

REVIEW

Foraging of seabirds on pelagic fishes: implications for management of pelagic marine protected areas

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ABSTRACT: Scientists and managers have become increasingly interested in how pelagic marine protected areas (PMPAs), or protected areas away from the coast, can be used to protect pelagic species. Subsurface-predator facilitated foraging ('facilitated foraging') between seabirds and subsurface predators, such as tunas, is a key ecological interaction in the tropical oceans where a number of large PMPAs have been created. In facilitated foraging, subsurface predators drive forage fish to the surface, where they are made available to seabirds. Because this is a critical interaction for seabirds, a reduction or cessation of fishing effort within tropical PMPAs may increase subsurface predator density, resulting in more foraging opportunities for seabirds closer to colonies. This interaction is well documented in the Eastern Tropical Pacific, and to a lesser extent in the Indian Ocean, but is poorly studied in the Central Tropical Pacific. Here, we review our current state of knowledge of facilitated foraging, particularly in relation to questions critical to PMPA management. We specifically consider 2 components of the foraging ecology of tropical seabird species: (1) diet and foraging methods, including flock feeding behavior, i.e. how species forage in association with other species or conspecifics, and (2) association with subsurface predators. We consider the spatial scale of this interaction as it pertains to the distribution of seabirds and tunas and to PMPA boundaries. We conclude with discussion of data gaps and the implications for managers. The present review of facilitated foraging will help focus future efforts and multidisciplinary collaborations on this important but understudied interaction.

KEY WORDS: Community ecology · Central Tropical Pacific · Fisheries management · Flock feeding · Foraging ecology · Multi-species interactions · Prey availability · Subsurface predator-facilitated foraging

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INTRODUCTION

There has been an increasing trend in the creation of mostly pelagic marine protected areas (PMPAs) to protect ocean ecosystems (Table 1). Marine ecosystems encompass 99% of the earth's biosphere volume (Angel 1993), and the vast majority of this volume occurs in the pelagic realm, or areas away from the coastal zone (e.g. non-neritic). Protection of

pelagic ecosystems, in addition to coastal regions, is necessary to meet global marine conservation targets, such as the Convention on Biological Diversity's call to establish 10% of the world's oceans as MPAs by 2020 (Convention on Biological Diversity 2010). Additionally, pelagic ecosystems provide >80% of global fish production (Pauly et al. 2002), are critical in the regulation of the Earth's climate (Field 1998), and support the majority of marine life during all or

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Table 1. Marine protected areas (MPAs) that contain large pelagic portions. *: areas strongly protected, >30% of the area in a no-take marine reserve. Data source: MPAPedia (www.mpatlas.org/learn/mpapedia)

Year designated	Name	Size (km ²)	Nation or authority
1975	Great Barrier Reef Marine Park*	345 000	Australia
1999	Macquarie Islands*	161 894	Australia
2006	Papah naumoku kea Marine National Monument*	362 074	United States
2006	Phoenix Islands Protected Area	408 250	Kiribati
2009	Pacific Remote Islands Marine National Monument*	225 040	United States
2009	Marianas Trench Marine National Monument	246 608	United States
2009	Prince Edward Islands MPA*	180 000	South Africa
2009	South Orkney Islands Southern Shelf MPA*	94 000	Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR)
2010	NE Atlantic high sea areas*	238 988	Oslo and Paris Commissions (OSPAR)
2010	Motu Motiro Hiva MPA*	150 000	Chile
2010	Chagos Archipelago MPA*	640 000	United Kingdom
2012	South Georgia & South Sandwich Islands MPA	1 000 700	United Kingdom
2012	Coral Sea	989 842	Australia
2012	Kermadec	620 000	New Zealand
2012	Marine Park of the Glorieuses & Marine Park of Mayotte	110 000	France

some part of their life history (Hays et al. 2005). Still, pelagic ecosystems face a number of threats, including overfishing, pollution, climate change, and species introductions (Halpern et al. 2008), and PMPAs have been proposed as one means of ameliorating these effects (Game et al. 2009). Protecting pelagic or wide-ranging species from effects is often cited as one of the primary reasons for designating PMPAs, but the areas must be large enough to incorporate significant portions of the habitat of far-ranging or migratory animal species or protect crucial life history phases (Hyrenbach et al. 2000, Norse 2005, Alpine & Hobday 2007, Ardron et al. 2008, Game et al. 2009). Additionally, protective measures must reflect effects managers are attempting to ameliorate (e.g. fishing must be reduced or prohibited to prevent overfishing), and areas must be effectively enforced (Walmsley & White 2003).

Several PMPAs, particularly in the Central Pacific and Indian Oceans (e.g. Chagos Marine Reserve, Phoenix Islands Protected Area, Papah naumoku kea Marine National Monument [MNM], and the Pacific Remote Islands MNM), are now in place (Table 1), and managers are beginning to grapple with the difficulties of developing and monitoring indicators of effectiveness for these protected areas within an ecosystem-based management context. This is particularly difficult in PMPAs because of the dynamic processes that occur in pelagic ecosystems (e.g. eddies and fronts) and the highly mobile species that are the focus of protection (Game et al. 2009).

Tropical seabirds are 1 example of a highly mobile species group that managers are aiming to protect. Many tropical seabirds are far-ranging foragers, breeding on small islands and atolls and carving out an existence in largely oligotrophic parts of the oceans (Owen 1981, Ballance et al. 1997). Many rely on dynamic and ephemeral oceanographic processes to forage. PMPAs may be of particular ecological significance to tropical seabirds because they are central place foragers during the breeding season, when they must return to colonies to incubate eggs and feed chicks (Ashmole & Ashmole 1967, Ballance et al. 2006). Seabirds may travel thousands of kilometers in a single foraging trip, but their long-distance movements are centered on the colony during the breeding season (King 1974, Flint 1991, Laniawe 2008, Catry et al. 2009a). This increases the chances that protection from PMPAs may influence seabirds throughout some or all of their foraging range because foraging opportunities may be increased through the additional protection of the resources they depend on.

