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VARIATION IN BODY SIZE OF *CONUS* SPECIES (FAMILY CONIDAE) FROM SEAWARD AND LAGOONAL REEFS OF ATOLLS IN THE TUAMOTU ARCHIPELAGO (FRENCH POLYNESIA)

Dedicated to Alan Kohn (1931-2022) and honoring his contributions to our understanding of the ecology and evolution of *Conus*

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ABSTRACT

Characteristics of cone snail (family Conidae) populations and communities are predicted to differ depending on habitat type. In particular, high wave energy and greater exposure at low tides are posited to restrict body sizes of cones at intertidal marine benches in comparison to subtidal reefs. Here, we tested this prediction by comparing shell sizes of cone-snail species that occur at both seaward and lagoonal sites at two atolls in the Tuamotu Archipelago: Makemo and Rangiroa. At Makemo, we also compared sizes of individuals from a seaward site, sites within a small channel or “hoa” that allows water exchange between the sea and lagoon, and sites at increasing distances from the hoa for species that occurred at these sites. Although eight species with adequate sample sizes for analyses occurred at both seaward and lagoonal sites at Rangiroa, we only observed sufficient sample sizes of two species at both seaward and lagoonal sites at Makemo. All of these species exhibited significantly larger body sizes at lagoonal sites that are largely composed of subtidal reefs than at seaward sites that represent intertidal marine benches. These results support the prediction that habitat type influences the body size of cone snails. We also found that body sizes of cone snails steadily increased from the seaward site, through the hoa, and with increasing distance from the hoa in the lagoon. These results as well as our infrequent observations of small-sized individuals at lagoonal sites suggest that cone-snail larvae settle at seaward sites and individual snails migrate through hoas and contribute to recruitment of lagoonal populations.

Key words: Atoll, body size, habitat type, intertidal bench, subtidal reef, *Conus*.

INTRODUCTION

Alan Kohn (1931–2022) pioneered ecological studies of cone snails (family Conidae) with an initial comprehensive analysis of the ecology of cones of Hawaii that was the subject of his Ph.D. dissertation (Kohn, 1959b) and later studies at other sites throughout the Indo-West Pacific (Kohn, 1959a, 1967, 1968, 1971, 1978a, b, 1983, 1997, 2001, 2003, 2015; Kohn & Almasi, 1993; Kohn & Nybakken, 1975; Kohn & Robertson, 1968; Kohn et al., 2005; Leviten & Kohn, 1980). Results from these works, for example, demonstrated that Conidae species exhibit preferences for particular prey items (e.g., Kohn, 1959b, 1968, 1971, 2001, 2003; Kohn & Nybakken, 1975), change diet with ontogeny (e.g., Kohn & Nybakken, 1975), and show ecological release and broader niche breadth at locations where congeneric competitors are absent (Kohn, 1978b). His work also revealed patterns of species richness, diversity, and body size that depend on habitat type (e.g., Kohn, 1968, 1971, 2015; Kohn & Nybakken, 1975).

Alan predicted that characteristics of cone snails occurring in intertidal marine benches (i.e., his “type II” habitat) differ from those inhabiting subtidal reefs (type III habitat) (type I habitats include subtidal areas with large areas

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of sand) (Kohn, 1967, 1968), including aspects of species diversity, population density, and body size (Kohn, 1971). In particular, cone snails in type III habitats should exhibit higher species diversity, lower population density, and larger body size than those in type II habitats (Kohn, 1971). The rationale for differences in species diversity was attributed to differences in habitat complexity with type III habitats being much more complex (e.g., in topography) than type II habitats and able to support a larger number of species (Kohn, 1971). Alan postulated that differences in density reflect an inverse relationship between species diversity and abundance (Kohn, 1968) or be "due to the more homogeneous or less patchy nature of type II substrate or prey populations or both, to reduced predation in a harsher environment, or to the relative advantage of small body size" (Kohn, 1971: 338). Alan proposed that differences in body size are due to physical factors (e.g., wave energy, exposure at low tides) that limit cone snails with large body sizes at type II habitats (Kohn, 1971, 2015).

Although several of his studies supported the first two predictions (e.g., Kohn, 1968, 1971, 2015; Kohn & Nybakken, 1975), the principal support for the third prediction came from results that showed that *Conus* Linnaeus, 1758, assemblages tend to be richer in large-sized species in type III than in type II habitats (e.g., Kohn, 1968, 1971, 2015; Kohn & Nybakken, 1975). Although his observations suggest that populations of species occurring in both habitat types tend to be larger in type III habitats, he either did not have adequate sample sizes to make comparisons (e.g., Kohn & Nybakken, 1975) or comparisons did not show significant differences in sizes (e.g., Kohn, 1968, 2015). For example, he compared sizes of several *Conus* species (*C. coronatus* Gmelin, 1791; *C. ebraeus* Linnaeus, 1758; *C. frigidus* Reeve, 1848; *C. miliaris* Hwass, 1792; and *C. rattus* Hwass, 1792) that occurred in both habitat types at atolls in the Maldives, but none were significantly larger in type III habitats (Kohn, 1968). Alan attributed this to his observations that "wave action is lighter at the Maldives type II stations with large censuses, located on lagoonal islands, than at type II habitats in general" (Kohn, 1968: 1054). Nonetheless, in a study of prey utilization of cone snails at intertidal benches and subtidal reefs, Paul Leviten, one of Alan's former Ph.D. students, found that six of seven *Conus* species (for which he had adequate sample sizes) showed significant differences in body size among type II and III habitats (Leviten, 1978). Leviten (1978) posited that differences in size are not only due to large body size being disfavored at intertidal benches, but also because of reduced availability of large prey items on benches, increased predation of small-sized snails at subtidal reefs, and differences in growth rates at the two habitat types.

