Associations between seabirds and subsurface predators around Oahu, Hawaii

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ABSTRACT: Many species of tropical seabirds rely on subsurface predators such as tuna and dolphins to drive prey close to the ocean's surface. We observed seabird foraging events from fishing vessels around the island of Oahu, Hawaii, to determine the prevalence and relative importance of different subsurface predators to seabird foraging. Sixty-nine seabird foraging events were observed, in 62 of which the presence and/or identity of subsurface predators could be determined. Of those 62, all but two involved subsurface predators and accounted for 99.8% of all foraging birds. Skipjack tuna *Katsuwonus pelamis* were the predominant (81%) subsurface predator involved in seabird feeding events, with odontocetes *Stenella attenuata* and *Pseudorca crassidens* (8%), mahimahi *Coryphaena hippurus* (6%), and yellowfin tuna *Thunnus albacares* (2%) being less common. Wedge-tailed shearwaters *Puffinus pacificus* and brown noddies *Anous stolidus* foraged in association with tuna schools more often than would be expected by chance alone. Red-footed boobies *Sula sula*, in contrast, did not associate with any subsurface predator in greater proportion than what would be expected by chance. Nine additional seabird species were observed foraging in association with subsurface predators, but not in numbers large enough for statistical analysis. This study highlights the value of regional investigations able to uncover the variable nature of seabird–subsurface-predator associations. The finding that, in Hawaii, at least 2 species of seabirds showed tight dependence on tuna underlines the need for tuna fishery management to address the potential indirect ecological effects of fishing.

KEY WORDS: Tropical seabirds · Subsurface predators · Skipjack tuna · *Katsuwonus pelamis* · Wedge-tailed shearwater · *Puffinus pacificus* · Hawaii · Pacific Ocean

INTRODUCTION

Uncovering the strength of interspecific relationships is a main thrust of ecological research, particularly when it is necessary to predict the ecosystem-wide ramifications of changes in the abundance or distribution of a given species (Krebs 1972). For example, the often-surprising trophic cascades caused by the removal or addition of one species illustrate the importance of tight ecological relationships to ecosystem structure (e.g. Estes et al. 2004, Myers et al. 2007). While predators in tropical pelagic systems have generally been found to be highly catholic in their diets (e.g. Harrison et al. 1983, Kitchell et al. 1999, Potier et al. 2007), there is mounting evidence of tight inter-specific associations involving oceanic birds and subsurface predators (cetaceans, large predatory fishes, sea turtles) (e.g. Au 1991, Pitman & Ballance 1992, Pitman 1993). These subsurface predators make prey available to the birds by driving and concentrating prey close to the ocean's surface, thus enhancing the foraging opportunities of surface-feeding and shallow-diving birds (Ashmole 1971). Because tuna, in particular, are harvested at such high global levels (5.1 million tons in 2005; FAO 2007), changes in their abundance and distribution may affect the foraging success of the associated seabirds.

If foraging opportunities were to become more sparse, that may further impair foraging success of the associated seabirds because of the tendency of sea-

birds to use each other to find prey patches, a process termed local enhancement (Grünbaum & Veit 2003). A critical first step to assess these potential impacts is to quantify the degree of reliance of seabirds on tuna and other subsurface predators.

Previous research has shown that the composition of the seabird assemblages associated with subsurface predators varies geographically, and that even within a given region, these associations may vary depending on the ecological setting and the species involved. In Hawaii, Harrison & Seki (1987) found that most (75%) foraging seabird flocks occurred over schools of skipjack tuna *Katsuwonus pelamis*. In the eastern tropical Pacific (ETP), Au & Pitman (1986, 1988) documented tight associations between several seabird species (terns, shearwaters, boobies, frigatebirds, petrels) and yellowfin tuna *Thunnus albacares* and spotted *Stenella attenuata* and spinner *Stenella longirostris* dolphins. Yet, while frigatebirds and sooty terns *Sterna fuscata* were obligate commensals with these subsurface predators, other species were more facultative. For instance, the shearwaters and petrels were often observed feeding on free-floating organisms away from subsurface predators (Au & Pitman 1988).

Ballance et al. (1997) expanded this analysis by documenting the influence of ocean productivity structuring the composition of seabird flocks associated with subsurface-predator schools in the ETP. Booby flocks predominated in high-productivity waters, flocks of wedge-tailed shearwater *Puffinus pacificus* and Juan Fernández petrel *Pterodroma externa* occurred in intermediate-productivity waters, and sooty tern flocks inhabited low-productivity waters. Several recent studies in other ocean basins have underscored the widespread incidence and regional variability in seabird–subsurface-predator associations. Off the Azores Islands (eastern Atlantic Ocean), Clua & Grosvalet (2001) documented that several species of dolphin, and occasionally large tuna, provide foraging opportunities for shearwaters. In contrast, off Reunion Island (Western Indian Ocean), Jaquemet et al. (2004) reported that tuna were the primary mediators for foraging shearwaters, terns and noddies; however, dolphins were the subsurface predators most commonly associated with tropicbirds. These results highlight the value of comparative regional and local studies of seabird and subsurface-predator assemblages within distinct geographic and oceanographic settings.

