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ORIGINAL PAPER

Current and historic distribution and abundance of the inarticulated brachiopod, *Lingula reevii* Davidson (1880), in Kaneohe Bay, Oahu, Hawaii, USA

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Abstract The inarticulated brachiopod, *Lingula reevii* Davidson (1880) is a filter-feeding invertebrate that burrows vertically in sandy or mixed sediments. Its only recorded occurrence is from Kaneohe Bay, Oahu, Hawaii, southern Japan, and Ambon, Indonesia. Past surveys of Kaneohe Bay populations suggested a distinct decrease in abundance following the diversion of sewage effluent from the bay in 1978/1979. In the summer of 2004 and 2007, visual surveys were conducted in areas of historical *L. reevii* abundance as well as in areas appearing to have suitable habitat. In 2004, approximately 2,950 m^2 at 20 sites within the bay were surveyed using quantitative belt transecting methods. A maximum density of 4 *Lingula*/m^2 was observed, a decrease from previous maximum estimates of 500 individuals/m^2 (Worcester, Dissertation, Zoology Department, University of Hawai′i, pp 49, 1969) and 100 individuals/m^2 (Emig, J Exp Mar Biol Ecol 52:47–61, 1981). When these 20 sites were revisited in 2007, many had fewer or no *L. reevii*; therefore, broader scale presence/absence surveys were conducted at 16 additional sites in the bay (also surveyed in 2004). The highest density of *L. reevii* found in 2007 was 0.94 individuals/m^2. The continued decline in abundance of *L. reevii* in Kaneohe Bay may be due, in addition to decreased organic enrichment from diversion of sewage discharge almost 30 years ago, to the more recent reduction of suitable habitat by the invasion of mat-forming alien algae species.

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Introduction

The abundance and distribution of the inarticulated brachiopod, *Lingula reevii*, was first surveyed in Kaneohe Bay, Oahu, Hawaii more than 35 years ago (Worcester 1969). The global distribution of *L. reevii* is apparently disjunct, being recorded only from Kaneohe Bay (Emig 1978, 1981, 1984), Ambon, Indonesia (Cals and Emig 1979), and southern Japan (Emig 1997). *L. reevii* is found in shallow, sandy reef flats in southern Kaneohe Bay, with a few reports from other areas within the bay (Emig 1978). It has not been reported elsewhere in the Hawaiian archipelago, despite extensive surveys (A. H. Banner, personal communication. to C.L.H., 1983).

Lingula reevii possess elongate, bilaterally symmetrical valves, with a characteristic blue-green or emerald color. They burrow vertically in sand, leaving a three-hole opening at the surface (Emig 1987). These lophophorates filter and ingest particles that may include diatoms, peridinians, foraminifera, filamentous algae, rotifers, polychaetes, oligochaetes, copepods, and organic detritus (Emig 1997). When disturbed by movement or shadow, a rapid contraction of the pedicle pulls the animal below the sand surface.

The reproductive biology of inarticulated brachiopods is not well understood. Known *Lingula* species are dioecious, reproducing by broadcast spawning; gametes are discharged from the median exhalent canal (Williams et al. 1997). The longevity of gametes and dispersal abilities of *Lingula* larvae are largely unknown, but larvae are reported to settle near adults in favorable habitats (Hyman 1959; Paine 1963). *Lingula* species spawn year-round at lower latitudes, but cooler water populations spawn seasonally (Chuang 1959; Hyman 1959; Hammond 1982). Sex can be determined by dissection; male gonads are white and fine-grained, while ovaries are tan to yellow and coarse in

