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Natural History Observations of Hawaiian Garden Eels, *Gorgasia hawaiiensis* (Congridae: Heterocongrinae), from the Island of Hawai‘i[1]

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Abstract: Garden eels occur worldwide in the tropics, but little is known about their biology and ecology. We studied Hawaiian garden eel (*Gorgasia hawaiiensis*) colonies near Kawaihae, Hawai‘i, to investigate multiple aspects of basic biology of this species. Colonies of *G. hawaiiensis* occurred at depths from 16 to 36 m in soft-bottom habitat adjacent to rocky reefs. Highest burrow densities (up to 40 eels m^{-2}) were in shallower water, and large (~10 mm diameter) burrows were more abundant, less dense, and commonly found in pairs in deeper water. Eels emerged around sunrise and withdrew and covered burrow entrances around sunset. Age was estimated from annual rings in sectioned otoliths ($n = 17$) and modeled to suggest fast growth to a maximum size of ~600 mm total length and a maximum age of 6 yr. Prey size and eel anatomy suggest that these fish feed by ingesting planktonic prey and processing them in the esophagus. The most common food items were small (<0.5 mm) demersal harpacticoid, cyclopoid, and calanoid copepods and unidentified fish eggs. These and other observations indicate that *G. hawaiiensis* is abundant, has a high population turnover rate, and may enrich sandy-bottom habitat within their beds by facilitating energy flow from the water column to the benthos.

Garden eels are anguilliform fishes that are often found in large colonies inhabiting soft-bottom habitats adjacent to tropical reefs. Currently there are two genera, *Heteroconger* and *Gorgasia*, with at least 28 species described from the subfamily Heterocongrinae of the congrid eel family Congridae (Smith 1989, Castle and Randall 1999, Miller et al. 2011). The genus *Gorgasia* is thought to be the more primitive of the two genera (Castle and Randall 1999), with the species *Gorgasia hawaiiensis* Randall & Chess, 1979 (Figure 1), being the only known species of garden eel from the Hawaiian Islands.

The majority of ecological knowledge available on garden eels has resulted from behavioral observations in tropical waters, where they form colonies in sandy habitat (Bohlke 1957, Herald 1970, Bohlke and Randall 1981). Garden eels inhabit individual burrows that they retreat into when disturbed. They are usually observed partially extended from burrows while swaying in the water column near the benthos, where they pick planktonic prey items (e.g., copepods, pteropods, shrimp larvae, etc.) from the passing currents (Randall and Chess 1979, Smith 1989, Vigliola et al. 1996). They seldom leave their burrows entirely and are usually only active during the daytime (Beebe 1938). One recent study, by Kakizaki et al. (2015), witnessed the spawning of *Gorgasia preclara* and

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Figure 1. Hawaiian garden eels, *Gorgasia hawaiiensis*, at Puakō Reef, Hawai'i. (Photo: Kelly Boyle.)

Heteroconger hassi in an aquarium during low light at night.

Nothing is known about the age and growth of the Heterocongrinae in general or the genus *Gorgasia*, specifically. Age and growth rates have been estimated from otolith sections of *Conger oceanicus* (Hood et al. 1988, Fahay 1993), vertebrae and otolith sections of *Conger conger* (O'Sullivan et al. 2003), and from otolith sections and tag recaptures of *Anguilla anguilla* (Moriarty and Steinmetz 1979, Deelder 1981, Moriarty 1983) and *Anguilla rostrata* (Ogden 1970, Helfman et al. 1984*a*,*b*), but these eel species all have ecology and life histories that differ from those of garden eels.

Gorgasia hawaiiensis was first described from collections off the island of Hawai'i, south of Puakō, on the Kona coast (Randall and Chess 1979). From anecdotal observations *G. hawaiiensis* appears to be abundant in semiprotected, soft-bottom habitats along the west coast of the island of Hawai'i. It has been reported from at least four other Hawaiian islands (Maui, Moloka'i, O'ahu, and Midway) and is endemic to the Hawaiian archipelago (Randall and Chess 1979) (Figure 2). *Gorgasia hawaiiensis* is found on sand bottoms as shallow as 14 m [Kealakakua Bay, Hawai'i (T. Hobson, National Marine Fisheries Service, pers. comm.)] and as deep as 60 m [Diamond Head, O'ahu (C. Kelley, Hawai'i Undersea Research Laboratory, pers. comm.)].

