IMPORTANCE OF MARINE INSECTS (HETEROPTERA: GERRIDAE, *HALOBATES* SPP.) AS PREY OF EASTERN TROPICAL PACIFIC SEABIRDS

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SUMMARY

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We analyzed the foraging ecology of seabirds in the eastern tropical Pacific Ocean during 1983–1991 on a series of oceanographic cruises during spring and fall of each year. We report details about the consumption of sea skaters *Halobates* spp., marine insects that are small, can hide well within sea foam, and can be very fast moving. One abundant sea skater of the four species present in the study area, *H. sobrinus*, is not taken by sea birds, and the reason is unknown. Among the predators, it appears that frigate storm-petrels, White-faced Storm-Petrel *Pelagodroma marina* and White-bellied Storm-Petrel *Fregetta grallaria* (likely also White-throated Storm-Petrel *Nesofregetta fuliginosa*), make directed efforts to consume sea skaters, a fact that may explain their unique flight and foraging behavior: slow, with extensive "kick splashing" against the sea surface, to incite movement in *Halobates*. The few other seabirds for which sea skaters constitute more than an incidental component of the diet (Herald Petrel *Pterodroma heraldica*, Bulwer's Petrel *Bulweria bulwerii*) also move slowly across and close to the sea surface. In the case of the White Tern *Gygis alba*, it readily hovers, an ability that would be advantageous to taking these insects. Among the avian species that rarely take a sea skater, almost all are included in the guild of seabirds that associate with tuna, and as a result they must fly quickly to keep pace.

Key words: foraging ecology, frigate storm-petrels, *Halobates*, sea skater, tropical Pacific, White-bellied Storm-Petrel, White-faced Storm-Petrel

INTRODUCTION

Sea skaters, genus *Halobates*, are the only insect known to live in the open ocean. More than 40 species have been described, but only five (*H. micans*, *H. sericeus*, *H. sobrinus, H. germanus* and *H. splendens*) are oceanic (Andersen & Cheng 2004). Their overall range lies between 40°N and 40°S, but within that expanse each species has a different specific range (Cheng 1989). In the eastern tropical Pacific Ocean (ETP), four of five oceanic species can be found; *H. germanus* occurs in the Indian and western Pacific oceans (Andersen & Cheng 2004). Sea skaters have been reported thus far in the diet of more than a dozen surface-feeding seabirds (Ashmole & Ashmole 1967, Cheng & Harrison 1983, Imber *et al*. 1995, Diamond 1983, Spear *et al.* 2007) and can be especially important prey for some. For example, they were found in 81% of regurgitations of the Blue-gray Noddy *Procelsterna coerulea* in the Hawaiian islands, appearing to be the only food item taken at certain times of the year (Cheng & Harrison 1983). Here, we further document the importance of sea skaters in seabird diets, reporting observations gathered at sea in the ETP.

STUDY AREA AND METHODS

The ETP extends roughly from the coast of the Americas to about latitude 170°W, and between latitudes 20°S and 20°N (Fig. 1). Data were collected during a nine-year period from 1983 to 1991; a full discussion of methods and localities is contained in Spear *et al.* (2007). Briefly, seabirds were collected during each of two National Oceanographic and Atmospheric Administration (NOAA) cruises each year: spring–summer and autumn–winter. Cruises lasted 2–3 months. To study general diet habits of tropical seabirds in the region (details in Spear *et al.* 2007), 6–7 (when possible) specimens per species present at sampling stations were shot and collected (Fig. 1). The stomach and gizzard were removed from each bird, and the food items were rough sorted. Specimens or fragments of *Halobates* were easily identifiable, as the insect cuticle is not easily digestible. They were preserved in 4% formaldehyde (or 70% ethanol) and later counted and identified to species in the laboratory on land. Preliminary results are contained in Spear *et al.* (2007), in which *Halobates* were not identified to species.

Scientific names of all seabird species included in our study are presented in Table 1.