PMPAs that reduce or eliminate commercial fishing may influence seabirds via direct and indirect mechanisms. (We refer to PMPAs that reduce or eliminate fishing effort when referring to PMPAs for the remainder of the text.) Reduced fishing within PMPAs may lower seabird bycatch or diminish the opportunities for seabirds to forage on fishery discards (Tasker et al. 2000, Lewison & Crowder 2003, Votier et al. 2004). Additionally, reduced pressure of

some fisheries may increase foraging opportunities for seabirds by increasing the abundance of prey species. However, unlike the majority of temperate seabirds, most tropical seabirds lack deep diving capabilities and instead must forage in the top-most surface layer (Ashmole & Ashmole 1968, Harrison et al. 1983). This has led to the evolution of subsurface-predator facilitated foraging (hereafter referred to as 'facilitated foraging') (Fig. 1). In this interaction, large pelagic fishes, such as tunas, drive forage fish into surface waters, making them available to surface predators (Murphy & Ikehara 1955, Ashmole & Ashmole 1967). Though this interaction occurs in many parts of the world (Burger 1988), it is of particular importance in the tropical waters of the world's oceans because it is one of the primary means by which tropical seabirds forage (Au & Pitman 1986, Spear et al. 2007). Because it is a critical interaction for seabirds, a reduction or cessation of fishing efforts targeting prey species or subsurface predators within tropical PMPAs may increase subsurface predator or prey density, resulting in more foraging opportunities for seabirds.

Facilitated foraging has been relatively well studied in the Eastern Tropical Pacific (ETP) (see Au & Pitman 1986, Spear & Ainley 2005, Spear et al. 2007), but it has been largely unstudied in the Central Tropical Pacific (CTP) (but see Ashmole & Ashmole 1967), although distinct differences in facilitated foraging occur between the 2 systems. For example, tunas, primarily skipjack *Katsuwonus pelamis* and yellowfin *Thunnus albacares*, are the main subsurface predators in the CTP, in contrast to dolphins and tunas in the ETP (Spear et al. 2007). These species have different vertical and horizontal movement patterns, which may influence facilitated foraging behavior. Additionally, seabird assemblages in the CTP differ from those in the ETP (Ashmole & Ashmole 1967). Still, it is unknown how variability in the interaction influences seabird populations. Given the correlations previously identified between fishery development and seabird crashes in many areas of the world (Harrison et al. 1983, Cury et al. 2011), there is a need to understand how seabirds interact with subsurface predators, particularly commercially important species, such as skipjack and yellowfin tunas, across the range where these interactions occur.

These interactions are of particular interest to managers of large PMPAs in tropical oceans as seabirds are often a guild that managers aim to protect. One such MPA is the US Pacific Remote Islands Marine National Monument (PRIMNM), created in

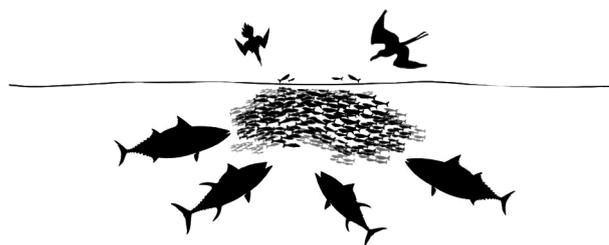


Fig. 1. Schematic of subsurface-predator facilitated foraging. Image credit: Drew Briscoe

2009 by Presidential Proclamation (Federal Register 2009), resulting in 225 038 km² of protected area in the CTP. It includes the far-flung and mostly unpopulated US territories of Wake Island, Johnston Atoll, Palmyra Atoll and Kingman Reef, Jarvis Island, and Howland and Baker Islands. These islands and atolls are home to as many as 4.4 million breeding seabirds representing at least 16 species (Table 2). Co-managed by the US National Oceanic and Atmospheric Administration (NOAA) and the US Fish and Wildlife Service (USFWS), monument managers want to know if the PMPA is likely to have a positive effect on seabirds and, subsequently, how to adequately monitor and manage seabird and pelagic fish populations.

To assess our current state of knowledge of facilitated foraging in the CTP and to determine the key research questions and methodologies for managing human activities that may influence facilitated foraging, we conducted a literature review and held an expert workshop. We focused specifically on the seabirds breeding on the PRIMNM islands and atolls (Table 2), though this information is applicable to other tropical areas. We further focused on a set of topics we identified in conjunction with managers at the NOAA Pacific Islands Regional Office, which is responsible for PRIMNM management. These topics were intended to focus future research on key elements of seabird and subsurface predator ecology and included the determination of the importance of subsurface predators to tropical seabird foraging, the distributions of seabirds and tunas, and the foraging behaviors and diets of seabirds in the PRIMNM region. At the heart of this review is this question: how do subsurface predator populations influence seabird population behavior and reproductive performance, and how can this knowledge be integrated into management of seabird and subsurface predator species in PMPAs? Below, we review current research aimed at answering this question.

Table 2. Tropical seabird ecology. Location where data are relevant is italicized with citations following. Data are primarily given for all locations for which there are data within the PRIMNM region. Otherwise, data is given for closest location. Isl: Island; Is: islands; ETP: eastern tropical Pacific; Squid: *Ommastrephidae* unless otherwise noted