The goal of the current study was to expand upon current ecological knowledge of *G. hawaiiensis* using scuba survey observations and collections at three sites on the northwestern shore of the island of Hawai'i. Specifically, we studied eel size, burrow size, and burrow dispersion and density as a function of depth, site fidelity, age and growth, co-occurring organisms, behavior, and feeding habits and morphology.

MATERIALS AND METHODS

Survey Sites

Three sites (at two locations) on the west side of the island of Hawai'i were chosen for surveys due to the previously documented occurrence of garden eels and easy access by small boat (Figure 2). Two of the three sites were located approximately 1 km north of Kawaihae and approximately 100 m offshore of Crystal Cove (19.971°N, 155.847°W). We hereafter refer to these two sites as Crystal Cove and South Crystal Cove. Our third study site was located farther south in Puakō Bay (20.053°N, 155.847°W). The Crystal Cove sites are approximately 35 m apart and divided by a volcanic/coral ridge extending westward from shore, 2–5 m above the bottom and 5–10 m wide. Surveys were conducted within 100 m north and south of the ridge. The Puakō Reef study site was located approximately 500 m westward from shore. All surveys and observations were made between January and May in 1988 and 1995. The time, current speed and direction, visibility underwater, and eel activity levels were noted during each dive.

Spatial Patterns and Burrow Size

At Crystal Cove and Puakō Reef, one 30 m transect was laid out along isobaths ($n = 3$), and 2 m^2 quadrats were placed at random along each transect. Transects were stratified by depth from the upper edge of each colony to a depth of 27 m (i.e., 21, 24, and 27 m water depth). All burrows inside the quadrats were counted, and all burrow diameters were measured to the nearest millimeter. Other organ-