RESULTS

Sea skaters were found in the guts of 60 seabird individuals (Table 2), 3.3% of the total collected. In many cases, the prey were almost complete specimens, or complete enough to allow for identification to species, sex and developmental stages. The frequency of

occurrence per year was variable. *Halobates* were found in the guts of fewer than five birds in most years, of none in 1983, of seven in 1990, but of 36 birds in 1987.

Three species of *Halobates* were identified: *H. micans, H. sericeus* and *H. splendens*. The most common species found was *H. micans*, in 31 samples, followed by *H. splendens* in 21 samples, and *H. sericeus* in only six samples. Two of the samples (RS87-88, OC88-123) consisted of bodies only and were not identifiable to species. Specimens of both *H. micans* and *H. sericeus* occurred together in two samples (RS87-144 and -183). We found no evidence that *H. sobrinus* was taken by birds, although this species is found in the eastern portion of the study area (Fig. 1).

A total of 267 insects were found among all samples (Table 2). Almost all were adults (86.9%: 120 males, 104 females, 8 sex not known). The remainder comprised either 5th or 4th instar nymphs (17 vm, 5 vf, 13 iv). The number of insects in each sample ranged from one to 25; only eight samples contained >10 individuals, and 24 samples contained only one insect. Among the eight samples with >10 insects each, four were identified as *H. micans* (23, 12, 18, 12), three were *H. splendens* (25, 15, 14), and the remaining sample contained 19 specimens of *H. sericeus*.

Although *Halobates* were found in the stomach samples of 19 species of seabirds (Table 1), they were a frequent food item, occurring in >10% of the samples, for only seven species. The White-faced Storm-Petrel appeared to be the most important predator in the ETP, with *Halobates* occurring in 93% of the samples. Other seabirds that preyed regularly on sea skaters were Herald Petrel, Bulwer's Petrel, Markham's Storm-Petrel, and White-bellied Storm-Petrel. *Halobates* was found in stomachs of several other seabirds, but samples sizes were too low to determine whether sea skaters were more than incidental to the trophic ecology of those species. Sea skaters were found in ≤1% of Leach's and Wedge-rumped Storm-Petrel, two of the most abundant seabird species in the study region (Spear & Ainley 2007). Likewise, the majority of ETP seabirds do not consume sea skaters to an appreciable degree.

DISCUSSION

Sea skaters

In the seabird guts sampled, we found three of the four *Halobates* species known to occur in the ETP. Interestingly, *H. sobrinus,* the most common and abundant species in the eastern portion of the area, was completely absent from our samples. This species