While performing field studies of *Conus* species at Rangiroa, the largest atoll in the Tuamotu Archipelago (French Polynesia) (Fig. 1), we observed tremendous differences in shell sizes of several species that were observed at both seaward sites that represent type II habitats and type III habitats in the lagoon. We were also struck by the absence or very low abundance of small-sized individuals in the lagoon. We collected shell-size data from these specimens as well as specimens observed during fieldwork at seaward and lagoonal sites at Makemo, another atoll in the Tuamotu Archipelago (Fig. 1). We compared shell sizes of *Conus* species at these sites to further test Alan's third prediction about body sizes and determine if individuals of species at seaward benches are significantly smaller than those from lagoonal, subtidal reefs. We also examined shell sizes of species at several locations within the lagoon at Makemo as well as several sites within a small channel connecting the lagoon to the sea (i.e., a "hoa"; Danielsson, 1954) to determine if and how sizes of individuals of *Conus* species vary in lagoonal habitats.

METHODS

We performed field studies over the course of several weeks at Avatoru, the principal isle or "motu" of Rangiroa, in November 2022 and at Makemo in late October and early November 2023. At Rangiroa, we collected, identified, and measured specimens from sites on the seaward side (-14°56′53.57″S, -147°40′33.44″W) and lagoonal side of Avatoru (-14°57′13.93″S, -147°40′18.79″W) (Figs. 1–3). At Makemo, we performed field collections at and measured specimens from sites on the seaward portion of the atoll, in the lagoon, and within a "functional hoa" (Chevalier, 1972, as cited by Stoddart & Fosberg, 1994) that was open to the sea and exhibited higher water flow into the lagoon during high tides (Figs. 1, 4–7). After maintaining specimens individually in cups with seawater (to obtain their feces), we returned them to the site where they were collected. Here, we report on results of surveys and measurements at Makemo from a seaward site close to the hoa (-16°33′10.40″S, -143°44′28.55″W), three sites within the hoa (-16°33′18.05″S, -143°43′47.19″W; -16° 33′20.98″S, -143°43′47.46″W; -16°33′26.17″S, -143°43′46.80″W), and three sites in the lagoon that are increasingly distant from the hoa (-16°33′29.34″S, -143°43′53.34″W; -16°33′26.46″S, -143°44′3.56″W; -16°33′ 24.37″S, -143°44′31.14″W) (Figs. 1, 4–7). We performed a minimum collection effort of 2 hr (i.e., two people searching for 1 hr each) at each site.

We measured shell length, shell width (i.e., maximum diameter of whorl), and shoulder height (i.e., aperture height or length of last whorl) to the nearest half millimeter using modified ("by rhinoplasty") vernier calipers (Kohn & Riggs, 1975). Because many of the samples of shell-size data did not exhibit normal distributions (as evaluated with Shapiro-Wilk normality tests; Shapiro & Wilk, 1965), we used Mann-Whitney U tests (Mann & Whitney, 1947) to determine if samples exhibited significant differences in shell sizes for all species with sample sizes > 5 from both seaward and lagoonal sites. We also compared shell sizes of samples from adjacent sites in the seaward,

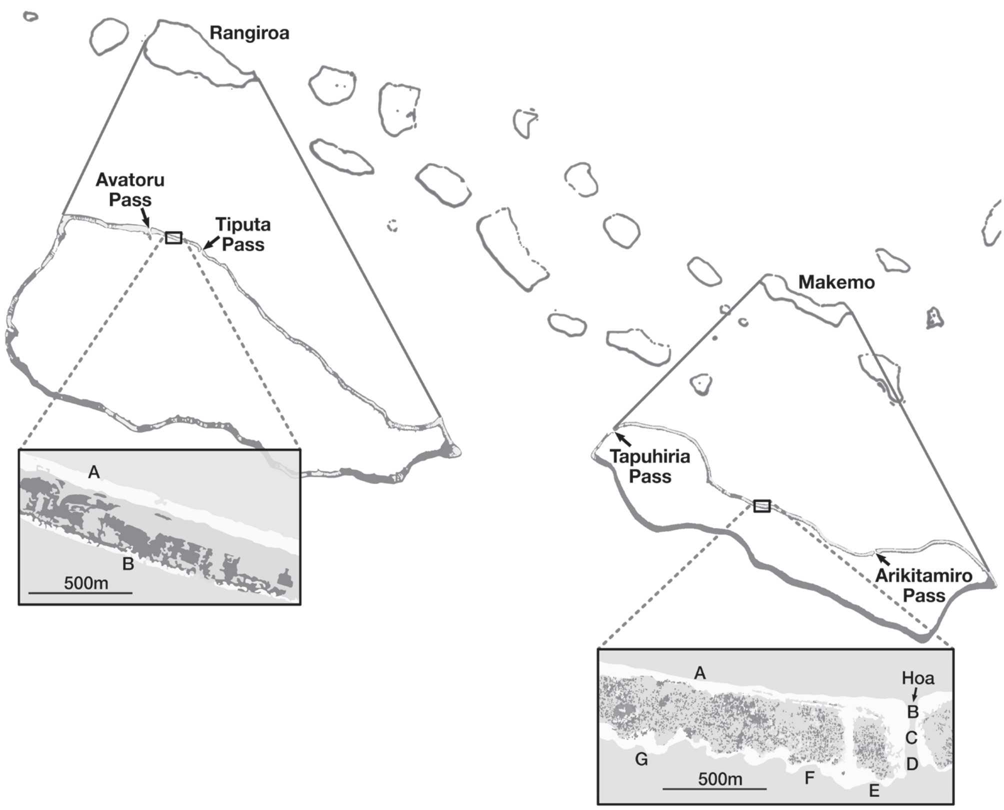

FIG. 1. Map of section of the Tuamotu Archipelago showing Rangiroa and Makemo as well as the locations of predominant passes and sampling sites at these atolls. Rangiroa: A = seaward site, B = lagoonal site; Makemo: A = seaward site, west of hoa, B = site at seaward entrance of hoa (hoa 1), C = site approximately in middle of hoa (hoa 2), D = site at lagoonal entrance of hoa (hoa 3), E = lagoonal; site, 200 m west of hoa, F = lagoonal site, 500 m west of hoa, G = lagoonal site, 1.5 km west of hoa. Image by John Megahan.