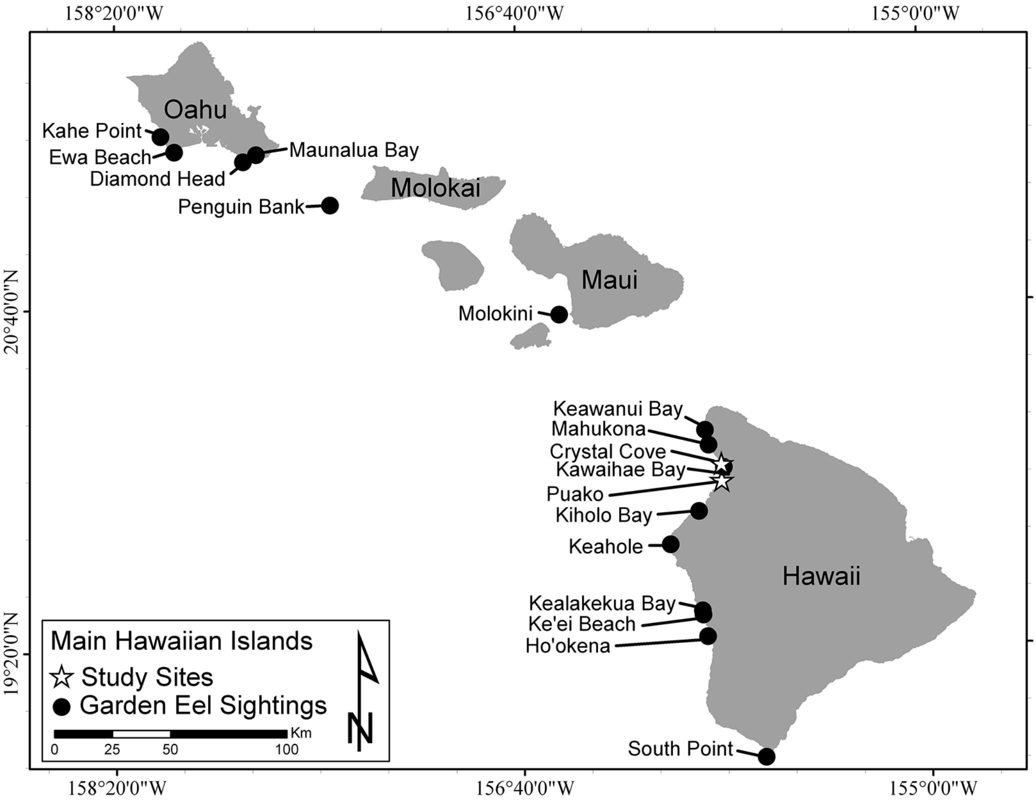

FIGURE 2. Sites in the Hawaiian Islands where garden eel, *Gorgasia hawaiiensis*, colonies were observed in this study, noted in the literature, or noted through personal communications (see text). The sites surveyed on the island of Hawai'i in this study were located at Crystal Cove and Puakō near Kawaihae.

isms within the quadrats were noted and collected, if possible. Logistical constraints and bottom time resulted in an unequal number of quadrats sampled per transect ($n = 4$–12). Therefore, for analyses, it was assumed that burrow diameters within a quadrat were independent (i.e., each burrow was used as a replicate). Only burrow diameters were surveyed at South Crystal Cove. Along each isobath ($n = 3$), 30 m transects were laid, random numbers were located along the tape, and the diameter of the closest burrow was measured to the nearest millimeter. Transects were stratified by depth from the upper edge of the colony to 30 m (i.e., 26, 27, and 30 m). Based on collections, garden eel burrows were easily distinguished from burrows created by other organisms due to a slightly raised lip, no surrounding mound or feces, and often a 20–50 mm radius halo of benthic diatoms (identified from samples collected and viewed under a microscope). Deeper dives (to 40 m) were made at all three sites to determine the lower depth limit of occurrence.

Recent observations of reproductive behavior suggest that females mate directly with males whose burrows are close in proximity rather than spawning generally into the water column (Kakizaki et al. 2015). Although difficulties visually sexing living eels made it impossible to discriminate between males and females, the proximity of eels to each other, which may be related to pairing, was also mapped at Crystal Cove. Three randomly selected 9 m^2 plots were located at 23 m depth. The coordinates of each burrow >5 mm diameter were measured to the nearest centimeter and the distance to the nearest burrow was calculated.

Our initial intent was also to examine the relationship between eel total length and burrow diameter, and use burrow diameter as a proxy for length. However, measuring burrow diameter and collecting an eel from the same burrow proved difficult given the limited time available at working depths and the eel's wary nature. To collect specimens, rotenone was injected into water glasses and inverted over burrows. Total eel length was measured from the tip of the mouth to the end of the tail and diameter measured using calipers. The limited data ($n = 3$) were tabulated to provide preliminary information on burrow size, total length, and body diameter.

Burrow fidelity of eels inhabiting larger burrows (>6 mm diameter) was measured over a 14-day period at Crystal Cove by installing permanent stakes as reference points. Coordinates at permanent stakes of 11 burrows were recorded and rechecked after 7 and 14 days to see if burrows were in the same place and had occupants.

Diel Patterns and Behavior

To evaluate diel patterns of activity, one dive was made to 25 m every hour for 24 hr at Crystal Cove from 15 to 16 April 1988. To avoid disturbance at night, divers used lines to guide themselves to the site and turned lights on upon reaching the seafloor. Upon reaching the bottom, divers recorded whether eels were extended from burrows and actively feeding or withdrawn into burrows.