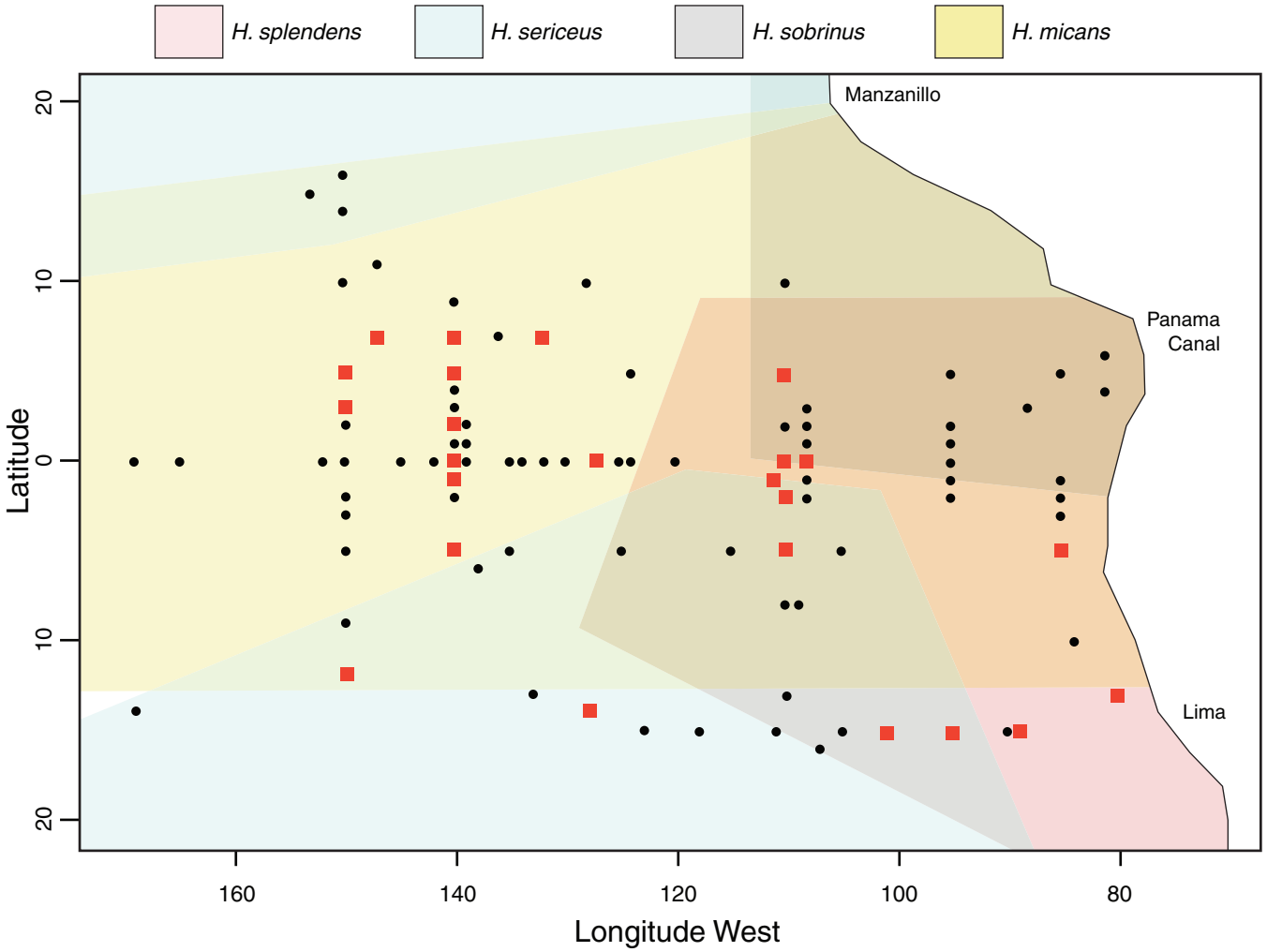

Fig. 1. The eastern tropical Pacific Ocean sites where seabirds were collected (n = 1807; 1983–1991) and the overlapping ranges of the four *Halobates* species that occur in the area (after Cheng & Shulenberger 1980, which contains detailed maps). Black dots are collecting sites; red squares are sites where *Halobates* specimens were found in samples.

is found off the coast of Central America to 115°W and between latitudes 20°N and 5°S (Cheng & Shulenberger 1980; Fig. 1), an area that contained at least a third of our sampling sites (see Spear *et al.* 2007). It seems that *H. sobrinus* possesses effective predator avoidance adaptations, at least with respect to birds.

The most common sea skater in our samples was *H. micans,* a cosmopolitan species widely distributed between latitudes 20°N and 20°S in the ETP (Cheng & Shulenberger 1980; Fig. 1). It was found in >50% of the seabird samples containing sea skaters and also accounted for half of the samples containing >10 specimens.

H. splendens, the rarest of the four species in the ETP, was found in 35% of bird samples containing sea skaters. This species is somewhat restricted in its distribution. It is found from the coasts of Central and South America to 125°W and between latitudes 10°N and 20°S (Cheng & Shulenberger 1980; Fig. 1). We found <10 specimens in most of the samples, but 25 insects were found in one seabird (a Tahiti Petrel) sampled at 2.5°N, 150°W.