Species	Body size	Flock feeding level, foraging method	Subsurface predator associations	Prey species	Prey size	Breeding foraging range	Non-breeding foraging range
White-tailed tropicbird	Small tropicbirds, 350 g (Diamond 1978)	Solitary foragers, surface plunging (Ashmole & Ashmole 1967, Spear et al. 2007)	Independent, <i>Christmas Is</i> , <i>ETP</i> , <i>Réunion Is</i> (Spear et al. 2007, Spear & Ainley 2005, Jaquemet et al. 2005) Yellowfin, skipjack, <i>ETP</i> (Spear & Ainley 2005) cetaceans, <i>Réunion Isl</i> (Jaquemet et al. 2005)	Squid, flying fish, <i>Christmas Is</i> (Gibson-Hill 1947)	10–18 cm, <i>Christmas Is</i> (Gibson-Hill 1947)	~120 km, not reported (Lee & Walsh-McGehee 1998)	Unknown
Red-tailed tropicbird	Large tropicbirds, 650–780 g (Schreiber & Schreiber 2009)	Solitary foragers, surface plunging (Ashmole & Ashmole 1967, Spear et al. 2007)	Independent, <i>Christmas Is</i> (Spear et al. 2007) Tunas, <i>ETP</i> (Spear & Ainley 2005)	53% fish, 47% squid, <i>Christmas Is</i> (Ashmole & Ashmole 1967); flying fish, squid, mackerel, <i>Hawaii</i> (Harrison 1990)	2–28 cm, <i>Christmas Is</i> (Ashmole & Ashmole 1967)	Mean 1034.3 ± 86 km, <i>Midway</i> (Laniawe 2008)	Several thousand km from colony, <i>ETP</i> (Spear & Ainley 2005)
Masked booby	Largest of boobies, 1.5–2 kg (Weimerskirch et al. 2008)	Flock feeders, plunge diving to 2 m (Weimerskirch et al. 2008, Grace & Anderson 2009)	Cetaceans, <i>ETP</i> (Au & Pitman 1986)	99% flying fish, remainder squid, <i>Palmyra</i> (Young et al. 2010b)	Average 26.6 cm, <i>Palmyra</i> (Young et al. 2010b)	Incubation: 103 km, <i>Clipperton</i> (Weimerskirch et al. 2008); early brooding: 30 km, <i>Palmyra</i> (Young et al. 2010b); chick-rearing: 144 km, <i>Clipperton</i> (Weimerskirch et al. 2008)	Unknown
Brown booby	Mid-size boobies, 1–1.7 kg (Schreiber & Norton 2002)	Flock feeders or independent, plunge diving to 0.9 m (Lewis et al. 2005, Yoda et al. 2007, Harrison et al. 1983)	Skipjack, <i>Hawaii</i> (Hebshi et al. 2008) cetaceans, <i>ETP</i> (Au & Pitman 1986)	Mainly flying fish, <i>Christmas</i> , <i>Johnston</i> (Harrison et al. 1984, Schreiber & Norton 2002)	5–40 cm, <i>Johnston</i> (Schreiber & Norton 2002)	Incubation, early brooding: 35 (males) to 75 (females) km, <i>ETP</i> (Gilardi 1992)	More coastal, <i>Palmyra</i> (Young et al. 2010a)
Red-footed booby	Smallest of boobies, 850–1100 g (Schreiber et al. 1996)	Flock feeders, plunge diving to 0.75 m (Lewis et al. 2005)	Skipjack, <i>Hawaii</i> (Hebshi et al. 2008) cetaceans, <i>ETP</i> (Au & Pitman 1986)	Mainly squid, remainder squid, <i>Palmyra</i> (Young et al. 2010b)	Average 20.6 cm, <i>Palmyra</i> (Young et al. 2010b)	Incubation, early brooding: 67.5 km max, <i>Palmyra</i> (Young et al. 2010b)	Unknown
Great frigatebird	1–1.8 kg (Metz & Schreiber 2002)	Flock feeders, surface snatchers, surface dipping or kleptoparasitism (Metz & Schreiber 2002)	Skipjack & yellowfin, <i>ETP</i> (Spear et al. 2007)	50% fish, 50% squid; flying fish, <i>Christmas</i> (Spear et al. 2007); other species' chicks <i>Pacific</i> (Metz & Schreiber 2002)	Variable, <i>Hawaii</i> (Harrison 1990)	Incubation: 612 km; brooding: 94 km, <i>Europa</i> , <i>Indian Ocean</i> (Weimerskirch et al. 2004)	600 km max, <i>Johnston</i> (Dearborn et al. 2003) 612 km, <i>Europa</i> , <i>Indian Ocean</i> (Weimerskirch et al. 2004)
Lesser frigatebird	0.75 kg (Le Corre 2001)	Flock feeders, surface snatchers, surface dipping or kleptoparasitism (Metz & Schreiber 2002)	Independent, tuna, cetaceans, <i>Mozambique Channel</i> (Jaquemet et al. 2005)	Flying fish, <i>Pacific</i> (BirdLife International 2012)	Unknown	Unknown	Unknown

Species	Body size	Flock feeding level, foraging method	Subsurface predator associations	Prey species	Prey size	Breeding foraging range	Non-breeding foraging range
Sooty tern	Largest of terns, 200 g (Schreiber et al. 2002)	Flock feeders, air dipping (Ashmole & Ashmole 1967)	Skipjack, cetaceans, <i>Hawaii</i> , <i>ETP</i> , <i>Réunion Is</i> (Hebshi et al. 2008, Spear et al. 2007, Jaquemet et al. 2008); independent, <i>ETP</i> (Spear et al. 2007)	38% fish, 62% squid; flying fish, mackerel/tuna, <i>Christmas</i> (Ashmole & Ashmole 1967)	0–18 cm, <i>Christmas</i> (Ashmole & Ashmole 1967)	Brooding: 290 km max; chick-rearing: 522 km max, <i>Johnston</i> (Flint 1991)	Unknown but completely pelagic
Gray-backed tern	Intermediate of terns, 95–145 g (Mostello 2000)	Flock feeders but independent of subsurface predators, plunge diving or air dipping (Gallagher 1960)	No data	92% fish, 4% squid; cowfish, flying fish, goatfish, <i>Hawaii</i> (Harrison et al. 1983) may take insects, <i>Christmas</i> , <i>Howland</i> (Gallagher 1960)	Average 20 cm (Harrison et al. 1983)	Unknown	Unknown
White tern	Smallest of terns, 77–157 g (Niethammer & Patrick 1998)	Solitary feeders independent of subsurface predators, air dipping (Ashmole & Ashmole 1967). Known to be flock feeders with tuna in <i>ETP</i> (Spear et al. 2007)	Skipjack, <i>Hawaii</i> (Hebshi et al. 2008); independent, <i>ETP</i> (Spear et al. 2007)	47% fish, 53% squid; blennies, flying fish, <i>Christmas</i> (Ashmole & Ashmole 1967)	0–16 cm, most 2–8 cm, <i>Christmas</i> (Ashmole & Ashmole 1967)	Unknown	Unknown
Brown noddy	Largest of noddies, 180 g (Chardine & Morris 1996)	Flock feeders, plunge diving or air dipping (Ashmole & Ashmole 1967)	Skipjack, <i>Hawaii</i> , <i>Réunion Is</i> (Hebshi et al. 2008, Jaquemet et al. 2005); tuna, <i>ETP</i> (Spear et al. 2007); cetaceans, <i>Réunion Is</i> (Jaquemet et al. 2005)	51% fish, 49% squid; flying fish, mackerel/tuna, <i>Christmas</i> (Ashmole & Ashmole 1967)	2–8 cm, <i>Christmas</i> (Ashmole & Ashmole 1967)	~20–80 km, <i>Hawaii</i> (Harrison 1981, King 1974)	Unknown
Black noddy	Intermediate noddy, 84–140 g (Gauger 1999)	Flock feeders, plunge diving or air dipping (Ashmole & Ashmole 1967)	Skipjack, <i>Hawaii</i> (Hebshi et al. 2008)	77% fish, 23% squid; flying fish, mackerel/tuna, blennies, <i>Christmas</i> (Ashmole & Ashmole 1967)	1–4 cm, <i>Christmas</i> (Ashmole & Ashmole 1967)	Within 9 km of land, <i>Christmas</i> (Ashmole & Ashmole 1967, 1968)	Unknown but thought to be close to nesting grounds (Gauger 1999)
Blue-gray noddy	Smallest of noddies, 58 g (Harrison 1990)	Flock feeders, plunge diving or air dipping (Ashmole & Ashmole 1967)	No data	75% fish, 10% squid; water-striders (insects), snake mackerels, squid <i>Loligo</i> spp., <i>Christmas</i> (Ashmole & Ashmole 1967)	1–10 cm, most 2 cm, <i>Christmas</i> (Ashmole & Ashmole 1967)	Within 9 km of land, <i>Christmas</i> (Ashmole & Ashmole 1968)	Unknown
Christmas shearwater	Small shearwaters, 354 g (Seto 2001)	Flock feeders, plunge diving (Ashmole & Ashmole 1967)	No data	29% fish, 71% squid; flying fish, mackerel/tuna, <i>Christmas</i> (Ashmole & Ashmole 1967)	0–14 cm, <i>Christmas</i> (Ashmole & Ashmole 1967)	Unknown	Unknown
Wedge-tailed shearwater	Largest of shearwaters; 390 g (Whittow 1997)	Small flock or solitary feeding, contact or air dipping (Ashmole & Ashmole 1967, Spear et al. 2007)	Skipjack, <i>Hawaii</i> , <i>Réunion Is</i> (Hebshi et al. 2008, Jaquemet et al. 2005) independent, <i>ETP</i> (Au & Pitman 1988)	66% fish, 28% squid; goatfishes, jacks, squids (fall), <i>Hawaii</i> (Harrison et al. 1983)	5.7 cm, <i>Hawaii</i> (Harrison et al. 1983)	Within 480 km, <i>Johnston</i> (King 1974)	Up to 3500 km, <i>Seychelles</i> (Catry et al. 2009b)