Age and Growth

Garden eels were collected for the age and growth portion of this study during February ($n = 11$), April ($n = 3$), and May ($n = 13$) 1988. Some fish were preserved initially in 50% isopropyl alcohol for 2 months and others frozen. Otoliths were removed and cleaned before age determination, and the longest (anterior–posterior) axis of each otolith was measured. Despite the relatively narrow annual temperature range at our sites, annual rings have been validated in tropical fishes previously (Fowler 2009) and were therefore used for age determination. Eel total length was plotted against otolith length, and regression analysis was used to determine if otoliths increased in size as the length of the fish increased.

Determination of age was first attempted on whole otoliths after rehydrating for 24–48 hr; however, preservation in isopropyl alcohol made the surface of otoliths of some specimens chalky and unreadable. Therefore, to obtain clear growth zones, one otolith from each fish was sectioned in the sagittal plane and used for subsequent age estimates. Sectioned otoliths ($n = 17$) were mounted on glass microslides with histoclad mounting medium and ground until annual rings could be detected and counted. In the case of several of the smallest fish, numerous fine increments could also be seen in the finely ground otoliths, which could have been daily in origin. However, due to the small sample size, no attempt was made to count these fine increments under higher magnification.

Otoliths were read by two independent readers. In all cases, there was agreement within a year; thus, no average percentage errors were calculated. Data on total length and estimated age were fit with the Von Bertalanffy growth equation using the nls function in R (R Core Team 2016). We used least squares fitting techniques to solve for the parameters of the Von Bertalanffy growth equation,

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \qquad (1)$$

where L_∞ is the predicted asymptotic length, K is the rate at which asymptotic length is achieved, and t_0 is the age at length = 0. We developed the model two ways: one solving for all three parameters (L_∞, K, and t_0) and the other solving only for L_∞ and K, and setting t_0 to zero (Moreau 1987, Cailliet et al. 2006).

Feeding Habits and Internal Morphology

Feeding habits were analyzed from gut contents ($n = 7$) and internal morphology of eels captured at midday during the 24 hr observations from 15 to 16 April 1988 at Crystal Cove. Eels were captured after observations of diel patterns and behavior were made to minimize any possible effect that the disturbance could have on eels in the surrounding area. Eels were injected with formalin within 30 min of capture. Gut contents were sorted into general taxonomic categories and individual items counted. To assess whether sufficient gut samples were used, we plotted the cumulative mean number of prey taxa (± standard deviation) versus the number of guts analyzed (the procedure was repeated six times with a different random order of samples each time), and we noted where this curve leveled and its standard deviation narrowed and became relatively constant (Ferry and Cailliet 1996).

To estimate food availability during this period, divers pushed a 10-cm-diameter, 20-micron-mesh plankton net 70 m over the eel colony at 0.5 m above the bottom. One sample was collected every hour over 12 hr (0700–1900 hours), preserved in 10% formalin, and sorted and counted to the same taxonomic level as the eel gut contents. To assess whether sufficient plankton samples were taken, the cumulative mean number of zooplankton taxa (± standard deviation) was plotted versus the number of tows analyzed (the procedure was repeated six times with a different random order of samples each time) and we qualitatively noted where this curve leveled and its standard deviation narrowed and became relatively constant (Ferry and Cailliet 1996).

To compare the taxonomic composition of prey and potentially available zooplankton, we used the Percent Similarity Index (PSI) and nonparametric rank correlation coefficients of pooled data sets (Cailliet and Barry 1978). In addition, a selectivity analysis was used to assess whether any prey items were consumed disproportionately to their availability in the water column. Manly's measure of preference, α, was calculated for all prey types present in the gut contents (Chesson 1983).

To complement behavioral information about feeding habits, the morphology of the head, mouth, esophagus, and alimentary tract were described. This included measurements of the gape (length of upper lip) and cleft (width of mouth) as a percentage of the head length (HL) for specimens described in Randall and Chess (1979). In addition, a complete internal dissection was performed on one garden eel, and its visceral morphology (guts, gonads, and swim bladder) was described and measured.