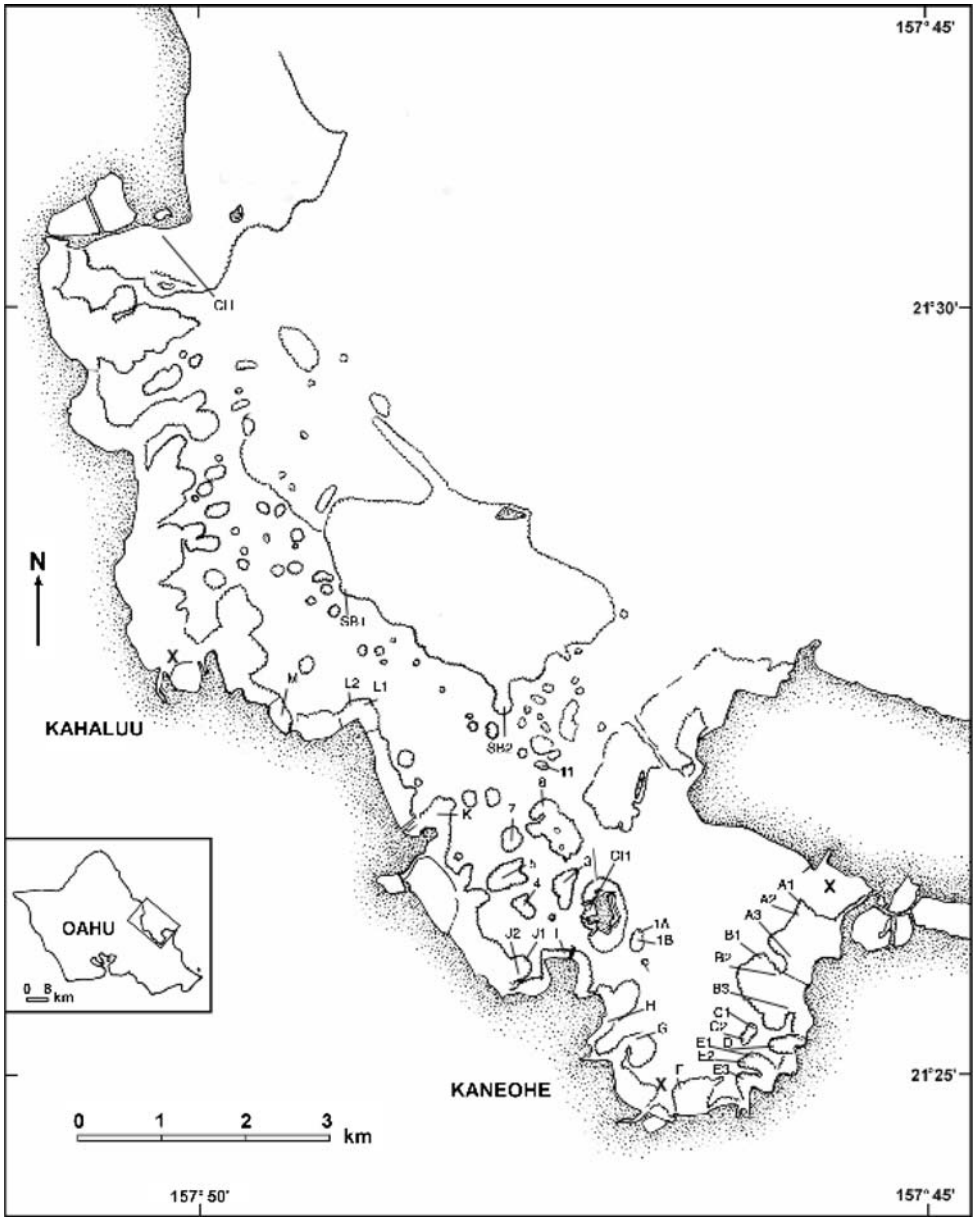

Fig. 1 Location of 37 sites surveyed for *Lingula reevii* in Kaneohe Bay, Oahu, in May–June 2004 and May–June 2007. Fringing reefs are labeled in alphabetical order (*A* through *M* from the southern region of the bay toward the north). Numbering of patchreef sites follows the convention of Roy (1970). Other abbreviations are as follows: *CH* Chinaman's Hat, *CI* Coconut island, and *SB* Sand Bar. *X* indicates sites of sewage discharges terminated between 1978 and 1986

texture (Worcester 1969). The lifespan of *Lingula* spp. is estimated to be 5–8 years (Emig 1997).