FIGS. 2–7. Photographs of sites at Rangiroa and Makemo. (2) Rangiroa: seaward reef flat (at low tide) (Rangiroa site A in Fig. 1); (3) Rangiroa: lagoonal shore (Rangiroa site B in Fig. 1); (4) Makemo: seaward reef flat (Makemo site A in Fig. 1); (5) Makemo: lagoonal shore just west of hoa (Makemo site E in Fig. 1); (6) Makemo: seaward entrance of hoa (Makemo site B in Fig. 1); (7) Makemo: lagoonal entrance of hoa (Makemo site D in Fig. 1).

hoa, and lagoonal sites to determine if shell sizes differed between samples from sites within and near the hoa. In addition, we applied a linear regression to determine if shell size and distance from the seaward side were correlated; we estimated distances from the seaward side using the "measure distance" tool on Google Maps (https://www.google.com/maps).

The seaward site at Rangiroa consisted of a large reef flat or bench (i.e., ~ 150 m from the shore/mean high-tide line to the reef crest) with algal-bound sand that exhibited greater topographic complexity toward the reef crest where waves of ~ 0.5–1 m height broke and spread across the bench (Fig. 2). The area immediately behind the reef crest was typically covered by no more than 10–20 cm of water at low tide and included small corals, plentiful macroalgae, and various sand-filled depressions, whereas the remainder of the bench was less complex, with little to no coral except in small depressions, and regularly exposed during low tides. In character with Alan's type III habitat, the lagoonal site consisted of a subtidal reef with larger corals; sandy areas; macroalgae; and large boulders, dead corals, and rubble that gradually deepened with further distance from the shore (Fig. 3).

The seaward nearshore habitats of Makemo that we observed consisted largely of a large bench with algal-bound sand that was narrower (i.e., shorter in distance between the shore and reef crest) than the bench at Rangiroa (i.e., ~ 50–75 m from shore to reef crest) and appeared to only be exposed during low tides at parts of the bench closest to the shore (Fig. 4). Wave energy appeared to have similar intensity as observed at the seaward site at Rangiroa. Many large pieces of rubble and/or boulders occurred close to the shore, although relative density and abundance varied depending on location. In addition, a large proportion of the area closest to the reef crest (~ 20 m shoreward from the crest) was very complex with many corals and depressions. We observed very little macroalgae on the bench. Lagoon habitats included large sandy/silty areas with occasional intertidal to mostly subtidal platforms as well as many large corals and boulders (Fig. 5). The lagoon only gradually deepened with a shallower bottom slope than observed at Rangiroa. Similar to the seaward areas at Makemo, macroalgae were also largely absent from the lagoonal sites examined.

We also surveyed cone snails within a hoa that was close to the seaward and lagoonal sites where we worked at Makemo (Fig. 1). The hoa was ~ 350 m in length (i.e., between the shores of the seaward and lagoonal sides of the motu), 30–50 m in width, and < 1 m in depth near the seaward side and up to several meters deep in areas near the lagoon. The area closest to the seaward side consisted largely of a subtidal platform with algal-bound sand and occasional pockets of sand, with large rubble and more conglomerated materials toward the seaward bench (Fig. 6). The habitat gradually transformed into a rubble-rich area with medium to large rubble in the middle of the hoa and then into an area with more sandy/silty areas and larger rubble/small boulders and corals closer to the lagoon (Fig. 7). Macroalgae were also largely absent in the hoa.

RESULTS

At Rangiroa, we observed 15 *Conus* species from the two sites examined: 13 at the seaward site and 12 at the lagoon site (Table 1). Although *C. pulicarius* Hwass, 1792, and *C. vitulinus* Hwass, 1792, were not observed at the seaward site, *C. coronatus*, *C. frigidus*, and *C. miles* Linneaus, 1758, were not observed in the lagoon. We collected and measured 731 individuals from the seaward site and 357 from the lagoonal site. Most individuals were collected within ~ 50 m from the reef crest at the seaward site (abundance of snails decreased dramatically closer to shore), whereas collections at the lagoonal site generally occurred within 20 m of the shore and to a depth of ~ 4 m. Given the abundance of certain species during initial collecting bouts (e.g., *C. ebraeus* and *C. sponsalis* Hwass, 1792, at Rangiroa), we did not collect additional individuals during later collections to focus on obtaining additional individuals of other species.

Although we only observed two to four species at the hoa and lagoon sites at Makemo, 11 occurred at the seaward site (Table 2). We collected and measured nearly 2,500 individuals representing 14 species from the sites for which we report data herein. In contrast to what we observed at Rangiroa, cone snails were distributed over nearly the entirety of the bench, including close to shore where *Conus ebraeus* and *C. sponsalis* were especially abundant.