Documenting whether these foraging associations happen more often than would be expected by chance alone, if these seabirds and subsurface predator were randomly distributed across all schools, uncovers subtle but critical aspects of this ecological phenomenon (Au & Pitman 1986, Pitman & Ballance 1992, Jaquemet et al. 2004). Characterizing such preferences

is an important component in assessing the strength of these ecological relationships and predicting whether cascading effects, as opposed to behavioral switching, would be likely in response to changes in the abundance of the dominant subsurface predator(s).

The present study expands the research of Harrison & Seki (1987), who characterized the seabird–subsurface-predator associations during the 1980s in Hawaii, but did not address these patterns statistically. Furthermore, a regime shift in the pelagic ecosystem of the Central Pacific Gyre (characterized by increased salinity, decreased sea-surface temperature and primary productivity, a shift in the composition of phytoplankton, and decreased reproductive successes of seabirds and monk seals) occurred after their study was conducted (Polovina & Haight 1999, Karl et al. 2001). To explore whether the subsurface predator community has changed since this regime shift took place, we compare the structure of this assemblage determined from our study (2000s) and during the 1950s and 1960s using the data of Harrison & Seki (1987).

MATERIALS AND METHODS

Surveys. At-sea surveys were conducted in summer and fall, June to November of 2000, 2001, and 2003, opportunistically aboard commercial and recreational fishing vessels around the island of Oahu, Hawaii. Eighteen trips were conducted (Fig. 1) for a total of 168 daytime survey hours. Most (14/18 or 77.8%) trips were conducted aboard a commercial vessel targeting skipjack tuna. Surveys were non-random; they targeted specific fishing areas known for higher densities of fish and seabirds, and deliberately sought out fish–seabird aggregations. Fishing effort occasionally targeted fish aggregation devices (FADs) but predominantly focused on free-ranging schools located by the presence of associated seabirds. When individuals or flocks (defined as 2 or more individuals) of foraging seabirds were observed either by A. J. Hebshi or the fishers, the vessel was directed towards the individual or flock. All foraging seabirds were counted and identified to species, and the identity of the subsurface predators, if present, was determined either through their capture or visual observations at the surface when no catches were made. The number and estimated mass of the fish harvested per school were determined when the fish were brought on deck, and the number of odontocetes per pod was estimated from surface observations.

Occasionally, schools were in close proximity with each other in time and space. If these schools consisted of different species or size classes of subsurface predators (size class was nearly uniform within all schools),
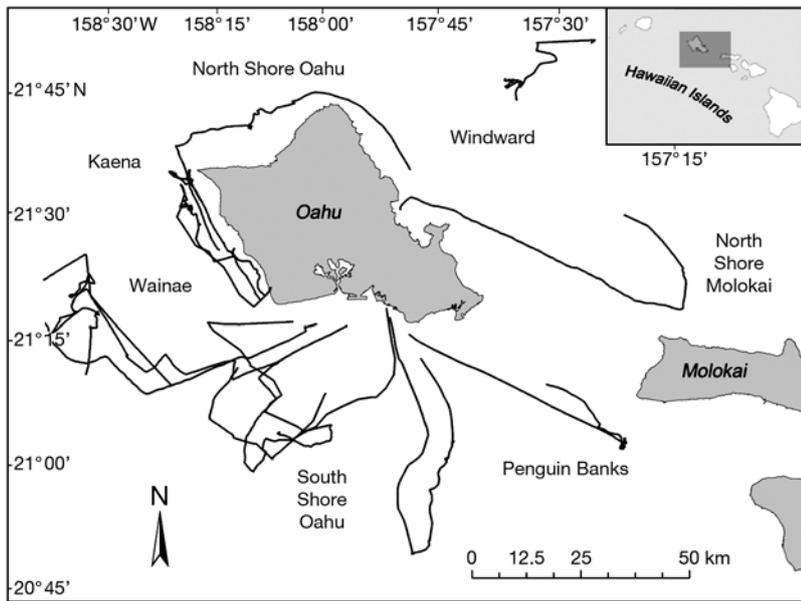
Fig. 1. Tracklines of at-sea surveys around Oahu, Hawaii, USA

they were considered to be distinct sightings. When no such determination could be made, the observations were pooled and the largest number of individuals recorded for each seabird species was used for any subsequent analyses.