RESULTS

Spatial Patterns and Burrow Size

Mean burrow densities in the colonies ranged from approximately 3 to 40 burrows m^{-2}. At Crystal Cove, isolated burrows occurred among coral rubble as shallow as 16 m but were not abundant until 21 m. Burrow densities decreased dramatically in deeper (>21 m) water, and only a few isolated burrows occurred below 32 m. At South Crystal Cove, the upper edge of the colony ended at a sand/rock interface at 24 m, and, again, only isolated burrows occurred below 32 m. The eel colony at Puakō Reef did not extend above 21 m or below 37 m, even though sandy substrate was available.

Burrow diameters ranged from 2 to 14 mm, and total lengths of all eels captured ranged between 282 and 686 mm ($n = 26$) with body depth and widths from 5.0 to 11.0 mm and 3.8 to 6.8 mm, respectively. From the burrow size frequency distributions for all three sites, larger burrows generally occurred in deeper water, especially at the South Crystal Cove site (Figure 3), and smaller burrows occurred over all depths. Smaller burrows were most common in shallow water and, although not sampled, were also common around the edges of the colonies at the lower depth limit as well as at sand/rock interfaces.

Results from burrow mapping suggest that larger burrows commonly appear to occur in pairs. Fifty-three burrows >5 mm in diameter were mapped. Defining a pair as any two burrows closer to each other than either was to the next closest burrow, 34 of these burrows were in pairs (binomial test of hypothesis that pairing was not significantly different from random, $0.1 > P > .05$). The mean distance

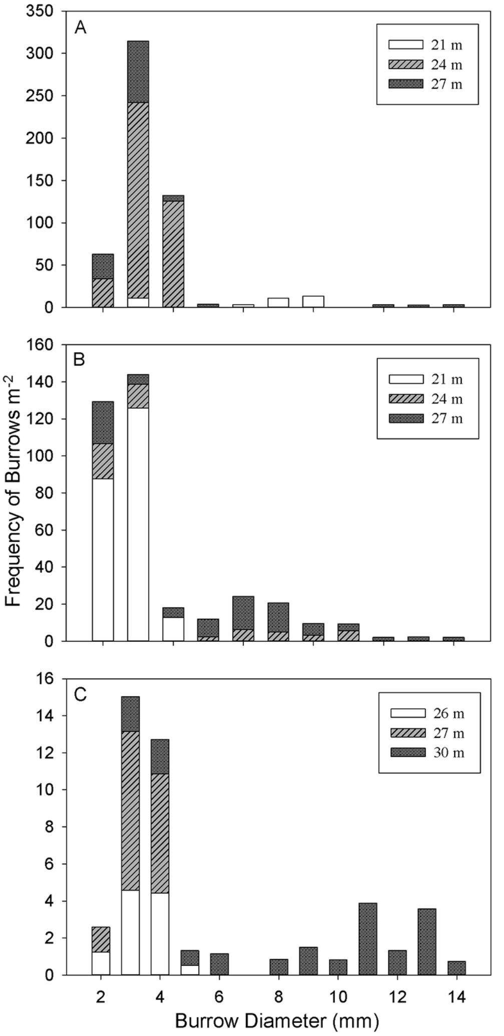

FIGURE 3. Frequency of burrow m^{-2} by size class at three water depths within each of three sites: *A*, Puakō Reef; *B*, Crystal Cove; *C*, South Crystal Cove.

between individuals in a pair was 29.4 cm ($n = 17$, SEM = ±1.7), between the individual in a pair and the nearest individual not in that pair was 73.1 cm ($n = 17$, SEM = ±4.4), and between unpaired individuals and the nearest eel was 53.8 cm ($n = 19$, SEM = ±4.5).

The three measurements of eel length and corresponding burrow diameter, as well as observations of eels extended from their burrows and burrow diameters after the eels retreated into their burrows, indicated that the diameters of the burrows reflected the sizes of the eels. A 282 TL garden eel with a body height of 5.0 mm and width of 3.8 mm had a burrow diameter of 5.0 mm. A 460 mm total length (TL) garden eel with a body height and width of 7.0 mm and 5.0 mm, respectively, had a burrow diameter of 7.0 mm. A third specimen had a TL of 530 mm, body height and width of 7.0 and 5.0 mm, respectively, and a burrow diameter of 7.0 mm. Therefore, burrows are not much wider than the bodies of the eels.