Many of the specimens collected from the lagoonal site at Rangiroa and a few individuals from the seaward site at Rangiroa were heavily encrusted by coralline algae; only occasional specimens had encrustations at Makemo. Because of this, measures of shell length and shell width of individuals could not accurately be determined without removing the encrustations (which we did not do because we returned specimens to their site of collection and did not want to further modify them). On the other hand, measures of shoulder height

TABLE 1. Number of individuals of *Conus* species observed and measured at Rangiroa. **Conus ebraeus* and *Conus sponsalis* were exceptionally plentiful at both sites; additional individuals were observed but not measured or included in counts.

	Number of individuals	
Species	Seaward	Lagoon
Conus catus Hwass, 1792	4	1
Conus chaldaeus (Röding, 1798)	45	11
Conus coronatus Gmelin, 1791	12	0
Conus ebraeus Linnaeus, 1758*	194	65
Conus flavidus Lamarck, 1810	15	7
Conus frigidus Reeve, 1848	7	0
Conus lividus Hwass, 1792	79	15
Conus miles Linneaus, 1758	14	0
Conus miliaris Hwass, 1792	146	17
Conus nanus G. B. Sowerby I, 1833	55	9
Conus pulicarius Hwass, 1792	0	28
Conus rattus Hwass, 1792	11	99
Conus sanguinolentus Quoy & Gaimard, 1834	4	16
Conus sponsalis Hwass, 1792*	152	85
Conus vitulinus Hwass, 1792	0	1

could be accurately determined in most cases; the only exceptions include one individual of *Conus chaldaeus* (Röding, 1798) from the seaward site, and three individuals of *C. ebraeus* from the lagoonal site at Rangiroa. Hence, all subsequent analyses of shell size were based on measures of shoulder height except for the individuals mentioned above which were not included in the following analyses.

Ten of the species (i.e., all except five) that were collected and measured at Rangiroa occurred at both seaward and lagoonal sites. Although samples sizes of *Conus catus* Hwass, 1792, and *C. sanguinolentus* Quoy & Gaimard, 1834, at lagoonal and seaward sites, respectively, were small, average shoulder heights of all species were less than those at seaward than lagoonal sites. Four of the 14 species observed at Makemo occurred at both seaward and lagoonal sites, but only one individual of both *C. chaldaeus* and *C. sanguinolentus* were observed at sites in the lagoon and so sample sizes were too small for formal analyses. Nonetheless, although the average shoulder height of specimens of *C. sanguinolentus* from the seaward site was smaller than that of the specimen from the lagoon, the individual of *C. chaldaeus* (shell length 12 mm, shell width 7.5 mm, shoulder height 9 mm) from the lagoon was smaller than individuals observed at the seaward site (Table 3). In addition, we only observed specimens of *C. sponsalis* at the lagoonal site closest to the hoa; we failed to even detect empty shells at sites farther away from the hoa. Also, even though we spent considerable collection efforts at the site that is 1.5 km west of the hoa (i.e., ~ 7 hr total), we only observed three live individuals of *C. ebraeus*; to increase the sample size of *C. ebraeus* from this location, we included size data of shells from 14 recently dead individuals (as gauged by the condition of the shell).

At Rangiroa, average shoulder height was larger in the lagoon (Table 3). P-values determined from Mann-Whitney U-tests were all < 10^{-6}, except for the comparison of samples of *Conus flavidus* Lamarck, 1810, which had a p-value of 0.0038. Histograms of size-frequency distributions of these populations also illustrate the large differences in shoulder height of

TABLE 2. Number of individuals of *Conus* species observed at sites at Makemo. Letters in parentheses refer to the locations of sites shown in Fig. 1. *Also collected and measured 14 empty shells from site that appeared to represent recently dead specimens. **Additional individuals were observed but not collected nor included in counts.

	Number of individuals						
Species	Seaward (A)	Hoa 1 (B)	Hoa 2 (C)	Hoa 3 (D)	Lagoon, 200 m W of hoa (E)	Lagoon, 500 m W of hoa (F)	Lagoon, 1.5 km W of hoa (G)
Conus catus Hwass, 1792	11	-	-	-	-	-	-
Conus chaldaeus (Röding, 1798)	7	-	-	-	-	1	-
Conus coffeae Gmelin, 1791	2	-	-	-	-	-	-
Conus coronatus Gmelin, 1791	-	-	-	1	-	-	-
Conus ebraeus Linnaeus, 1758	512	39	22	7	87	102	3*
Conus flavidus Lamarck, 1810	1	-	-	-	-	-	-
Conus leopardus (Röding, 1798)	-	-	-	-	-	17**	9**
Conus lividus Hwass, 1792	-	-	-	1	1	-	-
Conus miliaris Hwass, 1792	45	-	-	-	-	-	-
Conus nanus G. B. Sowerby I, 1833	92	-	-	-	-	-	-
Conus rattus Hwass, 1792	10	-	-	-	-	-	-
Conus rotifer Menke, 1829	2	-	-	-	-	-	-
Conus sanguinolentus Quoy & Gaimard, 1834	7	-	-	-	1	-	-
Conus sponsalis Hwass, 1792	982	171	33	7	39	-	-

individuals from seaward and lagoonal sites (Fig. 8). Although some plots appear to follow a normal distribution, others are skewed to the right (e.g., *C. ebraeus* at Rangiroa seaward site) or the left (e.g., *C. sponsalis* at Rangiroa lagoon site).