The southern sectors of Kaneohe Bay, Oahu, received municipal sewage discharges from the mid-1940s through the late-1970s (Smith et al. 1981). This anthropogenic disturbance led to eutrophic conditions within the southern and middle bay (where an additional, smaller sewage discharge continued until 1986), causing a phase shift from a coral-dominated reef ecosystem to one dominated by invasive algae and filter-feeding sponges, tunicates, and clams (Smith et al. 1981). Diversion of sewage from the bay in 1978/1979 resulted in a rapid change in water-column nutrient characteristics and decline in primary productivity (Smith et al. 1981). In the south bay, particulate organic carbon, phytoplankton biomass, and microplankton ash-free dry weight declined 36, 37, and 35%, respectively. Benthic algae declined and reefs slowly began to be recolonized by corals (Hunter and Evans 1995).

In recent years (since the mid-1990s), significant areas of shallow reef habitat have been undergoing invasion by several introduced seaweeds, *Kappaphycus* spp., *Eucheuma* spp., and *Gracilaria salicornia* (Rodgers and Cox 1999; Woo 2000; Smith et al. 2002, 2004). These mat-forming algae, introduced for aquaculture research in the 1970s, have more recently begun to rapidly overgrow living coral and other native benthic organisms. There have been no thorough qualitative nor quantitative surveys of the abundance of *L. reevii* either post-sewage diversion or during the more recent period of alien algal invasion of reef flats in Kaneohe Bay.

Table 1 Comparison of abundance of the inarticulated brachiopod *Lingula reevii* in Kaneohe Bay, Oahu, at sites qualitatively surveyed in 1969, prior to sewage diversion (Worcester 1969), in May–June 2004, and in May–June, 2007 (present study)

Site	Worcester 1969	Current study 2004					Current study 2007
	Abundance *Lingula*/m^2	No. transects	Area surveyed (m^2)	Max *Lingula*/m^2	Mean *Lingula*/m^2	SE	Max *Lingula*/m^2
A1	0.2–5.0	5	125	1.60	0.30	0.057	0.66
A2	0.2–5.0	5	125	0.40	0.01	0.008	–
A3	0.2–5.0	5	125	1.20	0.26	0.037	<0.01
B1	25.1–500	3	150	1.20	0.24	0.122	–
B2	25.1–500	3	150	4.00	1.42	0.279	<0.01
B3	0.2–25	5	125	2.00	0.36	0.081	–
C1	25.1–500	6	150	2.40	0.63	0.156	<0.01
C2	5.1–500	7	175	2.80	0.57	0.162	–
D	5.1–500	5	250	3.60	0.34	0.037	–
E1	0.2–5.0	5	125	1.20	0.14	0.032	–
E2	5.1–50	8	200	0.80	0.03	0.021	–
E3	0.2–25	5	125	2.00	0.32	0.068	–
J1		5	125	0.80	0.10	0.042	–
J2		5	125	0.40	0.04	0.013	–
L1		5	125	1.60	0.27	0.086	–
L2		5	125	1.20	0.20	0.073	–
1A		3	75	2.80	0.43	0.199	0.94
1B		3	75	2.40	0.71	0.167	<0.01
SB1		4	100	1.60	0.28	0.094	<0.01
CI1		15	375	2.80	0.42	0.094	–
		107	2,950				
Mean				1.80	0.35		
SE				1.00	0.32		

Worcester's qualitative abundance categories were L = 0.2–5.0/m^2, A = 5.1–25/m^2 and H = 25.1–500/m^2. Maximum and average density (individuals/m^2) and standard error (SE) of *Lingula reevii* abundance are reported for 20 sites censused in summer 2004 and maximum densities reported for these same sites censused in summer 2007. See Fig. 1 for site locations

– Indicates that no *Lingula reevii* were found in this census

Due to its limited distribution, and potential threats to its persistence (over-collection for scientific study, habitat degradation), *L. reevii* has been recently identified as a "Species of Concern", which means it is to be considered for listing as an Endangered Species in the United States (Federal Register 2004). The objective of this study was to survey sites throughout Kaneohe Bay, Oahu, to determine the current distribution and abundance of *L. reevii* and to make opportunistic observations of spawning. Sediment characteristics were measured at selected sites within the bay to examine correlation with current *L. reevii* distribution. This information will provide managers with an insight into the current status of these organisms and help to determine if protection is needed.