FACILITATED FORAGING

Facilitated foraging is a phenomenon that occurs in many parts of the globe, from temperate to tropic to polar regions. Facilitated foraging functions in 2 ways. In the first, defined as 'local enhancement' by Kiester & Slatkin (1974), birds use visual cues, such as other birds or the disturbance caused by subsurface predators at the water's surface, as indirect signals of available prey. This signaling is widespread in many parts of the world (Burger 1988, Au 1991, Clua & Grosvalet 2001, Silverman et al. 2004) and is also a common way for fishermen to identify the presence of fishing grounds (Murphy & Ikehara 1955, Au 1991). For example, off Newfoundland, Canada, common murre *Uria aalge* use the presence of other murre to signal the presence of their primary prey species, capelin *Mallotus villosus*, though they also rely on memory when prey and conspecific density is low (Davoren et al. 2003). Similarly, black-browed albatrosses *Thalassarche melanophrys* rely on local enhancement for locating krill in the Southern Ocean (Grunbaum & Veit 2003). Local enhancement is particularly important to tropical seabirds due to the relatively high patchiness of productivity in tropical regions and because tropical seabirds forage close to the water's surface (Ashmole & Ashmole 1967, Harrison et al. 1983).

The second mechanism of facilitated foraging involves the driving of prey fish to the surface by subsurface predators, such as tunas or dolphins. This mechanism forces prey to the surface, where it is within tropical seabirds' limited diving range (3 to 4 m maximum) (Ashmole & Ashmole 1967, Diamond 1978, Lewis et al. 2005, Weimerskirch et al. 2008). This component of facilitated foraging occurs at much greater frequency in tropical regions of the world's oceans, perhaps as a result of the reduced diving capacity of tropical seabirds (Diamond 1978).

This interaction has been studied extensively in the ETP and to some degree in the Indian Ocean, where the interaction is driven by a combination of marine mammals, sharks, tunas, and other predatory fishes (Au & Pitman 1986, Jaquemet et al. 2005, Spear & Ainley 2005, Ballance et al. 2006, Spear et al. 2007, Hebshi et al. 2008). In contrast, facilitated foraging in the CTP is driven almost exclusively by small tunas, such as yellowfin and skipjack, that occur closer to the surface than other tuna species (Sund 1981). This may be because of differences in productivity, frontal systems, the thermocline, or ecological drivers between the regions (Murphy & Ikehara 1955, Ashmole & Ashmole 1967, Barkley et al. 1978, Sund 1981, Spear et al. 2001, Allain et al. 2012, L. Ballance

pers. comm.). Further, ~90% of breeding seabird species in the CTP rely upon facilitated foraging, making it the major ecological driving force behind the pelagic community in the region (Ashmole & Ashmole 1967, King 1974). The differences between this interaction in the CTP and other regions highlight our need to better understand tuna-seabird associations across different regions and suggest caution in overly generalizing this phenomenon.

The benefits seabirds and tunas derive from facilitated foraging are unclear. Researchers have hypothesized that seabirds, such as frigatebirds *Fregata* spp. and sooty terns *Onychoprion fuscata*, are obligate commensals with tuna, while others, such as shearwaters *Puffinus* spp., are facultative because they forage in association with subsurface predators as well as independently of them (Au & Pitman 1986). The interaction may be beneficial for both tunas and seabirds as seabirds may prevent prey from leaping out of the water, further containing the school at the surface (Burger 1988). It is also possible that the interaction has a negative effect on tunas if seabirds compete for prey. However, a number of studies have shown that although tunas and seabirds utilize the same schools, the 2 groups largely forage on different prey, different prey sizes, or at different trophic levels (Murphy & Ikehara 1955, Ashmole & Ashmole 1967, Bertrand et al. 2002, Cherel et al. 2008, Young et al. 2010a). Also, tuna and seabirds use different hunting mechanisms (Burger 1988). Regardless of the benefits to tunas, the presence of subsurface predators is important to the successful foraging of seabirds in tropical oceans. For example, 76% of prey mass consumed by seabirds in one ETP study was made available to seabirds by subsurface foragers (Spear et al. 2007). Furthermore, sooty terns are the most abundant seabird in the CTP, and their success in this region may be predicated on interactions with tuna populations (Au & Pitman 1988).

Understanding how seabird populations respond to changes in tuna abundance is critical to determine to what extent facilitated foraging influences seabird behavior and demography. This influence will vary by species and will depend largely on 2 key components: (1) the foraging ecology of individual species, and (2) the foraging ranges and distribution of both seabirds and tunas. Below, we further explore these 2 components of seabird ecology in the context of facilitated foraging in the CTP. We focus on seabird species that breed on the islands that encompass the PRIMNM, which include tropicbirds *Phaethon* spp., boobies *Sula* spp., frigatebirds, terns, noddies (*Anous* and *Procelsterna* spp.), and shearwaters (Table 2).