At Makemo, average shoulder height was also larger in the lagoon (Table 4; Fig. 8). P-values from Mann-Whitney U-tests were all very small (i.e., “p-value: < 2.2e-16”) for comparisons of shoulder heights from seaward and lagoonal sites of *Conus ebraeus* and *C. sponsalis*. We also compared shoulder heights of samples from adjacent collection sites to evaluate how shell size changes between sites in the hoa and seaward and lagoonal sites (i.e., seaward to hoa 1, hoa 1 to hoa 2, etc.). Average shoulder height steadily increased from the seaward site, through sites in the hoa, and in the lagoon, including with increasing distance from the hoa (Fig. 9). After correcting for multiple tests, samples of *C. ebraeus* from all

TABLE 3. Average shoulder height of shells of *Conus* species that occur at both seaward and lagoonal sites at Rangiroa. Letters in parentheses refer to locations of sites shown in Fig. 1. *Value is not an average as only one individual was measured. **One individual not included in average as it was heavily encrusted by coralline algae. ***Three individuals not included in average as they were heavily encrusted by coralline algae.

	Shoulder height (mm)	
Species	Seaward (A)	Lagoon (B)
Conus catus Hwass, 1792	25.5	27.0*
Conus chaldaeus (Röding, 1798)	16.3**	26.3
Conus ebraeus Linnaeus, 1758	11.9	26.8***
Conus flavidus Lamarck, 1810	27.5	33.1
Conus lividus Hwass, 1792	25.3	30.5
Conus miliaris Hwass, 1792	14.9	21.9
Conus nanus G. B. Sowerby I, 1833	9.4	14.7
Conus rattus Hwass, 1792	20.7	26.8
Conus sanguinolentus Quoy & Gaimard, 1834	30.0	30.5
Conus sponsalis Hwass, 1792	11.3	17.3

adjacent sites exhibited significant differences in shoulder heights (p-values $< 10^{-3}$) except for three comparisons involving the samples from the hoa 2 and hoa 3 sites (i.e., original p-value of 0.033 would be greater than the adjusted significance level of 0.025), the hoa 3 site and the lagoonal site that is 200 m west of the hoa (i.e., p-value = 0.70), and the lagoonal sites that are 200 and 500 m west of the hoa (i.e., original p-value of 0.031 would be greater than the adjusted significance level of 0.0125). For *C. sponsalis,* all comparisons except for the one between the samples from the hoa 2 and hoa 3 sites (p-value = 0.33) revealed significant differences in shoulder height (p-values $< 10^{-4}$) (Fig. 9).

To further evaluate how shell sizes change from seaward to lagoonal sites and with increasing distance from the hoa, we performed a linear regression of shoulder heights to distances of sampling locations from the seaward reef. Analyses of both species revealed significant (i.e., "p-value: < 2.2e-16") association of shoulder height and distance with R-squared values of 0.670 and 0.808 for *Conus ebraeus* and *C. sponsalis*, respectively.

DISCUSSION

In accord with Leviten's (1978) observations, we found strong support for Alan Kohn's prediction that body sizes of cone snails at marine bench habitats are smaller than those at subtidal reefs. Indeed, populations of *Conus* species that occurred at seaward and lagoonal sites of two atolls in French Polynesia were significantly larger at sites within the lagoon than at seaward sites. In addition, at Makemo, we also observed a significant correlation between shell size and distance from the seaward reef for samples of *Conus ebraeus* and *C. sponsalis* in the lagoon and a hoa.

As discussed earlier, Alan proposed that higher wave energy or exposure during low tides can limit the sizes of cones that occur at intertidal marine bench habitats (Kohn 1968), whereas Leviten (1978) suggested that predation at subtidal reefs might affect the abundance of small-sized cones. The differences in shell sizes that we observed at Rangiroa and Makemo largely reflect an absence of both large-sized individuals at seaward sites and small-sized individuals at lagoonal sites. Exceptions to this trend include *Conus rattus* and *C. sponsalis* at Rangiroa (Fig. 8) and *C. chaldaeus* at Makemo (Table 4) in which small-sized individuals of these species were observed within the lagoon. On the contrary, the largest shells of all species occurring at both seaward and lagoonal sites were always detected within the lagoon. These observations support Alan's view that body sizes of