Species-specific patterns. There were sufficient numbers of observations (n > 30 feeding flocks per event) for 3 seabird species — wedge-tailed shearwater, brown noddy *Anous stolidus*, and red-footed booby *Sula sula* — to perform univariate statistical tests to investigate whether these species associated with particular types of subsurface predators beyond what would be expected if the birds were distributed randomly across all schools. Because there were few observations of non-tuna subsurface predators, mahi-mahi and odontocete schools were lumped into a single functional group and compared with the observations of tuna schools. This dichotomous comparison is biologically justifiable due to the substantial difference in prey size (a key variable in seabird niche partitioning; Harrison et al. 1983) between tuna and the other predators (Roger 1994, Robertson & Chivers 1997, Santos & Haimovici 2001, Olson & Galván-Magaña 2002, Ménard et al. 2006). For each of the 3 species of birds, means and medians tests were used to determine whether the average number of individuals per flock was significantly different between the 2 subsurface predator groups. Contingency tests (χ^2) were used to detect if the bird species were associated with either group of subsurface predator disproportionately from what would be expected by chance.

Seabird assemblages. A multivariate test (non-metric multidimensional scaling, NMDS) was used to com-pare seabird assemblages among different subsurface-predator types (PC-ORD; McCune & Mefford 1999). NMDS is ideal for characterizing the distributions of patchy organisms because it does not impose any assumptions on the shape of the underlying habitat−wildlife relationships. Furthermore, NMDS does not assemble discrete groupings of species or samples, but plots them along a multidimensional continuum representing combinations of the explanatory variables. The species and samples from similar habitats are thus plotted closer together in multivariate space (Kenkel & Orloci 1986). This analytical technique has been used previously to characterize the structure of seabird assemblages and their habitat associations (Smith & Hyrenbach 2003, Hyrenbach et al. 2007).

The NMDS analysis relied on a similarity matrix created using the Sorensen (Bray-Curtis) index from the raw seabird counts and 13 explanatory variables describing the type of fishing (commercial vs. sport), the type of subsurface predators (skipjack tuna, mahimahi, spotted dolphin, false killer whale, yellowfin tuna, unknown), and the geographic location around Oahu (Waianae, Penguin Bank, Kaena Point, other). Only those locations contributing at least 10% (7 or more) observations were considered in the analysis.

RESULTS

Surveys

A total of 69 independent seabird foraging observations were recorded. The presence and identity of subsurface predators were not ascertained in 7 (10.5%) of the schools. In two of the remaining 62 observations (2.9% of total), no subsurface predators appeared to be present. These were short-lived (<10 s) feeding events, after which the birds quickly dispersed from the site, suggesting an absence of subsurface predators. Thus, for the subsequent analyses we considered a sample size of 62 seabird foraging observations, 60 of which involved subsurface predators.

While skipjack tuna were the predominant associated subsurface predator, 4 other species were involved in feeding associations with seabirds: mahimahi *Coryphaena hippurus*, false killer whale *Pseudorca crassidens*, spotted dolphin, and yellowfin tuna (Fig. 2). These 5 species of subsurface predators were widely
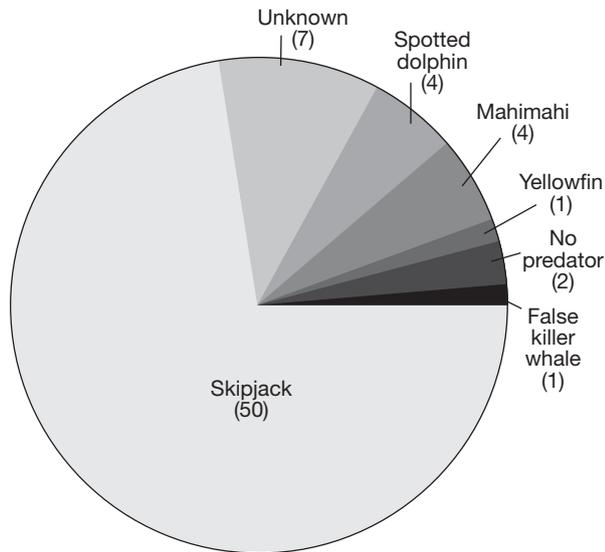
Fig. 2. Relative abundances of subsurface predators associated with foraging seabirds (n = 69 schools). See Table 1 for scientific names