Of the 11 permanently marked burrows, only three disappeared after 14 days, and these did so at 7 days. In four cases, fanning over a burrow at night revealed a flap of mucous material covering burrow entrances. The top of the flap was covered with a thin layer of sand.

Diel Patterns and Behavior

All-day surveys (0800–1700 hours) at Crystal Cove from 15 to 16 April 1988 indicated eels were extended 10 to 30 cm out of their burrows, with their upper body and head bent forward while orienting into the current, until late afternoon, when their body orientations were more variable. If there was no current, heads were oriented in various directions. Eels made sweeping motions while extended, often nearly touching the substrate with their heads. There were no obvious associations between current velocity and amount of extension out of burrows. We could not get close enough to observe mouth movements that might indicate feeding. Observations using scuba revealed that *G. hawaiiensis* withdrew into and covered their burrows at dusk and emerged again at dawn.

Age and Growth

Whole otoliths were thick and oval, with a sulcus covering approximately half of the medial side. Otolith length (OL, mm) increased significantly and linearly with eel body size (TL, mm), following the equation: $OL = 0.77 + 0.002*TL$ ($r^2 = 0.83$, $n = 19$). Thus, otoliths provided necessary informa-

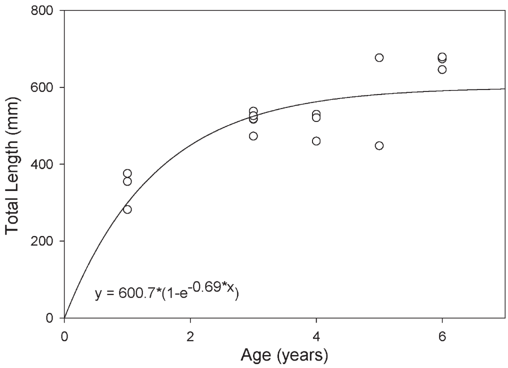

FIGURE 4. Von Bertalanffy growth curve constructed from total length and age (number of pairs of opaque and translucent growth increments) of 17 garden eels. The von Bertalanffy growth function was fit using nls in R. The t_0 value was set at 0.

tion on age and growth of these fish. Age estimates were possible for 17 otoliths, and ages ranged between 1 and 6 yr. The von Bertalanffy growth function (VBGF), fit to these limited data in two different ways, produced different results. In the first approach, when t_0 was allowed to vary, L_∞ was estimated to be 1,172 mm TL (SE = ±1,346; CV = 1.15), $K = 0.09$ (SE = ±0.18; CV = 2.015), and $t_0 = -2.95$ (SE = ±2.88; CV = 0.98). In the second approach, in which t_0 was set at 0, L_∞ was estimated to be 600 mm TL (SE = ±33; CV = 0.06) and $K = 0.69$ (SE = ±0.15; CV = 0.22). Although our three-parameter model produced slightly better fit [Akaike Information Criterion (AIC) = 192.2] than our two-parameter model (AIC = 196.1), the latter approach produced the most reasonable estimates of L_∞ (close to our maximum reported length of 686 mm) and K, and therefore the growth curve from this approach was plotted in Figure 4.

Feeding Habits and Internal Morphology

The plot of cumulative mean number of prey taxa versus the number of guts analyzed leveled off and its standard deviation decreased at approximately five guts. Our sample size of seven guts therefore appears sufficient to characterize the feeding habits of *G. hawaiiensis*. Likewise, the curve of cumulative mean number of zooplankton taxa for plankton tows leveled off and its standard deviation narrowed and became constant at approximately seven plankton tows. Thus, our 12 plankton tows were adequate to characterize available prey items.