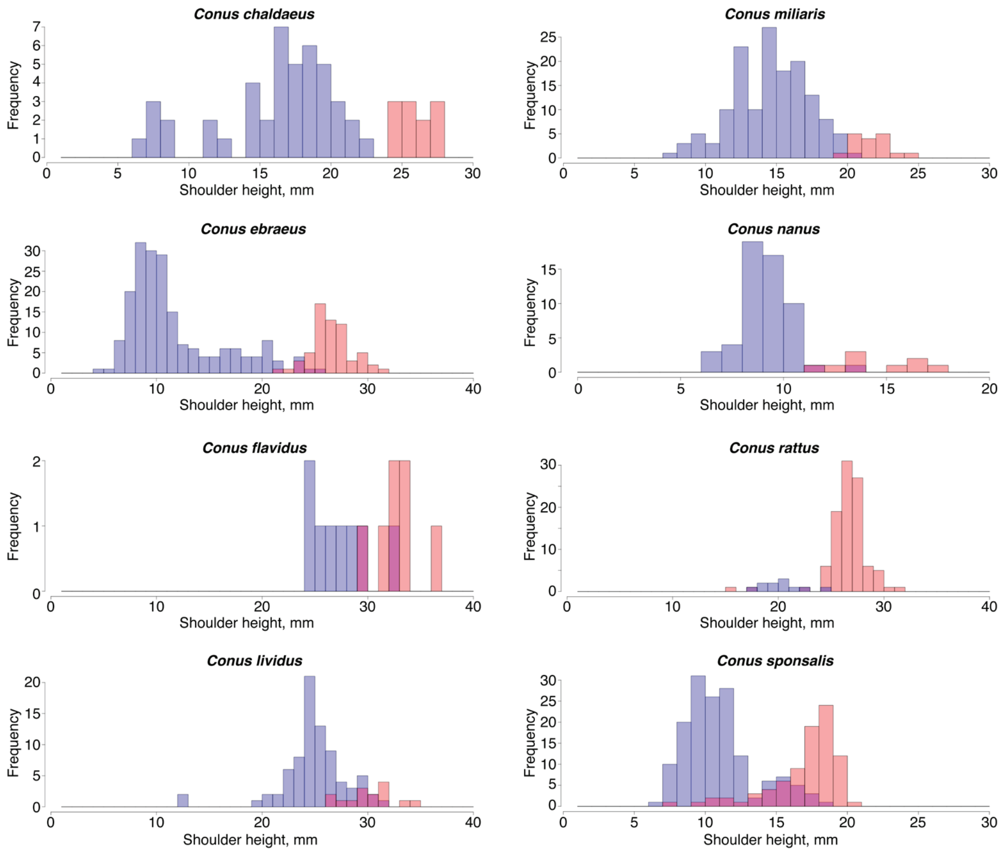

FIG. 8. Size frequency distributions of eight *Conus* species that occur at seaward (blue bars) and lagoonal sites (red bars) at Rangiroa. The x- and y-axes of the different plots do not necessarily utilize the same scales.

cone snails are limited on seaward intertidal benches as well as Leviten's (1978) proposals that densities of small-sized cones at subtidal reefs are reduced because of size-dependent predation.

Although high rates of predation of small-sized cones in lagoons could be responsible for the patterns that we observed, the absence or low abundance of small-sized individuals at lagoonal sites also suggests that larval recruitment is much lower or more episodic in lagoons of atolls than at seaward sites, a phenomenon observed for other lagoonal species. For example, whereas rates of passive migration of fish larvae into lagoons of atolls in the Tuamotu Archipelago are estimated to be low (Leis et al., 2003), recruitment of most lagoonal fish species appears to derive from settlement of larvae that enter the lagoon and not via completion of life cycles within lagoons (Leis et al., 1998).

The significant association between shell size and distance from the seaward habitat for the two species at Makemo (Fig. 9) suggests that recruitment in the lagoon is largely limited to migration of postsettlement individuals from seaward sites through passes or hoas. Indeed, whereas both *Conus ebraeus* and *C.*

TABLE 4. Average shoulder height of shells of *Conus* species that occur at both seaward and lagoonal sites at Makemo. Letters in parentheses refer to locations of sites shown in Fig. 1. *Value is not an average as only one individual was measured.

	Shoulder height (mm)						
Species	Seaward (A)	Hoa 1 (B)	Hoa 2 (C)	Hoa 3 (D)	Lagoon, 200 m W of hoa (E)	Lagoon, 500 m W of hoa (F)	Lagoon, 1.5 km W of hoa (G)
Conus chaldaeus (Röding, 1798)	15.1					9.0*	
Conus ebraeus Linnaeus, 1758	12.6	15.2	17.6	21.2	21.8	22.2	35.3
Conus sanguinolentus Quoy & Gaimard, 1834	27.4				29.0*		
Conus sponsalis Hwass, 1792	11.2	13.3	16.8	17.6	21.5		

sponsalis occurred at sites within the lagoon, we only observed individuals of *C. sponsalis* at the lagoonal site that was ~ 200 m west of the entrance to the hoa and none were observed at sites further to the west. In addition, many of the specimens of *C. sponsalis* that we observed at the lagoonal site nearly reached what is considered their maximum shell length (i.e., 34 mm; Rockel et al. 1995) at this site. This observation suggests that specimens of *C. sponsalis* are reaching their maximum size and senescing before they migrate farther away from the hoa. *Conus ebraeus* might extend further into the lagoon given that it has a larger maximum size than that of *C. sponsalis* (i.e., 62 mm; Rockel et al., 1995). Nonetheless, the abundance of this species (N = 3) declined with increasing distance from the hoa (Table 2) and so it too might not be able to occupy sites further into the lagoon. Furthermore, we did not observe any living cone-snail species during ~ 4 hr of collection effort at a lagoonal site that was ~ 3 km to the northeast of Tapuhiria Pass (and only found a few empty shells of *C. pulicarius*). Hence, although we did not sample throughout the lagoon, lagoonal populations of cones at Makemo largely appeared to be restricted to areas that are adjacent to the hoa where we sampled, which suggests that populations are being maintained via migration from seaward sites. Alternatively, although we favor the hypothesis that the relationship between shell size and distance from the seaward habitat reflects differences in ages of specimens, it could also reflect differences in growth rates and predation rates of small-sized cones among habitat types if these rates both increase within the lagoon with increasing distance from seaward sites.

Our observations of a small-sized individual of *Conus chaldaeus* in the lagoon at Makemo (Table 4) and several small-sized individuals of *C. rattus* and *C. sponsalis* in the lagoon at Rangiroa (Fig. 8) imply that recruitment of cone snails in these lagoons is also realized occasionally through larval settlement because it seems unlikely that these individuals, especially the small *C. chaldaeus* individual, migrated into the lagoon after settling as larvae on the seaward side of the atoll. How each potential source of recruits (i.e., larvae and migration of juvenile or subadult individuals from seaward habitats) contributes to establishment and replenishment of lagoonal populations is likely related to aspects of the biology of individual species as well as the physical characteristics of the atoll (e.g., water renewal rates and presence and location of passes and functional hoas).

