models is insufficient or unreliable data for parameterisation, which can significantly compromise the reliability and the usefulness of model outputs for ecological or tactical fisheries applications (Plaganyi & Butterworth, 2004). Fortunately, in the case of the Warm Pool model, decades of region-specific biological, ecological and fisheries research data were available to build the static Ecopath model and to calibrate and validate the performance of the Ecosim dynamic model.

In particular, high-quality stock assessment model output data were available for 14 functional groups that extended for periods of up to 59 years, also 17 years of catch time series for non-target species and 12 years of annual biomass estimates for forage species and large phytoplankton. Together, these datasets spanned a broad spectrum of trophic levels and allowed the Ecosim model to produce good fits to the data. This study therefore overcame one of the major criticisms of Ecosim models, specifically that calibration, if performed, is often based on data for species that occupy only a narrow trophic level range, as time series of data are often available only for the most economically important species (Griffiths et al., 2010). The validity of the vulnerability parameter (v) estimates used by Ecosim to tune the model to time series data for a particular functional group can be compromised by the absence of complementary time series for a group's predators and prey, which would help to constrain the biomass and mortality estimates used in the model for these predator and prey groups to more ecologically realistic values.

A brief assessment of the impacts of not including bycatch groups in the model calibration is presented in Supporting information Appendix S3, which shows poorer model fits across most species groups if data for bycatch species were excluded from the Ecosim model calibration process. This emphasises the importance of a well-designed observer programme to monitor the catches (and discards) of a wide range of species caught in pelagic fisheries, as recommended by Nicol et al. (2013). Demonstrating that an ecosystem model can reproduce a long history of observed data, as was achieved with the Warm Pool model, lends greater credence to the model's forecasts about the potential effects of fishing or other impacts (e.g., climate change) on the ecosystem beyond the existing time series, on which management measures may be more reliably based.

5 | CONCLUSIONS AND CONSIDERATIONS FOR FUTURE WORK

This exploratory ecosystem modelling study provided valuable insights into the changes in the Warm Pool ecosystem over decades of industrial fishing and the plausible ecological impacts of future alternative effort regimes for the purse-seine fishery. The enormous complexity of trophic interactions within the Warm Pool pelagic ecosystem means that ecosystem models may be one of the few ways in which "what-if" scenarios regarding the ecological effects of fishing may be explored.

Although the model was based upon the highest quality data sets available, the input parameters are by no means without error or uncertainty, and there are several areas where the model can be improved. Basic studies are required on the feeding ecology, age and growth, and standing biomass of several functional groups, especially those of low commercial value that occupy low-to-intermediate trophic levels (e.g., forage species), to improve estimates of key model parameters (e.g., P/B, Q/B). Until such data on these ecosystem components become available, we can only speculate as to the true ecosystem-level responses to fishing.

The results presented in this study focus on the ecological impacts of the imposed FAD fishing effort scenarios, and therefore assess the efficacy of each scenario as a potential fisheries management measure based on the expected changes in the biomass or catch of particular functional groups. However, the management measures that best satisfy ecological or biological objectives might not be feasible due to unacceptable impacts on fishery value. Although the potential economic impacts of the various scenarios were not explored in the current study, Ecopath is capable of translating ecological impacts into economic impacts by including off-vessel prices and non-market prices for each functional group through the value chain module (Christensen, de la Puente, Sueiro, Steenbeek, & Majluf, 2014). Future work in this area may assist fisheries managers in finding optimal economic and ecological outcomes on which to base future management measures for fisheries supported by the western Pacific Warm Pool ecosystem.

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