FORAGING ECOLOGY

Foraging ecology defines the mechanisms and strategies by which seabirds forage, the prey species they target, and how seabirds interact with their environment (Ashmole & Ashmole 1967). Here, we specifically consider 2 components of foraging ecology of PRIMNM seabird species: (1) diet and foraging methods, including flock feeding behavior (i.e. how species forage in association with other species or conspecifics), and (2) association with subsurface predators. We consider how these components related to facilitated foraging, and the implications for managers. We also identify gaps in our knowledge.

Diet and foraging methods

At-sea foraging behavior defines a large portion of the ecological niche of a species. The oligotrophic nature of pelagic and particularly tropical ocean ecosystems means that foraging resources are often patchy and widely dispersed (Longhurst & Pauly 1987), and multiple species and taxa (e.g. seabirds and tunas) often forage in the same patch above and below the water's surface (Buckley 1997, Spear et al. 2007). Likely to reduce intra-specific competition, species occupy specific niches, targeting different size classes of prey or utilizing different methods of capture, though overlaps in niches do occur (Ashmole & Ashmole 1967, Spear et al. 2007).

The majority of seabird species in the CTP forage as part of multi-species flocks in association with subsurface predators (Table 2), including frigatebirds, noddies, shearwaters, terns, and booby species, though brown boobies *Sula leucogaster* usually forage independently (Gould 1971 in Harrison et al. 1983). These flocks can be as large as 4300 ind. from 15 bird species, span an area of 5 km, and persist for multiple hours (King 1974, Au & Pitman 1988, Balance et al. 1997, Spear et al. 2007). Variations in target prey, proportion of overlapping prey items, and foraging methods among species allow for multi-species foraging flocks (Harrison et al. 1983). This diversification of foraging patterns in the Central Pacific, however, is limited because tropical seabirds capture a smaller range of prey species than in other regions of the world, although individual species target different prey, as well as different size classes (Harrison et al. 1983, Spear et al. 2007), and employ different foraging methods (e.g. plunge diving, surface plunging, contact dipping, etc.; Table 2) (Ashmole & Ashmole 1967).

Sooty terns and masked boobies *Sula dactylatra* are 2 of the most common flock feeders in the CTP, and a comparison between their foraging methods and diets illustrates how seabirds in the CTP carve out niches effectively. Sooty terns are the largest of the CTP tern species at 200 g (Schreiber et al. 2002), but they are still considerably smaller than all of the boobies, especially the masked booby (1.5 to 2 kg, Weimerskirch et al. 2008). Sooty terns are not well adapted to water and spend long stretches of time in the air, foraging mainly by dipping from several meters above the surface (Ashmole & Ashmole 1967). These heights give them a unique vantage point from which to spot prey, though their small size limits their target prey size (2 to 8 cm) (Ashmole & Ashmole 1967). The diet of sooty terns consists of squid and fish, but the percentages vary by location. For example, at Christmas Island, seabirds' diets consisted of ~62% ommastrephid squids and 38% fish by volume, while this percentage was reversed in the ETP (Ashmole & Ashmole 1967, Cherel et al. 2008). Masked boobies, by contrast, are well adapted for foraging within the water column, plunge diving to a depth of up to 2 m and targeting flying fish (Weimerskirch et al. 2008, Young et al. 2010b). They will, however, eat prey of a much smaller size, as evidenced on Rose Atoll, where prey averaged 7.4 cm (range 5.6 to 8.9 cm) (Harrison et al. 1984). Masked booby diets primarily consist of fish followed by squid (Harrison et al. 1984, Spear et al. 2007, Young et al. 2010b). Though there is some overlap in diet preferences, sooty terns and masked boobies use different strategies and prey on different size classes. This niche partitioning was observed in diet composition studies in the Hawaiian Islands and on Christmas Island across seabird assemblages consisting of over 15 seabird species (Ashmole & Ashmole 1967, Harrison et al. 1983). Isotopic signature studies in the Central Pacific and Indian oceans delivered similar results (Cherel et al. 2008, Young et al. 2010a).

Associations with subsurface predators

Most tropical seabirds associate with subsurface predators to some degree, and flock feeding behavior often occurs concurrently with facilitated foraging. Because almost all CTP seabirds flock feed to some extent, almost all are thought to engage in facilitated foraging (Ashmole & Ashmole 1967, Harrison & Seki 1987, Spear et al. 2007). Owing to the remoteness of the CTP and therefore lack of research, most of our knowledge of seabird–subsurface predator interactions comes from studies elsewhere. The nature of

seabird and subsurface predator interactions varies among species and regions (Table 2), and interactions are largely influenced by oceanographic conditions, such as thermocline depth and frontal systems. Thus, how studies in other regions of the world translate to the CTP should be interpreted with caution.

In the ETP and Hawaii, several species largely forage in association with subsurface predators (wedge-tailed shearwaters, white terns *Gygis alba*, and sooty terns) but also appear to have the ability to forage independently (Spear et al. 2007, Hebshi et al. 2008). For example, wedge-tailed shearwaters and sooty terns are typically obligate commensals with tunas (Au & Pitman 1988, Hebshi et al. 2008). However, they sometimes forage over floating objects (e.g. logs) in the ETP (Au & Pitman 1988). Tropicbirds forage independently of other seabirds or subsurface predators, though they are more frequently in small groups in association with subsurface predators, including yellowfin and skipjack tuna in the ETP and cetaceans near Réunion Island (Jaquemet et al. 2005, Spear & Ainley 2005). Sooty terns, white terns, great frigatebirds, and wedge-tailed shearwaters are occasionally nocturnal, and both blue-grey noddies and white terns are thought to forage independently of predators in the ETP (Ashmole & Ashmole 1967), though this is not the case in the CTP, where they are found in association with skipjack tunas (Spear et al. 2007).

There are some species for which our understanding of their at-sea behavior is extremely limited. For example, Christmas shearwaters *Puffinus nativitatis* are flock feeders, but their level of association with subsurface predators is largely unknown (Ashmole & Ashmole 1967). Both grey-backed terns *Sterna lunata* and blue-grey noddies *Procelsterna cerulean* have been poorly studied, but it is unlikely that they frequently forage in association with subsurface predators because they are thought to be largely coastal species (Harrison et al. 1983). Blue-grey noddies are particularly interesting because they forage within ~3 km of land though still largely in the pelagic realm, due to the sharp slope of the shelf of many tropical islands. Their varied diet, which includes insects when they are abundant, suggests that they are an opportunistic and sometimes coastal species (Ashmole & Ashmole 1967, Harrison et al. 1983, Rauzon et al. 1984).