Finally, given that the abundance and diversity of mollusks in lagoons of atolls in French Polynesia appear to be strongly influenced by the level of connectivity of lagoonal and seaward waters (e.g., Salvat, 1983; Adjeroud et al., 2000), the greater species richness that we observed at our lagoonal site at Rangiroa compared to Makemo could be due to its proximity to two major passes (both ~ 4.5 km

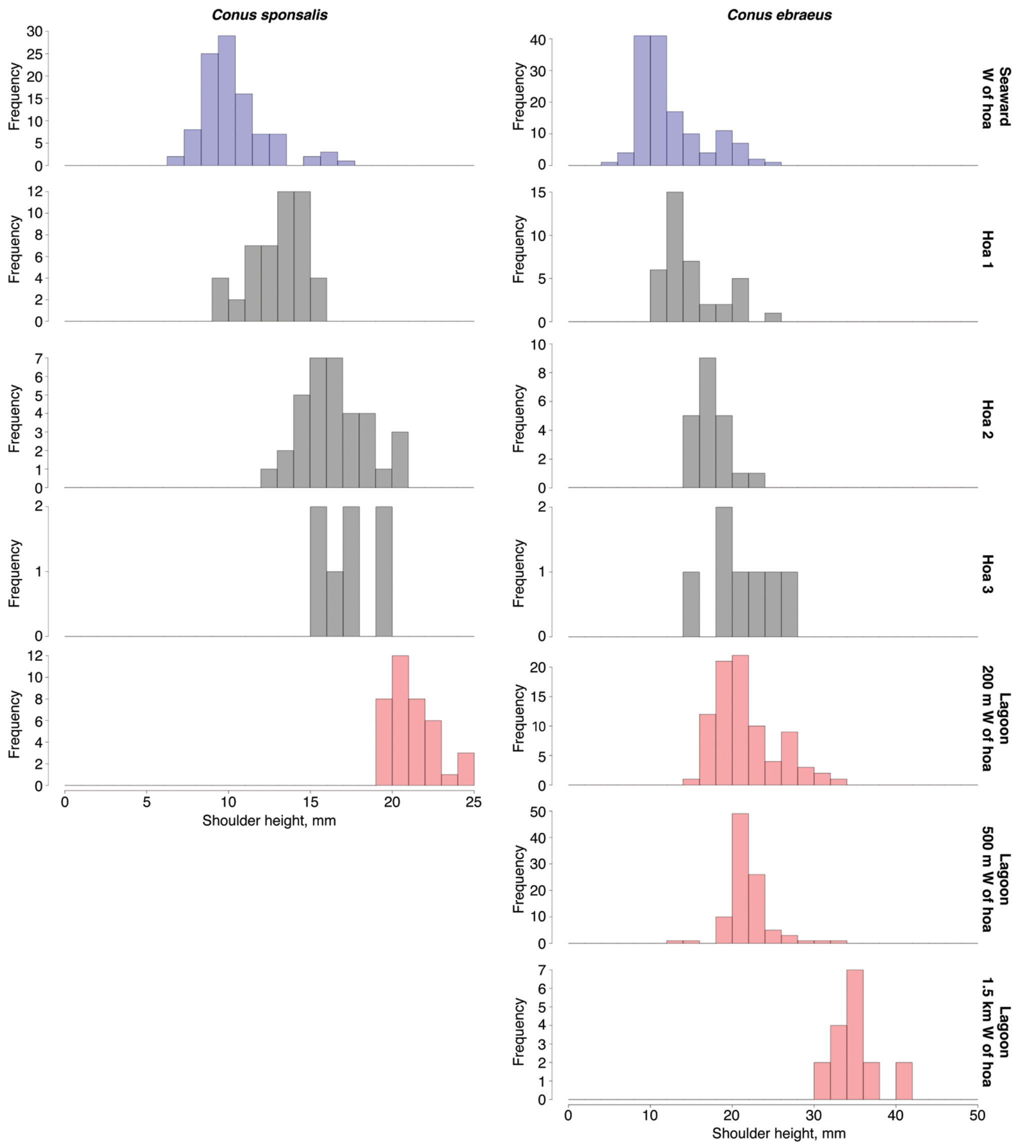

FIG. 9. Size-frequency distributions of *Conus sponsalis* and *Conus ebraeus* that occur at seaward sites (blue bars), sites within the hoa (gray bars), and lagoonal sites (red bars) at Makemo. Although x-axes are the same for each species but differ among species, y-axes of the different plots do not necessarily utilize the same scales.

away from our site) and the nearby presence of functional hoas that could facilitate greater migration of individuals and/or larvae into the lagoon (Fig. 1). On the contrary, the hoa at Makemo where we performed our surveys appeared to be the only functional hoa on the entire motu and the major passes are ~ 20 and 27 km away from our principal collection sites in the lagoon (Fig. 1).

In conclusion, our studies of cone-snail populations at seaward and lagoonal sites at two atolls in the Tuamotu Archipelago support Alan's hypothesis that sizes of individuals inhabiting marine bench habitats are potentially limited due to physical factors (i.e., wave energy and exposure during low tides). Nonetheless, the relative dearth of small-sized individuals in the lagoon could be due to recruitment limitation at lagoonal sites. We posit that the large individuals at lagoon sites, especially at Makemo, represent older individuals that migrated into the lagoon from nearby seaward sites and that larval recruitment in the lagoon is much more episodic and/or less intense than at seaward sites.

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LITERATURE CITED

Adjeroud, M., S. Andréfouët, C. Payri, & J. Orempüller, 2000, Physical factors of differentiation in microbenthic communities between atoll lagoons in the central Tuamotu Archipelago (French Polynesia). *Marine Ecology Progress Series*, 196: 25–38.

Chevalier, J.-P., 1972, Observations sur les chenaux incomplets appelés hoa dans les atolls des Tuamotu. Pp. 477–488, in: C. Mukundan & C. S. Gopiinadha Pillai, eds., *Proceedings of the Symposium on Corals and Coral Reefs, Mandapam Camp, 12–16 January 1969*. Marine Biological Association of India, Cochin.