Materials and methods

Distribution and abundance surveys

Surveys were conducted throughout Kaneohe Bay in May–June, 2004, and May–June, 2007, with more extensive efforts targeting areas in the southern end of the bay that had been shown previously (pre-sewage diversion) to have highest densities of *L. reevii* (Fig. 1; Worcester 1969). Belt transects were conducted by snorkelers at depths of 0.25–1.0 m at 20 sites in the bay. Two snorkelers surveyed each transect (1×25 or 1×50 m, as noted), swimming in reverse directions on opposite sides of the transect line. Numbers of *L. reevii* burrows were counted in 1×5 m increments along the transect line. Similar surveys were conducted using scuba diving at three deeper water sites in 2004 (>5 m; Fig. 1; sites 1A, 1B, and A4). In addition, qualitative surveys of presence or absence of *L. reevii* were made at 17 additional reef flats in Kaneohe Bay in both 2004 and 2007, and at two sites outside of the bay (Kailua and Lanikai reef flats; approx. 3.5 and 6 km southeast, respectively).

Plankton tows

Plankton tows were done in daylight hours in areas of highest *Lingula* densities to sample for *Lingula* larva. A 25-cm diameter plankton net with 30-μm mesh was towed at the surface either by boat or a snorkeler in open water, along reef slopes and over reef flats. Tow speed and time varied

(10–20 min per tow at 0.1–1 knot) with sea conditions and size of sampling area. Plankton samples were run through 500 and 63 μm sieves. Material from the 63 μm mesh sieve was examined under a dissecting microscope for *Lingula* larva.

Sediment analysis

Sediment grain size was compared with present *L. reevii* distribution patterns at six sites where *L. reevii* density had been quantified. Two replicate sediment samples were taken by hand at each site, using 50 ml plastic tubes (32 × 118 mm) as cores. The samples were sieved through a series of screens with mesh sizes of 63, 125, 250, 500, 2,000, and 4,000 μm (phi classes of 4, 3, 2, 1, −1 and −2, respectively). The contents of each sieve were transferred to aluminum weigh boats, dried at 80°C for 24 hours, and weighed to obtain dry weight.

Sediment depth at each site was measured by inserting a stiff metal wire (2 mm in diameter) vertically into the sediment until solid substratum was reached. Ten measurements were made at each of nine sites.

In situ and laboratory observations of spawning

Opportunistic observations were made of *Lingula reevii* individuals releasing eggs or sperm into the water column. Animals were collected and held in the lab for observation in flow-through seawater aquaria, and subsequent field surveys were made at different times, tidal periods and moon phases in attempts to determine the conditions under which *L. reevii* spawns.

Results

Field surveys of *L. reevii* in 2004 and 2007 indicated that small populations occurred in the southern bay (fringing reef sites A–K and patchreefs 1A–1B) and at the Sand Bar (SB1) in mid-Kaneohe Bay (Tables 1, 2). Individuals of mixed sizes (1.5 to 10 cm total shell length) were present at water depths ranging from 0.5–4.0 m, primarily in areas with fine sand mixed with coral rubble.