The dominant prey items were small (0.2–0.4 mm) harpacticoid, cyclopoid, and calanoid copepods (Table 1). Fish eggs, gastropod larvae, radiolaria, and foraminifera made up the rest (~28%) of the diet. The plankton samples contained a wider variety of taxa than found in the stomachs but exhibited considerable overlap with a Percent Similarity Index of 70.3% and a correlation coefficient (r) of 0.84 (Table 1). Harpacticoid, cyclopoid, and calanoid copepods were abundant, along with fish eggs, in plankton tows, whereas radiolaria and foraminifera were present in small numbers. Gastropod larvae and eggs were eaten disproportionately to their abundance in zooplankton samples, suggesting selection of these items (Manly's $\alpha = 0.59$ and 0.22, respectively). Two prey types (cyprid and "other" larvae) were not found in the guts but were relatively abundant and common in the zooplankton samples.

Analysis of feeding morphology suggests interesting adaptations for a planktivorous lifestyle (Figure 5). Both the gape (length of upper lip) and cleft (width of mouth) were small, relative to fish size, ranging from 25.9% to 29.5% of the head length (HL) and 10.6% to 18.0% HL, respectively [$n = 8$, from Randall and Chess (1979)]. This is partly because the head length measurement included a relatively long distance from the tip of the snout to the opercular opening, which lies just in front of the pectoral fins.

The gill rakers of the 686 mm (TL) specimen that was analyzed were quite small and stubby, suggesting little prey size selection or filtering. The esophagus was 85 mm long (12% TL), with 55 mm of its surface having small, triangular, downward-facing papillae, often called rugae (Cailliet et al. 1986), which suggest the retention and processing of small, zooplanktonic prey. The stomach (30 mm) and intestine (195 mm) were relatively long (33% TL), indicating a long and efficient

TABLE 1

Summary of Garden Eel Feeding Habits from Gut Content Analysis ($n = 7$)

	Gut Contents		Zooplankton Samples		
Prey Item	Mean % N (±SEM)	% FO	Mean % N (±SEM)	% FO	Manly's α
Harpacticoid and cyclopoid copepods	56 (±12.1)	100	45 (±3.2)	100	0.10
Eggs	21 (±13.1)	71	8 (±2.4)	75	0.22
Calanoid copepods	16 (±6.6)	71	18 (±2.8)	100	0.07
Gastropod larvae	7 (±4.2)	57	1 (±0.7)	17	0.59
Cyprid larvae	0	0	21 (±2.3)	100	0.00
Radiolarians and foraminifera	0.3 (±0.5)	14	3 (±1.3)	42	0.01
Bivalve larvae	0	0	0.3 (±0.3)	8	0.00
Other	0	0	4 (±1.0)	58	0.00
PSI = 70.3%					
$r = 0.84^{**}$					

Note: Potential prey availability from epibenthic zooplankton samples ($n = 12$). Values are mean percentage number (mean % N; ±standard error in parentheses), percentage frequency of occurrence (% FO), and Manly's α. The Percent Similarity Index (PSI) and correlation coefficient (r, with ** indicating statistical significance at the .001 level) between the taxa in guts and zooplankton samples are listed at the bottom.

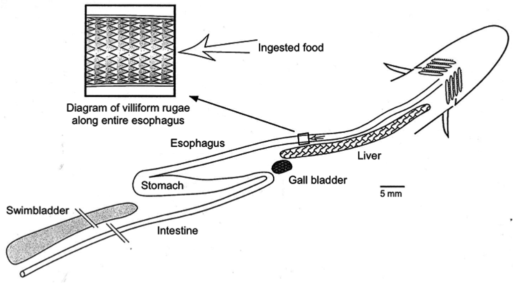

FIGURE 5. Diagram of the intestinal tract and its location in *Gorgasia hawaiiensis*, showing details of the triangular, villiform, posteriad rugae found in the esophagus and presumably used to retain and process prey items. Also shown are parts of the liver, the gall bladder, and the swim bladder, which starts right behind the stomach and continues to the end of the intestine.

digestive process. Together, the alimentary tract composed 45% TL.