Management implications and data gaps

Comprehensive knowledge of what seabirds eat, how they find prey, and to what extent they rely on

facilitated foraging are critical components to evaluating the potential benefits of PMPAs (Maxwell & Morgan 2011a). The tuna species involved in facilitated foraging are commercially important, meaning that fishing regulations will be an inherent consideration in both ecosystem dynamics and how seabird–tuna interactions are managed (Essington et al. 2002, Hebshi et al. 2008). Understanding the extent to which seabirds rely on subsurface predators will also give insights into how adaptable seabirds are if populations of subsurface predators are reduced by fishing or by changes in the oceanographic environment.

Studies that include diet, at-sea surveys, and behavioral observations of seabird-tuna interactions are necessary to better understand how management measures might influence seabird-tuna interactions (Maxwell & Morgan 2011b). A number of studies have been conducted to specifically characterize facilitated foraging in the ETP (Ballance et al. 1997, Spear et al. 2007), but no comprehensive studies have occurred in the CTP outside of Hawaiian waters (Harrison & Seki 1987, Hebshi et al. 2008), although there is anecdotal evidence that this interaction is markedly different than in other regions in the world and in other regions of the Pacific Ocean (Murphy & Ikehara 1955, Barkley et al. 1978, Maxwell & Morgan 2011a). Diet studies conducted in the CTP using stable isotopes and wet diet samples (Ashmole & Ashmole 1967, Harrison et al. 1983, Young et al. 2010a) are relatively few and are geographically and temporally limited. Thus, many questions remain regarding how the diets of seabirds change over a larger spatial and temporal seascape. Understanding the benefit that fishery closures have on tropical seabirds requires a strong commitment to better our understanding of the foraging ecology of seabird assemblages and how they relate to subsurface predators.

FORAGING RANGES AND DISTRIBUTION

While a detailed examination of trophic structure and foraging ecology is necessary to understand the association between seabirds and tunas, the spatial scale over which animals move is similarly important in order to understand the degree of potential interaction. Tunas are constrained by thermal tolerance and oxygen levels in the CTP (Blackburn & Williams 1975, Zagaglia et al. 2004), while in contrast, seabirds are spatially constrained by parenting duties during the breeding season (Ashmole & Ashmole 1967). These constraints vary by species because of life history strategies and body size (Ashmole & Ashmole

1967). As a result, seabirds and tuna interactions are restricted to relatively small scales during seabird breeding seasons. Understanding the association between seabirds and tunas requires knowledge of the distribution of both seabirds and tunas.

Seabird distribution

Seabirds partition themselves based on body size, prey species, and foraging range (Ashmole & Ashmole 1967). Foraging range is particularly pertinent to management because it dictates whether protected area boundaries are effectively incorporating foraging habitat. Several studies in the Central Pacific have used either telemetry or stable isotopes to determine foraging ranges. Enrichment in stable carbon isotopes in prey species increases from pelagic to coastal regions. Hence, this signature can be determined from the tissues of seabirds, showing the origin of their prey in relative distance from their breeding grounds (Bearhop et al. 2002). Of 7 seabird species studied at Palmyra Atoll in the equatorial Pacific, all had distinctly different levels of stable carbon isotope enrichment, showing that they each utilized different foraging areas (Young et al. 2010a). Smaller birds generally had a more pelagic signature than larger birds. This is probably because when near-shore resources are abundant, larger birds out-compete smaller birds (Ballance et al. 1997).

Studies incorporating satellite or radio telemetry, at-sea surveys, or time away from the nest were used to estimate foraging ranges (Gilardi 1992, Bradley et al. 2004, Young et al. 2010b). However, these studies range across a number of breeding stages, which can have marked effects on foraging ranges. For example, non-breeding birds are often presumed to have the widest distribution because they are not tied to land due to parental constraints. During breeding, birds early in the brooding stage appear to have the most restricted ranges because chicks must be fed frequently. Birds incubating eggs often have the most extensive ranges because the time they are away from the nest is only limited by their mate's ability to go without food while on the nest (e.g. Weimerskirch et al 2004). Across species and breeding stages, there is considerable variability in foraging ranges, with the ranges of some species largely unknown (Table 2, Fig. 2). Additionally, intensity of fishing has been shown to affect foraging ranges (Pichegru et al 2010) and should be taken into account. With the continued development of smaller and lighter tracking devices (Hazen et al. 2012a), our

understanding of foraging ranges will increase. At-sea surveys and stable isotopes can provide estimates of foraging ranges for species too small to carry satellite tags.

Tuna distribution

Tunas have a strong relationship with the physical environment as their distributions are limited by suitable temperature and oxygen concentrations where food is also abundant (Blackburn & Williams 1975, Zagaglia et al. 2004, Sund 1981, Andrade & Garcia 1999, Weng et al. 2009). They must be able to attain high swimming speeds and travel great distances, all the while maintaining body temperatures above ambient temperatures (Sund 1981, Andrade & Garcia 1999). Moreover, tuna distribution is driven by oceanographic features that concentrate prey, including fronts, thermoclines, and mixed layers (Sund 1981, Fiedler & Bernard 1987, Brill & Lutcavage 2001, Zainuddin et al. 2006).