TABLE 1
Frequency of occurrence of *Halobates* in seabirds collected in the ETP, 1983–1991

Bird species	Sample size	Frequency (%)
Stejneger's Petrel *Pterodroma longirostris*	48	2
De Filippi's Petrel *Pterodroma defilippiana*	7	43
White-winged Petrel *Pterodroma leucoptera*	139	2
Black-winged Petrel *Pterodroma nigripennis*	89	1
Herald Petrel *Pterodroma heraldica*	13	15
Juan Fernandez Petrel *Pterodroma externa*	214	1
Tahiti Petrel *Pseudobulweria rostrata*	154	3
Bulwer's Petrel *Bulweria bulwerii*	43	16
Thin-billed Prion *Pachyptila belcheri*	5	60
Cape Petrel *Daption capense*	4	50
Markham's Storm-Petrel *Oceanodroma markhami*	15	20
Leach's Storm-Petrel *Oceanodroma leucorhoa*	503	1
Wedge-rumped Storm-Petrel *Oceanodroma tethys*	411	3
White-faced Storm-Petrel *Pelagodroma marina*	15	93
White-throated Storm-Petrel *Nesofregetta fuliginosa*	15	4
White-bellied Storm-Petrel *Fregetta grallaria*	22	23
White Tern *Gygis alba*	12	8
Grey-backed Tern *Onychoprion lunatus*	5	80
Sooty Tern *Onychoprion fuscatus*	93	1

The third species taken by ETP seabirds, *H. sericeus*, has an anti-tropical distribution in the Pacific Ocean. It usually occurs farther west than *H. sobrinus* and is distributed roughly between latitudes 15°–40°N and 05°–40°S (Cheng 1997; Fig. 1). We found this species in abundance in one sample (White-faced Storm-Petrel) at 15°S, 101°W. It co-occurred with *H. micans* in one sample collected at 12°S, 150°W, and with *H. splendens* in another sample collected at 15°S, 95°W.

Seabird predators

Sea skaters are taken by a number of ETP seabirds, but only incidentally in most. White-faced Storm-Petrels apparently make a directed effort to prey on these insects. In that category as well, among species for which sample size was >10, might be Herald Petrel, Bulwer's Petrel, Markham's Storm-Petrel, White-bellied Storm-Petrel and White Tern. However, *Halobates* occurrence is extremely patchy on the small scale (Cheng & Shulenberger 1980); for instance, prevalence in neuston net tows can range from 0 to >180 insects. Therefore, an appreciable sample size of birds is needed to gauge how important sea skaters may be in their diet. In contrast, a number of seabirds for which we had appreciable sample sizes (>80) obviously almost never consume a sea skater, e.g., White-winged and Black-winged petrels, Juan Fernandez Petrel and Sooty Tern.

The degree to which a seabird species preys on sea skaters says something about its foraging tactics and may relate also to the size of the bird. Sea skaters are only about 1 cm in diameter (including legs) and are capable of moving very quickly, at speeds on the order of 1 $m \cdot s^{-1}$ (Cheng 1985); they do not dive but can easily avoid nets. However, they are often stationary among bubbles at the sea surface. Given the small size of sea skaters, therefore, a bird predator would need to travel slowly and close to the sea surface to find them, and then be ready to move very quickly to take one.

White-faced and White-bellied storm-petrels (as well as White-throated, see below) have disproportionately large feet compared with other storm-petrels. As well, they fly in a curious fashion, smacking the water with their feet ("kick-splashing") as they rapidly change direction while actually covering little horizontal distance. Besides aiding to maneuver in light winds, this could be a way to frighten sea skaters into moving, thus revealing their presence to the birds, and to pursue them effectively, with rapid changes in flight direction. In the analysis of flight speeds by Spear & Ainley (1997), the frigate storm-petrel category, which included these two (three) species, were quite separate from the more rapidly flying *Oceanodroma* group. Therefore, the fact that Markham's Storm-Petrel, quite unlike the Leach's or Wedge-rumped storm-petrels, preys occasionally on sea skaters represents an outlier in the *Oceanodroma* group. Otherwise, on the basis of diet, Markham's Storm-Petrel is in the same cluster as the other *Oceanodroma* (Spear *et al.* 2007), which tend to feed more on fish, especially myctophids found at the surface at night. Conversely, the White-bellied Storm-Petrel feeds more on fish than the other frigate storm-petrels; on the basis of overall diet, it thus clusters more closely to the *Oceanodroma* species. The Black-bellied Storm-Petrel *Fregatta tropica*, despite the misnomer, rarely occurs in warm seas (except the Indian Ocean). It too exhibits the flight behavior of its tropical relative and may represent a southern colonization that has retained the kick-splashing habit. We had no data on its diet, and virtually none is available from its wintering grounds in temperate waters. Finally, we did not effectively sample White-throated Storm-Petrels in the frigate petrel category and thus cannot judge the degree to which they prey on sea skaters. On the