Quantitative surveys of 107 transects covering 2,950 m^2 revealed average site densities of *L. reevii* ranging from 0.01 to 1.4 individuals/m^2 with a maximum observed density of 4 individuals/m^2 in 2004 (site B2, a fringing reef). Up to 0.94 individuals/m^2 were observed in 2007, but at a different site (site1b, a dredged patchreef). In 2004, 10 of the 17 additional sites surveyed had estimated densities of less than 0.01 individual/m^2, the lowest average found in any of the quantitative surveys; *L. reevii* were present in only 6 of the 17 sites in 2007 surveys. No *L. reevii* were observed in qualitative surveys either year at Chinaman's Hat (CH), or outside Kaneohe Bay at Kailua Boat Ramp or Lanikai.

Table 2 Qualitative surveys of 17 additional sites in 2004 and 2007 with low densities of *Lingula*

	Approx. area surveyed × 1.000 m^2	Presence/ absence 2004	Presence/ absence 2007
Site			
3	97	+	+
4	54	+	+
5	148	+	0
7	65	+	0
8	160	0	0
11	22	0	+
F	125	+	0
G	40	+	0
H	45	+	+
I	174	+	0
K	130	0	0
M	0.5	0	0
CH	150	0	0
SB2	65	0	0
CI2	100	+	+
CI3	100	+	+
A4	0.1	0	Not surveyed
Total area searched	1,476,000		

+ Indicates the presence of one or more *Lingula reevii* and 0 indicates that no *Lingula* were found

Dominant sediment grain sizes in habitats where *L. reevii* were observed varied from 125–250 μm, although one small population was found at the sand bar (SB1; 0.3 individuals/m^2) in sediment with a dominant grain size of 500 μm (Fig. 2). Linear regression revealed a low correlation between *Lingula* density and sand depth ($r^2 = 0.076$). When the outlier (highest *L. reevii* density recorded, mean = 1.4 individuals/m^2) was excluded from this analysis, the r^2 value dropped to 0.0137.

Lingula reevii were observed spawning on 26 May 2004 on Coconut Island (site CI1), at ≈3:30 p.m. during a slack tide. *L. reevii* were not observed spawning at any other time; however, mature gonads with sperm or eggs were found previously during limited dissections. A single living *Lingula* larva (shell diameter = 0.7 mm) was found in a surface plankton tow in southern Kaneohe Bay at 1100 h on 30 May 2004. A range of size classes evidenced by burrow opening size suggests that recent recruitment is occurring within this population.