Yellowfin and skipjack tuna are the 2 primary subsurface predators in the CTP. Very little detailed work has been done examining the distribution of tunas in the PRIMNM region. At the Line Islands (Palmyra Atoll and Christmas Island), yellowfin tunas were dominant closer to land, while skipjack tunas were more common offshore (Murphy & Ikehara 1955). Despite their ability to travel large distances, yellowfin tunas are confined to relatively restricted geographic areas (Hilborn & Sibert 1988). Tag recoveries determined that median lifetime displacement of yellowfin tuna was 337 to 380 km and that a substantial proportion of individuals remained within the EEZs of Western Pacific nations for up to 6 mo (Fig. 2, Sibert & Hampton 2003). Off the coast of Baja California, 95% of all tagged tuna remained within ~1500 km of their tagging location (Schaefer & Fuller 2007). Three of the studied individuals were sexually mature and traveled south to warmer waters (>25°C) over 1500 km away to spawn. Additionally, the majority of yellowfin tuna tagged in Hawaii stayed within a few hundred kilometers of the tagging location over the course of ~1 yr (based on mark-recapture) (Itano & Holland 2000). Two individuals from Hawaii traveled over 4000 km to Japan and Mexico, respectively. It is possible that they were traveling to spawning grounds, although some yellowfin are known 'resident' spawners in Hawaii (Itano & Holland 2000). In the larger Central and Western Pacific, yellowfin travel from the Western Pacific into the Central Pacific in the second and third quarter of the

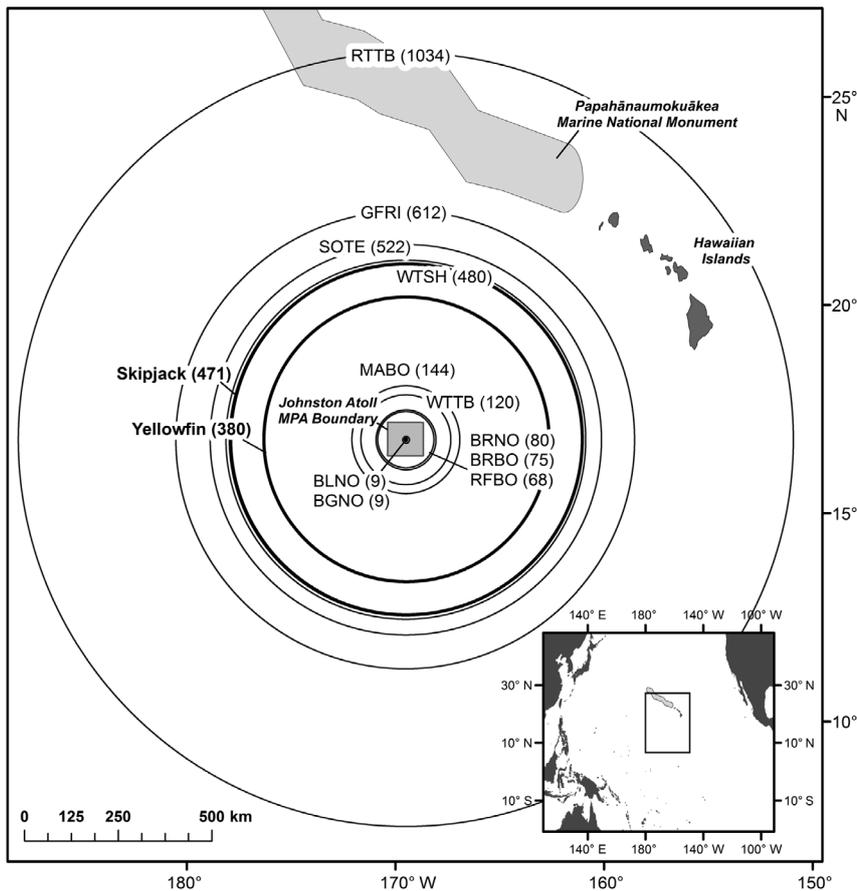


Fig. 2. Foraging ranges of breeding tropical seabirds (thin lines; from Table 2) and tuna (thick lines; from Sibert & Hampton 2003), centered around Johnston Atoll, part of the US Pacific Remote Islands Marine National Monument. Maximum foraging ranges and median lifetime displacement are shown in () following species names. Centering tuna movements around an island is hypothetical and done to show maximum potential overlap between tunas and seabirds (RTTB: red-tailed tropicbird; GFRI: great frigatebird; SOTE: sooty tern; WTSH: wedgetailed shearwater; MABO: masked booby; WTTB: white-tailed tropicbird; BRNO: brown noddy; BRBO: brown booby; RFBO: red-footed booby; BLNO: black noddy; BGNO: blue-grey noddy)

year, though the majority of yellowfin spawning occurs year-round within 10° of the equator, where sea surface temperatures are $>26^\circ\text{C}$ (Itano 2000).

Skipjack tuna are relatively geographically confined, although their distributions are somewhat greater than yellowfin (Hilborn & Sibert 1988). The median lifetime displacement for skipjack tuna is 411 to 471 km (Fig. 2, Sibert & Hampton 2003), though most skipjack in the ETP have spawning origins in the Central Pacific west of 130° W (Blackburn & Williams 1975). They generally follow a pattern of spawning in the Central Pacific where waters are warm enough for larvae, migrating to cool productive waters of Central American coast as adolescents, and returning to the Central Pacific to spawn again (Blackburn & Williams 1975).

Spatial and temporal interactions between seabirds and tunas

The spatial and temporal scale over which the 2 predator groups operate is critical to understanding

their interaction. For example, if skipjack remain highly resident to a region (e.g. moving on scales of 100 km over several weeks), and red-footed boobies are able to forage within those same distances, it may be possible for boobies to reliably find facilitated foraging opportunities. This also implies that fisheries management at the local scale can have appreciable influences on the regional ecosystem and facilitated foraging. In contrast, if tunas are not resident to a region (e.g. they move over scales of hundreds of kilometers in the order of days tracking oceanographic features or prey resources), seabirds constrained by breeding activities will be less likely to encounter tunas and opportunities for facilitated foraging. In this second scenario, seabirds could be characterized as interacting with patchily distributed prey resources because tuna are ephemeral in the region. This has important implications for managing fisheries resources and PMPAs. It implies that managing fisheries on a localized scale (e.g. at the scale of a single island nation EEZ or PMPA) may have reduced influence on facilitated foraging and, potentially, the subsequent foraging success of seabirds.

Although tunas and seabirds interact on different scales, they are likely to overlap to some extent (Fig. 2). Their overlap is difficult to characterize given that the movements of tuna are not centered on a single location. Hypothetically, however, if tuna were centered around the same point as seabirds, the potential range overlap could cover the full foraging ranges of up to 8 of the 11 species for which foraging ranges are known (Fig. 2, Table 2). Tuna movements, however, are not known to center around islands, and the fish may move much larger distances over their lifetime than seabirds. Additional research on the localized spatial and temporal movements of tunas will help to elucidate both the movements of tunas and their overlap with breeding seabirds.