TABLE 2
Predator and prey, by year and cruise, and collecting details, for *Halobates* species whole enough for identification

Sample no.[a]	Seabird species	Lat	Long	Date mo/d	*Halobates* sp.	No.	Stages[b]
RS84-103	Black-winged Petrel	0	-140	04/26	*micans*	1	1f
RS84-52	Leach's S-P	0	-140	04/26	*micans*	1	1f
DS85-41	White-bellied S-P	-5.0	-110	06/04	*micans*	1	1vm
OC86-29	White-bellied S-P	-15.0	-89	05/02	*splendens*	3	1m 2f
OC86-314	Leach's S-P	2.0	-140	10/27	*micans*	1	1m
RS87-02	Leach S-P	0	-108	04/26	*micans*	2	1m 1f
RS87-18	Wedge-rumped S-P	5.0	-110	04/28	*micans*	1	1vm
RS87-19	Leach's S-P	5.0	-110	04/28	*micans*	1	1m
RS87-50	White-faced S-P	0	-140	05/11	*micans*	23	9m 11f 3vm
RS87-51	White-faced S-P	0	-140	05/11	*micans*	9	1m 5f 3A
RS87-53	Bulwer's Petrel	0	-140	05/11	*micans*	2	2A
RS87-58	Tahiti Petrel	0	-140	05/11	*micans*	2	1m 1f
RS87-88	Leach's S-P	5.0	-150	06/05	*?micans*	1	1A
RS87-106	Tahiti Petrel	2.5	-150	06/07	*splendens*	4	3m 1f
RS87-107	Tahiti Petrel	2.5	-150	06/07	*splendens*	25	20m 5f
RS87-108	White-faced S-P	2.5	-150	06/10	*splendens*	2	1m 1f
RS87-109	White-faced S-P	2.5	-150	06/10	*splendens*	2	1f 1vm
RS87-110	White-faced S-P	2.5	-150	06/10	*splendens*	1	1m
RS87-113	Tahiti Petrel	2.5	-150	06/10	*micans*	12	5m 7f
RS87-126	White-faced S-P	2.5	-150	06/10	*micans*	18	1m 8f 2vm 1vf 6 iv
RS87-128	Black-winged Petrel	2.5	-150	06/10	*micans*	1	1m
RS87-131	Grey-backed Tern	2.5	-150	06/10	*micans*	6	1m 5f
RS87-132	Grey-backed Tern	2.5	-150	06/10	*micans*	9	2m 7f
RS87-133	Grey-backed Tern	2.5	-150	06/10	*micans*	1	1f
RS87-134	Grey-backed Tern	2.5	-150	06/10	*micans*	5	3m 1f 1vm
RS87-144	Tahiti Petrel	-12.0	-150	06/16	*micans*	2	1f 1vm
RS87-144	Tahiti Petrel	-12.0	-150	06/16	*sericeus*	1	1m
RS87-150	White-bellied S-P	-14.2	-128	07/03	*sericeus*	1	1f
RS87-174	White-faced S-P	-15.0	-101	07/13	*sericeus*	19	8m 5f 3vm 1vf 2 iv
RS87-175	White-faced S-P	-15.0	-101	07/13	*sericeus*	5	1m 2f 1vm 1vf
RS87-180	White-winged Petrel	-15.0	-101	07/13	*sericeus*	1	1m
RS87-181	Herald Petrel	-15.0	-101	07/13	*splendens*	1	1m
RS87-183	White-faced S-P	-15.0	-95	07/15	*sericeus*	2	1m 1f
RS87-183	White-faced S-P	-15.0	-95	07/15	*splendens*	1	1vm
RS87-197	Leach's S-P	-13.6	-80.4	07/21	*splendens*	2	1m 1f
RS87-200	Markham's S-P	-13.6	-80.4	07/21	*splendens*	2	2m
RS87-203	Thin-billed Prion	-13.6	-80.4	07/21	*splendens*	4	4m
RS87-204	Thin-billed Prion	-13.6	-80.4	07/21	*splendens*	15	12m 3f
RS87-205	Thin-billed Prion	-13.6	-80.4	07/21	*splendens*	14	9m 5f
RS87-210	De Filippi's Petrel	-13.6	-80.4	07/21	*splendens*	9	9m
RS87-214	Cape Petrel	-13.6	-80.4	07/21	*splendens*	2	2f