Danielsson, B., 1954, Native topographical terms in Raroia, Tuamotus. *Atoll Research Bulletin*, 32: 92–96.

Kohn, A.J., 1959a, Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Journal of Natural History*, 2(17): 309–320.

Kohn, A.J., 1959b, The ecology of *Conus* in Hawaii. *Ecological Monographs*, 29: 42–90.

Kohn, A. J., 1967, Environmental complexity and species diversity in the gastropod genus *Conus* on Indo-West Pacific reef platforms. *American Naturalist*, 101: 251–259.

Kohn, A. J., 1968, Microhabitats, abundance and food of *Conus* on atoll reefs in the Maldive and Chagos Islands. *Ecology*, 49: 1046–1062.

Kohn, A. J., 1971, Diversity, utilization of resources, and adaptive radiation in shallow-water marine invertebrates of tropical oceanic islands. *Limnology and Oceanography*, 16: 332–348.

Kohn, A. J., 1978a, The Conidae (Mollusca: Gastropoda) of India. *Journal of Natural History*, 12: 295–335.

Kohn, A. J., 1978b, Ecological shift and release in an isolated population: *Conus miliaris* at Easter Island. *Ecological Monographs*, 48(3): 323–336.

Kohn, A. J., 1983, Microhabitat factors affecting abundance and diversity of *Conus* on coral reefs. *Oecologia*, 60(3): 293–301.

Kohn, A. J., 1997, Ecological and biogeographic attributes of *Conus* on the Indian Ocean's southernmost coral reefs. Pp. 113–131, in: F. E. Wells, ed., *The Marine Flora and Fauna of the Houtman Abrolhos Islands, Western Australia; Proceedings of the Seventh International Marine Biological Workshop*. Western Australian Museum, Perth.

Kohn, A. J., 2001, Maximal species richness in *Conus*: diversity, diet and habitat on reefs of northeast Papua New Guinea. *Coral Reefs*, 20: 25–38.

Kohn, A. J., 2003, Biology of *Conus* on shores of the Dampier Archipelago, northwestern Australia. Pp. 89–100, in: F. E. Wells, D. I. Walker, & D. S. Jones, eds., *The Marine Flora and Fauna of Dampier, Western Australia, Volume 1.* Western Australian Museum, Perth.

Kohn, A. J., 2015, Ecology of *Conus* on Seychelles reefs at mid-twentieth century: comparative habitat use and trophic roles of co-occurring congeners. *Marine Biology*, 162: 2391–2407.

Kohn, A. J., & K. N. Almasi, 1993, Comparative ecology of a biogeographically heterogeneous *Conus* assemblage. Pp. 523–538, in: F. E. Wells, ed., *The Marine Flora and Fauna of Rottnest Island, Western Australia, Volume 2.* Western Australian Museum, Perth.

Kohn, A. J., & J. W. Nybakken, 1975, Ecology of *Conus* on eastern Indian Ocean fringing reefs: diversity of species and resource utilization. *Marine Biology*, 29: 211–234.

Kohn, A. J., & A. C. Riggs, 1975, Morphometry of the *Conus* shell. *Systematic Zoology*, 24(3): 346–359.

Kohn, A. J., & R. Robertson, 1968, The Conidae (Gastropoda) of the Maldive and Chagos Archipelagoes. *Journal of the Marine Biological Association of India*, 8: 273–277.

Kohn, A. J., K. M. Curran, & B. J. Mathis, 2005, Diets of the predatory gastropods *Cominella* and *Conus* at Esperance, Western Australia. Pp. 235–244, in: F. E. Wells, D. I. Walker, & G. A. Kendrick, eds., *The Marine Flora and Fauna of Esperance, Western Australia.* Western Australian Museum, Perth.

Leis, J. M., T. Trnski, P. J. Doherty, & V. Dufour, 1998, Replenishment of fish populations in the enclosed lagoon of Taiaro Atoll (Tuamotu Archipelago): evidence from eggs and larvae. *Coral Reefs*, 17: 1–18.

Leis, J. M., T. Trnski, V. Dufour, M. Harmelin-Vivien, J.-P. Renon, & R. Galzin, 2003, Local completion of the pelagic larval stage of coastal fishes in coral-reef lagoons of the Society and Tuamotu Islands. *Coral Reefs*, 22: 271–290.

Leviten, P. J., 1978, Resource partitioning by predatory gastropods of the genus *Conus* on subtidal Indo-Pacific coral reefs: the significance of prey size. *Ecology*, 59(3): 614–631.

Leviten, P. J., & A. J. Kohn, 1980, Microhabitat resource use, activity patterns, and episodic catastrophe: *Conus* on tropical intertidal reef rock benches. *Ecological Monographs*, 50(1): 55–75.

Mann, H. B., & D. R. Whitney, 1947, On a test of whether one or two random variables is stochastically larger than the other. *Annals of Mathematical Sciences*, 18: 50–60.

Röckel, D., W. Korn, & A. J. Kohn, 1995, *Manual of the Living Conidae, Volume 1, Indo-Pacific*. Christa Hemmen Verlag, Wiesbaden.

Salvat, B., 1983, La faune benthique du lagon de l'atoll de Scilly, archipel de la Société. *Journal de la Société des Océanistes*, 77: 5–15.

Shapiro, S. S., & M. B. Wilk, 1965, An analysis of variance test for normality (complete samples). *Biometrika*, 52(3/4): 591–611.

Stoddart, D. R., & F. R. Fosberg, 1994, The hoa of Hull Atoll and the problem of hoa. *Atoll Research Bulletin*, 394: 1–26.

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