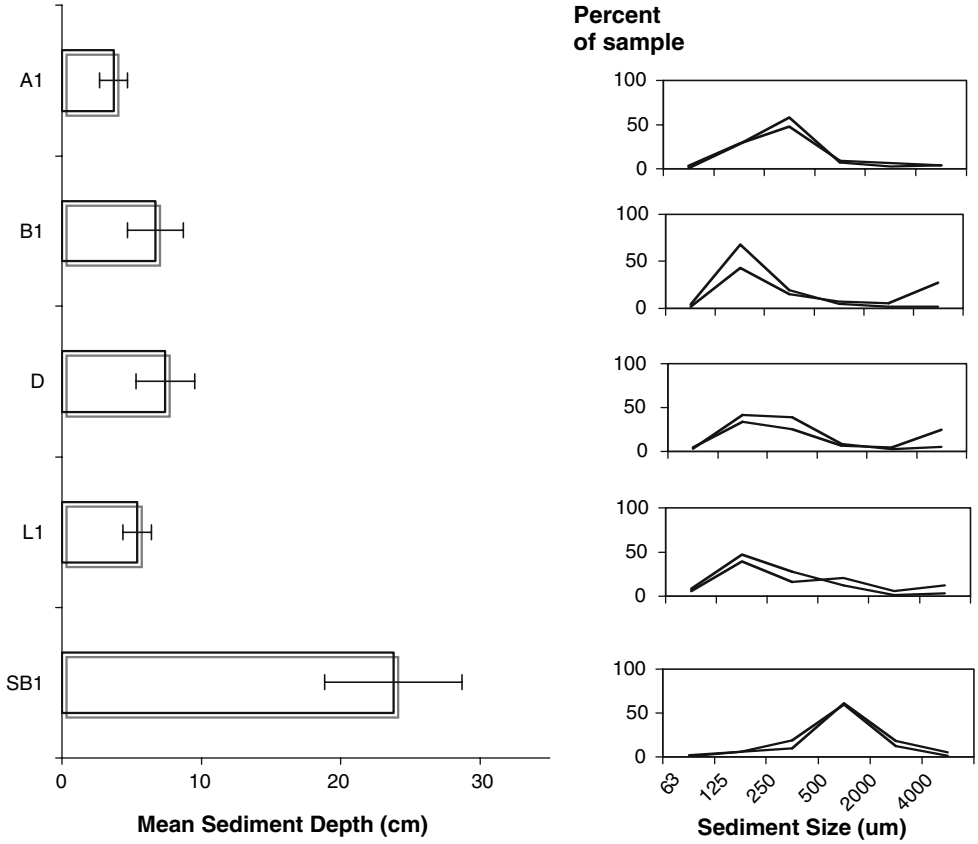

Fig. 2 Comparisons of grain size and mean sediment depth (+SE) for five sites in Kaneohe Bay where *Lingula reevii* surveys were conducted

Discussion

The current population of *Lingula reevii* in Kaneohe Bay has undergone substantial decline in comparison to past assessments of population densities. Worcester's (1969) surveys from 1966–1969 found densities as high as 500 individuals/m^2, with an average of 25–50 individuals/m^2. A similar species, *Lingula anatina,* occurred at densities of over 400 individuals/m^2 in northern Australia (Kenchington and Hammond 1978) and up to 100 individuals/m^2 in Japan (Emig 1984). In another study reporting the presence of *L. reevii* in Ambon, Indonesia, mixed populations containing both of the above-mentioned species were estimated at up to 220 individuals/m^2 (Cals and Emig 1979). At higher latitudes (Kunsan, South Korea; 36°N), Park et al. (2004) found an average annual density of *Lingula anatina* of 277 individuals/m^2, with a range from 27–687 individuals/m^2.

Compared to estimates from Worcester (1969) and Emig (1981), *L. reevii* populations have declined steeply from their previous abundance in the southern regions of Kaneohe Bay (Table 1). Potential reasons for this decline may include collection for scientific purposes (200–500 individuals removed on at least five different occasions; personal observation, C.L.H.), decreased sediment deposition, or lower particulate organic food supply following the diversion of the sewage discharge in 1978–1979 as suggested by Emig (1981). Raut et al. (2005) found an almost complete loss of *Lingula* sp. off the east coast of India over a 40-year period, attributable to either natural or anthropogenic factors.

There was no correlation between *L. reevii* density and sand depth among the survey sites. Dominant grain sizes of sediment collected within the range of habitats in which *L. reevii* were observed in Kaneohe Bay were fine sands, ranging from 125–250 µm in the present study. Emig (1981) reported that maximal abundance of *L. reevii* occurred in areas where over 80% of the sediment grain size was between 132 and 290 µm, suggesting that there has been only a small, if any, change in sediment size characteristics in the intervening 25-year sampling interval at these sites. For the temperate *Lingula anatina,* populations in intertidal flats in Korea occurred within a similar range of sediment grain size (Park et al. 2004).

In addition to the decrease in sewage-based nutrient subsidy to Kaneohe Bay in the late 1970s, much of the preferred habitat for *L. reevii* has been more recently invaded by mat-forming alien seaweeds (Rodgers and Cox 1999; Woo 2000; Smith et al. 2002, 2004). It is unknown if this change in habitat structure (i.e., physical overgrowth, swaying of seaweeds with water motion) deters the extension of the feeding lophophore by *L. reevii*, but this may be

a second contributing factor to the continuing decline in population numbers and may provide an area for future investigation.

The currently low and declining population size of *Lingula reevii* in Hawaii suggests that protective efforts are warranted. These might include restoration of reef flat habitats by removal of invasive algae and/or undertaking efforts for in situ or ex situ nursery facilities to enhance reproductive capabilities of this species.

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