RS87-216	Cape Petrel	-13.6	-80.4	07/21	*splendens*	3	3f
RS87-251	Wedge-rumped S-P	-6.4	-79.9	07/27	*micans*	7	1m 2f 1vm 1vf 2A
OC88-123	White-faced S-P	0	-135	06/24	*?micans*	1	1 iv
OC88-134	White-faced S-P	-5.0	-110	06/29	*splendens*	1	1m
OC88-139	Wedge-rumped S-P	-2.0	-110	06/30	*splendens*	1	1f
RE89-74	Juan-Fernandez Petrel	5.0	-140	05/23	*micans*	1	1f
DS89-130	Leach's S-P	7.0	-132	12/05	*micans*	2	1m 1f
DS89-131	Leach's S-P	7.0	-132	12/05	*micans*	3	2m 1f
RE90-20	Bulwer's Petrel	2.0	-140	04/30	*micans*	1	1f
DS90-12	Wedge-rumped S-P	7.0	-140	10/21	*micans*	1	1f
DS90-109	White-bellied S-P	-5.0	-140	10/29	*sericeus*	2	1m 1f
DS90-148	Leach's S-P	7.0	-148	11/05	*micans*	1	1m
DS90-158	Tahiti Petrel	7.0	-148	11/05	*micans*	1	1f
DS90-181	Leach's S-P	-1.5	-111	11/26	*micans*	2	1m 1f
DS90-183	Leach's S-P	-1.5	-111	11/26	*splendens*	1	1m
DS90-204	Leach's S-P	-2.0	-110	11/28	*splendens*	3	2m 1f
RE91-09	Wedge-rumped S-P	5.0	-110	04/03	*micans*	1	1f
RE91-24	White-faced S-P	-5.0	-110	04/07	*micans*	12	6m 2f 1vm 3 iv
RE91-25	Leach's S-P	-5.0	-110	04/07	*micans*	1	1 iv
RE91-74	White Tern	1.75	-140	05/06	*splendens*	6	1m 4f 1vf
RE91-115	White-faced S-P	0	-110	05/16	*micans*	3	3f

[a] Letters indicate the vessel, and the first number indicates the year.

[b] f = adult female, m = adult male, A = adult with body only, vf = fifth instar female, vm = fifth instar male, iv = fourth instar nymph.

basis of general diet, however, they clustered very closely with White-faced Storm-Petrels (Spear *et al.* 2007). Consistent with the above, the frigate storm-petrels consume tiny (1 mm) plastic pellets that float on the sea surface more so than other ETP seabirds (Spear *et al.* 1995). This too says something about a foraging style that is efficient at taking sea skaters, as the birds clearly fly slow and close enough to the sea surface to see such tiny particles.

Among the other ETP species that feed relatively more on sea skaters, White Terns readily hover, which certainly would be an advantage in taking these tiny insects when in a predatory mode, i.e., not transiting from island to foraging area. The other species that may consume sea skaters more than incidentally also exhibit a slow, meandering flight at times. Those seabird species that very rarely take a sea skater are all very fast flyers (Spear & Ainley 1997), spending much of their time chasing flying fish (Exocetidae) and squid as part of multi-species flocks, catching their prey on the wing and otherwise keeping up with tuna (Spear *et al.* 2007).

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