distributed across the study area (Fig. 3), even though only skipjack were captured north of the island. There was a significant difference in the occurrence (presence or absence) of skipjack as a function of fishing trip type (commercial vs. recreational) ($\chi^2 = 17.2$, df = 1, p < 0.0005) (Fig. 4) because recreational boats targeted logs and buoys where mahimahi were more likely to be found. Schools were typically larger for the tuna than for the odontocetes and the mahimahi. In those instances when nearly the entire tuna school was
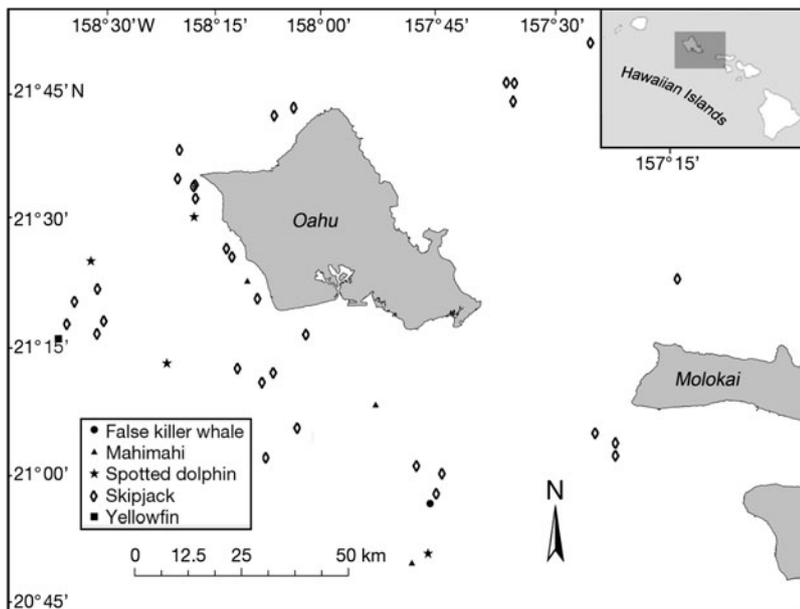

Fig. 3. Geographic locations of seabird flocks associated with subsurface-predator schools

harvested (n = 13), thus allowing for a minimum school-size estimation, 204 ± 182 tuna (mean ± SD) were harvested. In contrast, the mahimahi schools ($\bar{x} = 4.75$, n = 4, maximum = 11) and odontocete pods ($\bar{x} = 13.8$, n = 5, maximum = 22) encountered were substantially smaller. In the 13 harvested tuna schools, only 2 contained mixed species. Skipjack comprised >99% of these 2 schools, with yellowfin tuna and rainbow runners *Elagatis bipinnulata* present in very small numbers.

Twelve species of foraging seabirds (5508 individuals) were observed (Fig. 5), of which 75% were wedge-tailed shearwaters, the most abundant breeding seabird in the Hawaiian Archipelago during summer and fall (Harrison et al. 1984, Spear et al. 1999). When we considered the 62 observations where the presence or absence of subsurface predators was ascertained, almost all (99.8%) of the foraging birds were associated with subsurface predators. In particular, the vast majority (96.0%) of these birds were associated with skipjack tuna (Table 1).

Species-specific patterns

For 3 seabird species (wedge-tailed shearwater, brown noddy, red-footed booby), numbers of feeding events were large enough to conduct univariate tests. Non-parametric tests were used to test differences in the median number of birds per school as a function of subsurface-predator type for the first 2 species, because they did not meet the required assumption of equal variances. A Mann-Whitney test was performed for the wedge-tailed shearwater, and a sign test was performed for the brown noddy due to the large number of null values. A parametric *t*-test was used to detect differences in the mean number of red-footed boobies across different subsurface-predator schools.