Management implications and data gaps

Data gaps exist in our knowledge of seabird ranges, but even our current knowledge shows a potential mismatch between the size of some PMPAs, such as PRIMNM, and the distribution of seabirds (Fig. 2). Though the goal of PRIMNM is not to encompass the entirety of seabird foraging ranges, additional research is necessary to determine if the boundaries of PRIMNM are effectively capturing seabird facilitated foraging habitat during the breeding season. Additionally, comprehensive at-sea distribution is known only for a few of the seabird species in the CTP (Table 2), and no studies exist for lesser frigatebirds, gray-backed terns, white terns, or Christmas shearwaters anywhere. Further, the distributions in all breeding stages, particularly during the non-breeding stages, are known for only a few species (Table 2). The distribution of yellowfin tuna is comparatively well understood, while information on skipjack is largely still lacking, although they may be more important to seabirds (Harrison & Seki 1987). Data on distributions of both seabirds and tunas are critical to understanding the overlap between seabirds and subsurface predators as well as evaluating if PMPA boundaries are effectively capturing the ranges and critical areas of the populations they are aiming to protect. Protective measures, such as reductions in fishing, may also be seasonally effective, particularly during seabird breeding seasons. However, tropical seabird breeding cycles are highly variable and may occur year-round (Ashmole & Ashmole 1967).

Foraging ranges of seabirds and tunas are constrained by reproduction, body size, and thermoregulation. Oceanographic features that dictate

where prey can be found also influence their movements (Lehodey et al. 1998, Kappes et al. 2010). Knowledge of oceanographic drivers is critical to drawing conclusions about seabird distribution at a scale that is relevant to management. Very few studies have linked predator distribution with both oceanographic features and prey species, and those that have (e.g. Croll et al. 2005, Wingfield et al. 2011) were not conducted in the CTP. Seabird foraging success is likely dictated not only by the presence of prey but also by the presence of subsurface predators. This adds an additional layer of complexity in determining the oceanographic influences that affect seabird foraging success. This is further complicated by the fact that seabirds and tunas appear to move on different spatial scales, with tunas able to cover a much larger and less restricted area. Conducting integrated field studies that determine seabird foraging success using multiple data sets (e.g. environmental variables, prey, and subsurface predator distribution data) across different spatial and temporal scales, and linking this success to tuna presence and distribution, is critical to ensuring that the seabirds' foraging habitat is adequately protected (Maxwell & Morgan 2011b). Cost-effective methods, such as the use of remotely sensed data, can be employed once initial relationships between species and oceanographic parameters are determined.

CONCLUSIONS

While some of the topics highlighted here can aid management of seabirds, a more integrated understanding of the mechanisms of the interactions and the components that drive the relative success of seabird foraging within the interactions is critical. For example, the relationship between tuna school size and its influence on foraging success in seabirds is still unknown. Is there a school size that results in optimal foraging success or a school size threshold below which facilitated foraging breaks down? Does the presence of seabirds help or hinder tuna foraging? Could an increase in seabird populations actually depress tuna populations as a result of interspecies competition? Anecdotal information suggests the relationship is commensal or mutualistic (Au & Pitman 1986, Burger 1988), but integrated studies will provide more concrete evidence. The answers to these questions are critical for understanding the influence of fishing on facilitated foraging, both within PMPAs and outside.

Greater knowledge of seabird foraging behavior will also help managers better understand how seabirds will respond to a reduction or increase in fishing effort. Will an increase in fishing effort result in cascading effects on seabirds and their survival, or will seabirds be capable of switching behaviors with little population level influences? How will effects differ when fishing levels change locally versus at the ecosystem level? Hebshi et al. (2008) suggested that there is little indication that seabirds are able to shift behaviors easily. They also suggested that despite the global increase in skipjack populations (Sibert et al. 2006), localized depletion due to fishing or environmental influences may have a disproportional influence on seabird populations because of their limited foraging ranges. Hinke et al. (2004) also suggest that large-scale reductions in yellowfin tuna may lead to increases in mahi mahi *Coryphaena hippurus*, a species that is not preferred by seabirds for facilitated foraging (Hebshi et al. 2008).

These questions are particularly pertinent for PMPAs as the influences of climate change increase. Just as fishing effort can change the abundance and potential distribution of tunas, so can climate influences (Hazen et al. 2012b). Lehodey et al. (2010) and Loukos et al. (2003) predict that increasing water temperatures may open up additional habitat in subtropical latitudes as well as farther west, but we may also see decreases in habitat in the tropics due to sea surface temperatures beyond the thermal tolerance of some tuna species. Off Australia, Hobday et al. (2010) predict that the core habitat of most pelagic species will contract. Climate change may increase dissolved oxygen concentrations in deeper waters, allowing tuna to forage deeper in the water column and away from the surface where seabirds are able to forage (Lehodey et al. 2010). Climate change may also bring increased El Niño events (Timmermann et al. 1999), which may result in increases in tuna populations (Loukos et al. 2003) but these events are known to have sometimes devastating effects on tropical seabirds (Schreiber & Schreiber 1984).

In summary, there is much to be learned about this complex interaction. Still, with the increase of pelagic marine protected areas, particularly in the tropical oceans where this interaction is most critical, managers will continue to grapple with making decisions that will be in the best interests of the species they are aiming to protect. We hope that in addition to summarizing our present state of knowledge surrounding facilitated foraging, this review also will serve as a call for seabird and pelagic fish biologists, as well as oceanographers and those in related disci-

plines, to collaborate and focus effort on this important and fascinating but understudied interaction. A better understanding of facilitated foraging and its effects on seabird populations will allow for better and more informed management decisions to protect seabirds, fishes and the pelagic ecosystem.

Acknowledgements. We are grateful to the participants of the Pelagic Fish and Seabird Inter-Relationships in the Central Tropical Pacific Workshop: D. Ainley, L. Ballance, C. Boggs, E. Breuer, P. Dalzell, D. Duffy, B. Flint, A. Hebshi, H. Hirsh, K. Holland, D. Hyrenbach, A. Katekaru, M. Naughton, P. Pinto da Silva, D. Polhemus, K. Rivera, S. Shaffer, M. Seki, N. Shoji, M. Tosatto, S. White, H. Young, L. Young, and K. Weng. Their insights, along with the comments of 2 anonymous reviewers, greatly informed this work. We are grateful to staff of the National Marine Fisheries Service, including H. Hirsh and C. Boggs, the Fish and Wildlife Service, especially B. Flint, and Marine Conservation Institute, especially B. Chandler, S. Magier, and B. Rubin, for their assistance in organizing the workshop. This work was supported by a grant from the National Oceanic and Atmospheric Administration (NA10NMF429028).

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Editorial responsibility: Matthias Seaman,
Oldendorf/Luhe, Germany

Submitted: June 27, 2012; Accepted: January 9, 2013
Proofs received from author(s): April 10, 2013