There was a significant difference in the median number of foraging wedge-tailed shearwaters as a function of subsurface-predator type. Higher numbers of shearwaters foraged over tuna (skipjack and yellowfin) than over the other predators combined (Mann-Whitney $U = 1543.5$, df = 1, p = 0.0009) (Fig. 6). However, the presence/absence data revealed a non-significant result ($\chi^2 = 1.988$, df = 1, 0.25 > p > 0.10), with no difference in the proportion of tuna schools and non-tuna schools attended by wedge-tailed shearwaters, suggest-
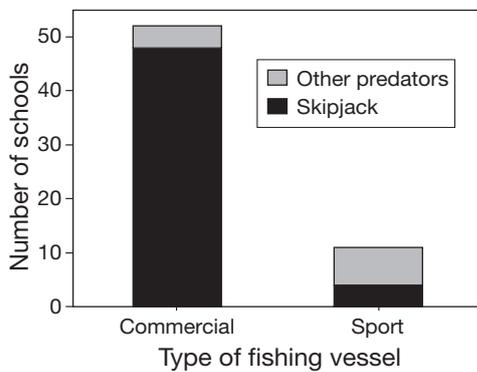
Fig. 4. Composition of subsurface-predator schools observed as a function of fishing-vessel type
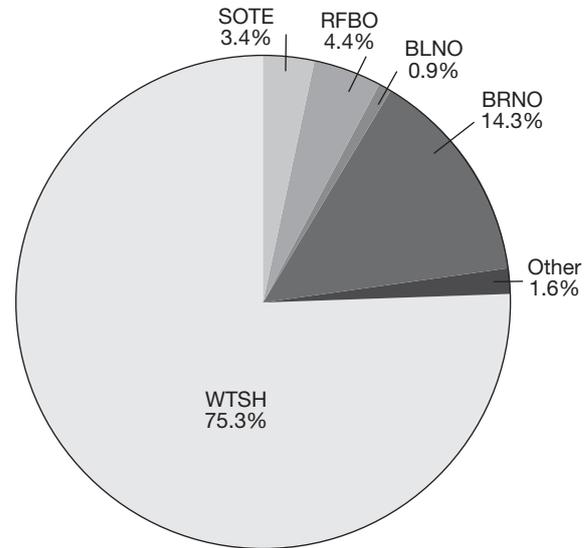

Fig. 5. Relative abundance of seabirds associated with subsurface-predator schools. WTSH = wedge-tailed shearwater, BRNO = brown noddy, BLNO = black noddy, RFBO = red-footed booby, SOTE = sooty tern. 'Other' includes 7 species: brown booby, white tern, great frigatebird, Newell's shearwater, pomarine jaeger, south polar skua, and sooty or short-tailed shearwaters. See Table 1 for scientific names

ing that members of this species are not limited to foraging over tuna despite their larger number of individuals associated with these predators.

All the foraging brown noddies recorded during the present study were observed over tuna schools. Thus, there was a significant difference in the median number of individuals over tuna schools versus non-tuna schools (sign test: $\chi^2 = 10.16$, df = 1; p = 0.001) (Fig. 6). The proportion of tuna schools attended by brown noddies was higher than would be expected if these birds had foraged randomly across subsurface predator types ($\chi^2 = 8.663$, df = 1, p = 0.013, 0.01 < p < 0.025).

There was no significant difference in the mean number of red-footed boobies as a function of subsurface predator type (tuna vs. non-tuna) ($t = 0.77$, df = 11, p = 0.455) (Fig. 6). Moreover, there was no significant difference among the proportions of subsurface-predator schools associated with boobies ($\chi^2 = 3.088$, df = 1, p = 0.214, 0.10 < p < 0.25).

Seabird assemblages

The multivariate NMDS analysis identified 2 axes with high (99.3%) orthogonality (r = −0.082), which best described the seabird community structure and explained 67.9% of the cumulative observed variance (axis 1: $R^2 = 0.502$; axis 2: $R^2 = 0.178$) (Fig. 7). The stress of the best-fit NMDS was 17.873, suggesting that the performance of the test was fair (McCune & Grace 2002).

Table 1. Numbers of observed individuals of each seabird species as a function of subsurface-predator type. Values in parentheses indicate the number of schools of subsurface predator in which at least 1 individual of a given seabird species was observed. Skipjack = *Katsuwonus pelamis*; yellowfin = *Thunnus albacares*; spotted dolphin = *Stenella attenuata*; mahimahi = *Coryphaena hippurus*; false killer whale = *Pseudorca crassidens*

|		Skipjack (50)	Yellowfin (1)	Spotted dolphin (4)	Mahimahi (4)	Unknown (7)	False killer whale (1)	No predator (2)
Puffinus pacificus	Wedge-tailed shearwater	3918 (49)	60 (1)	71 (4)	4 (3)	80 (7)	5 (1)	12 (2)
Anous stolidus	Brown noddy	730 (27)	0	0	0	58 (5)	0	0
Sula sula	Red-footed booby	189 (32)	4 (1)	22 (4)	12 (2)	12 (6)	5 (1)	0
Anous minutus	Black noddy	50 (11)	0	0	0	2 (1)	0	0
Sula leucogaster	Brown booby	23 (11)	0	6 (2)	1 (1)	0	0	0
Gygis alba	White tern	28 (11)	0	1 (1)	2 (1)	3 (1)	0	0
Sterna fuscata	Sooty tern	166 (9)	0	0	0	19 (3)	0	0
Puffinus auricularis	Newell's shearwater	6 (4)	0	0	0	0	0	0
Fregata minor	Great frigatebird	6 (6)	0	1 (1)	4 (2)	0	0	0
Catharacta maccormicki	South polar skua	4 (4)	0	0	0	0	0	0
Stercorarius pomarinus	Pomarine jaeger	3 (3)	0	0	0	0	0	0
Puffinus griseus or *P. tenuirostris*	Sooty or short-tailed shearwaters	1 (1)	0	0	0	0	0	0
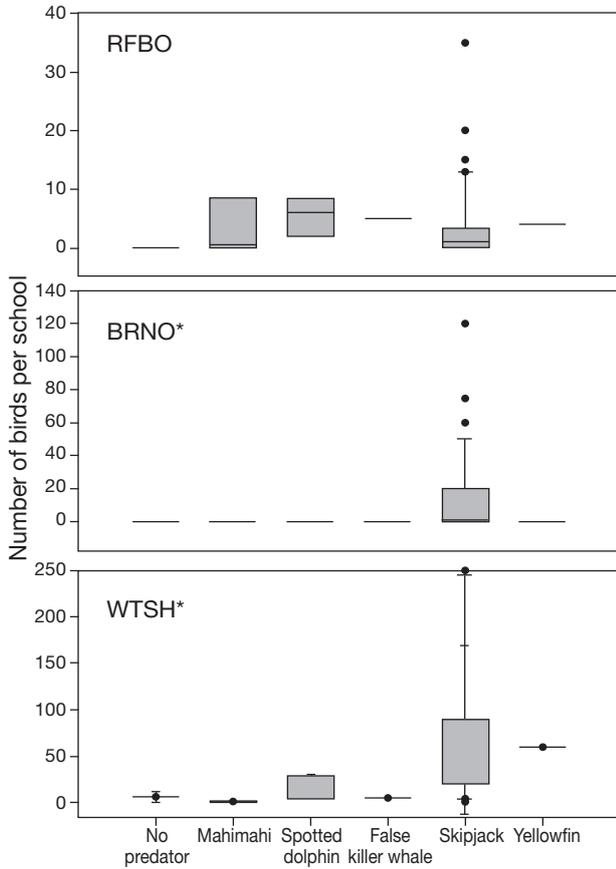
Fig. 6. *Sula sula* (red-footed booby, RFBO), *Anous stolidis* (brown noddy, BRNO), and *Puffinus pacificus* (wedge-tailed shearwater, WTSH). Boxplots showing the medians, quartiles, 95% bars, and outliers of the numbers of 3 focal seabird species as a function of subsurface-predator type. *Significant differences at the p < 0.05 level in the average number of birds per school over tuna vs. non-tuna species

The non-parametric (Kendall) cross-correlations between the explanatory variables and the 2 significant axes revealed that the seabird community structure was influenced primarily by the presence of wedge-tailed shearwaters and brown noddies, the 2 most abundant seabird species, with significant correlations with both axes (Table 2). These results suggest that the first axis captured the differences between commercial and sport fishing vessels, while the second axis captured the variability across geographic locations. This analysis also revealed significant Kendall correlations with the first axis for 2 subsurface predators: mahimahi (n = 67, tau = +0.281, 0.05 < p < 0.005) and skipjack (n = 67, tau = −0.452, 0.001 < p < 0.005). These results reinforced the observation from the univariate analyses that wedge-tailed shearwaters and brown noddies tend to forage in greater proportion over skipjack tuna schools. The sooty tern was the only species significantly correlated with the second axis (n = 67, tau = −0.329, 0.05 < p < 0.005).
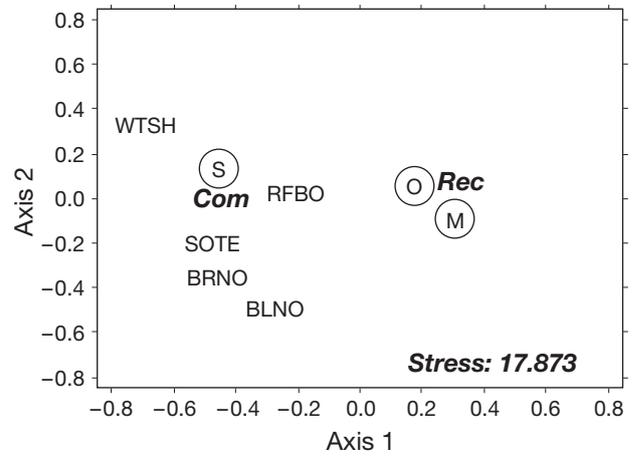

Fig. 7. NMDS plot showing 2-dimensional distances among the 5 most abundant seabirds (WTSH = wedge-tailed shearwater, SOTE = sooty tern, RFBO = red-footed booby, BLNO = black noddy, BRNO = brown noddy), 2 fishery types (commercial [Com] vs. recreational [Rec]), and 3 subsurface-predator types (M = mahimahi, O = odontocete, S = skipjack)

Table 2. Kendall correlations with first and second ordination axes (n = 67). Significant values are in bold. Significance levels are: $\alpha_{0.005} = 0.341$, $\alpha_{0.05} = 0.241$. See Table 1 for scientific names of seabird species and predator type

	Axis 1 tau	Axis 2 tau
Seabird species		
Wedge-tailed sheawater	**−0.779**	**0.427**
Brown noddy	**−0.242**	**−0.537**
Black noddy	−0.168	−0.103
Brown booby	−0.037	−0.144
Red-footed booby	−0.093	−0.017
Sooty tern	−0.106	**−0.329**
White tern	−0.007	0.119
Sooty or short-tailed shearwaters	−0.089	−0.147
Pomarine jaeger	−0.104	−0.098
South polar skua	−0.163	0.201
Newell's shearwater	−0.237	0.237
Great frigatebird	0.059	0.091
Vessel type		
Sport	**0.351**	−0.011
Commercial	**−0.351**	0.011
Location		
Waianae	−0.078	**0.315**
Penguin Banks	0.050	0.017
Kaena	−0.006	−0.125
Windward	−0.008	**−0.288**
Other	0.080	−0.125
Predator type		
Spotted dolphin	0.185	0.040
Mahimahi	**0.281**	−0.070
False killer whale	0.141	−0.016
Skipjack	**−0.452**	0.134
Yellowfin	−0.037	0.094
Unknown	0.241	−0.199

Long-term changes in the subsurface-predator community

In the present study, we found no evidence of qualitative changes in the seabird–subsurface-predator associations as a result of a regime shift in the Central North Pacific Gyre in the 1980s. Harrison & Seki (1987) concluded that skipjack were the dominant predators over which seabirds feed in waters around the main Hawaiian Islands, with 75% of the 681 bird flocks observed on cruises in the 1950s and 1960s being associated with schools of this predator. This historical result is comparable with the proportion of 81% (50/62) documented in the present study.

DISCUSSION

Our research corroborates previous assessments of the importance of subsurface predators to the foraging ecology of many species of tropical seabirds (Au & Pitman 1986, Harrison & Seki 1987, Jaquemet et al. 2004), and provides new information about seabird associations with specific subsurface predators within the commercial and sport fishing grounds surrounding the island of Oahu. In this area, at least 2 species of seabirds forage in association with tuna schools (primarily skipjack) disproportionately more frequently than would be expected if the birds were randomly distributed across all types of predator schools. We hypothesize that tuna schools are the most profitable for seabirds, particularly for the smaller species, for 2 reasons: (1) the larger size and greater persistence of tuna schools increases the duration of the foraging opportunity, and (2) these schools provide prey of greater suitability (i.e. size class, species, quantity).

Although we were unable to determine whether these larger foraging schools of subsurface predators were more visible and long-lasting, Au & Pitman (1986) found that the number of seabirds in a flock was positively correlated with the size of the subsurface predator school. We hypothesize that larger schools are indicative of larger prey concentrations and provide a larger surface area for a greater number of seabirds to access these prey resources.

Differences in prey types may also be driving the observed segregation of seabird species across subsurface-predator schools. Because mahimahi and odontocetes generally feed on larger prey than do the tuna (Roger 1994, Robertson & Chivers 1997, Santos & Haimovici 2001, Olson & Galván-Magaña 2002, Ménard et al. 2006), these larger prey may be outside of the size range suitable for the smaller birds, particularly the terns and to a lesser extent the shearwaters. For example, mahimahi stomach contents from the ETP revealed an average prey length of 160.0 mm (Olson & Galván-Magaña 2002), whereas yellowfin tuna stomach contents from the same geographic area contained an average prey length of 38.2 mm (Ménard et al. 2006). A comprehensive diet study of Hawaiian seabirds revealed that different species feed on distinct prey size ranges: up to 145 mm for wedge-tailed shearwaters, 93 mm for brown noddies, and 200 mm for red-footed boobies (Harrison et al. 1983). Therefore, the shearwaters and noddies — but not the boobies — appear to be morphologically constrained from consuming even the average prey size of mahimahi. Because tropical seabirds are fairly diverse in their prey taken within their preferred size class (Harrison et al. 1983), prey taxonomy by itself probably has no bearing on seabird–subsurface-predator associations. Rather, any apparent taxonomic preferences are probably residual effects from feeding behaviors of the associated subsurface predators (Spear et al. 2007).

Potential biases and limitations of this study

The majority of the seabird interactions with subsurface predators observed in the present study involved skipjack tuna. Due to the low densities of seabird flocks in tropical waters, we resorted to using fishing vessels to locate subsurface predators rather than using random survey tracks. This approach has been used previously in other regions to facilitate otherwise logistically difficult and expensive surveys (Jaquemet et al. 2004). Because the sampling was not random, however, these data may not accurately reflect the actual relative proportions of subsurface predator schools in the waters around Oahu. In fact, the different proportions of school types from commercial versus sport vessels highlights this lack of randomness. Nevertheless, it is likely that the observations from commercial vessels, which were dominated by skipjack tuna, were more akin to a random sampling. Conversely, the sport-fishing vessels yielded a somewhat biased perspective by targeting FADs and other floating objects where mahimahi aggregate (Kojima 1956).

Our observations may also have been biased towards sampling seabirds associated with subsurface predators, while other foraging methods may have been underrepresented. First, night feeding (which may or may not involve the participation of subsurface predators) is supported by direct observations in wedge-tailed shearwaters and sooty terns (Gould 1967), and by evidence that wedge-tailed shearwater colony attendance during full moon nights is lower than during new moon nights (Shallenberger 1973). However, the greater numbers of birds attending the colonies at night versus during the day underscores the notion

that nocturnal foraging is probably a minor contributor to overall feeding in tropical 'tuna birds' (Whittow 1997, Gauger 1999, Schreiber et al. 2002).

Second, the present study likely underestimated the overall incidence of solo or small-flock feeding in the absence of subsurface predators on surface-dwelling prey. This behavior is more transient and therefore less conspicuous and harder to detect at sea. For instance, only two out of the 62 feeding events characterized during the present study were of this type. However, previous research has shown the rarity of solo or small-flock feeding for some of these species. In central Pacific cruises performed in the 1960s, King (1974) and Gould (1974) reported that 93% of all wedge-tailed shearwaters and 77% of all sooty terns were observed feeding in mixed-species flocks. These data were collected along transect lines and limited to a distance of no greater than 0.75 miles (1.2 km), a range explicitly chosen by the researchers to exclude birds whose behavior could not be determined (Gould 1974).

Finally, because these data have a seasonal bias (summer and fall) and a limited geographic scope (waters around Oahu), they do not represent the entire Hawaiian seabird community. In particular, sooty terns, which breed in spring and early summer, were not recorded in large numbers despite their large breeding densities around Oahu (Harrison et al. 1984).

Implications for fishery management and seabird population health

Despite the limitations and potential biases of the present study, it appears that skipjack tuna are important mediators of food availability for several species of seabirds around Oahu. Skipjack comprise the bulk of the subsurface predators involved in foraging associations with seabirds, and at least 2 seabird species forage in association with tuna schools in greater numbers than would be expected by chance alone. These observations are in line with previous observations on the relative importance of skipjack to seabirds in Hawaiian waters (Harrison & Seki 1987). The qualitative nature of this relationship appears stable despite an oceanographic regime shift and long-term climate change. Despite evidence that skipjack biomass is increasing on a global scale (Sibert et al. 2006), localized depletion due to heavy fishing and redistribution or declines in abundance due to large-scale interannual and longer-term oceanographic fluctuations (e.g. Lehodey et al. 1997, Karl et al. 2001, Polovina 2005) could reduce skipjack abundance within the foraging range of seabirds, especially during the breeding season when these central-place foragers are constrained to return to their colonies. For instance,

Boggs & Kikkawa (1993) documented a decline in the catch per unit effort of skipjack tuna around Hawaii through the 1970s. Moreover, ecosystem-level modeling has shown that substantial increases in fishing pressure on yellowfin tuna could, through a complex community-level response, lead to a decline in skipjack abundance and an increase in mahimahi (Hinke et al. 2004).

Our empirical observations and the modeling results from Hinke et al. (2004) have important implications for the development of ecosystem-level fishery practices that incorporate an understanding of the ecological relationships and the consequences of oceanographic variability and management actions. In particular, our research suggests that seabirds may not readily switch to using other subsurface predators such as mahimahi, in the event of redistributions or population declines in skipjack tuna. Therefore, the heavy reliance of seabirds on tuna may affect their ability to successfully find prey and maintain healthy populations. Based on the particular characteristics of the tuna schools and their prey, we anticipate that the smaller-sized seabirds—shearwaters, terns, and noddies—would experience reduced foraging opportunities. For this reason, we concur with the warning of other authors (e.g. University of Alaska Sea Grant College 1999, Yaffee 1999, Link 2002, Hinke et al. 2004, Worm et al. 2006) against the reliance on stock-viability management as the sole driver of our fishery-management policies. Instead, we advocate the adoption of broader ecosystem-based management considerations, including the ecological interactions between the target and non-target species.

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