Co-Occurring Organisms

Fishes commonly co-occurring with eels in their colonies included the razorfishes (family Labridae: *Hemipteronotus niger* and *H. niveilatus*), the lizard fish (family Synodontidae: *Synodus variegatus*), and the wormfish (family Microdesmidae: *Gunnellichthys curiosus*). Other associated fish species included the ophichthiid *Apterichtus flavicaudus*, and ulua (jacks in the family Carangidae) were also occasionally observed swimming over the colonies.

Burrowing helmet snails (*Cassis cornuta*) and auger snails (*Terebra maculata*) frequently co-occurred with garden eels at Crystal and South Crystal Coves. Other infaunal organisms producing large burrows and mounds could not be excavated. Benthic diatoms and small, filamentous red algae were common around the mouths of eel burrows. Predation on garden eels was observed once when a hogfish (family Labridae: *Bodianus bilunulatus*) swam quickly into an eel colony from a rocky outcrop and preyed upon a protruding eel before it could retreat to its burrow.

DISCUSSION

Our study provides important insights into the natural history of the Hawaiian garden eel, *G. hawaiiensis*. By coupling observations on spatial distribution with diet and life history data we are able to further understanding of the role of garden eels in marine ecosystems. Results suggest that *G. hawaiiensis* is a fast-growing species with unique adaptations enabling persistence in sandy bottom habitats.

Spatial Patterns and Burrow Size

Distinct distribution patterns with depth occur, but it is uncertain what causes them. The shallow limits are perhaps set by substrate availability and water motion. Garden eels have been found only on sand and can perhaps experience burrow disturbance in shallow water. Similarly, it is unclear what factors may limit the lower depth distribution at our sites. *Gorgasia hawaiiensis* has been found much deeper (>30 m) at Penguin Bank (C. Courtney, pers. comm.).

Some of the within-bed depth-related patterns (i.e., smaller burrows in shallow water, deeper burrows in deeper water and often in pairs) documented in this study may be due to behavioral interactions. Other studies on garden eels have documented agonistic and territorial behaviors between eels from different burrows (Fricke 1970, Robison and Lancraft 1984). Smaller burrows occurred more commonly and were denser in shallow water and at the edges of colonies, perhaps reflecting displacement from preferable sites by larger or older individuals. Larger burrows were found deeper and in pairs. Due to potentially decreased disturbances, deeper areas may be preferable for more permanent burrow establishment.

The burrow diameters of our study (2–14 mm) were more widely varied than those reported by Randall and Chess (1979). Individual burrows appear to conform generally to the sizes and shapes of the eels that occupy them. Tyler and Smith (1992) found garden eel burrows to be approximately 2 mm wider than the greatest body depth of the eel, excluding the fins. Fricke (1970) indicated that burrow diameters were correlated with length but provided no data. Our field observations and limited sampling of eel size and corresponding burrow diameter seem to support these findings; however, *G. hawaiiensis* seems to fit more tightly in its burrows. The size composition of *G. hawaiiensis* appears to be similar to that of other species in this genus. The original description of *G. hawaiiensis* (Randall and Chess 1979) included eels ranging from 333 to 553 mm TL. Our samples increase the maximum size to 686 mm TL.

Without being able to tag and recapture individuals, it was impossible to ascertain the permanency of burrows. However, our 14-day study of marked burrows and 24-hr observations suggest that burrow fidelity is high. Fricke (1969) tagged burrows of *G. sillneri* and did not find evidence of movement, with most changes in burrow location due to young eels coming into the area or mating activity. This is further supported by our diel observations, which indicate that although eel behavior may change in a 24-hr period, garden eels seldom or never leave their burrows and retreat into them at night. *Gorgasia hawaiiensis* was found to cover burrow entrances with a protective flap, possibly produced by specialized secretory cells such as those found in *G. sillneri* (Fishelson 1996).

Qualitative information collected on burrow spacing and dispersion (i.e., burrow mapping) indicates that larger burrows are generally separated widely or occur in pairs. It is possible that these paired burrows represent male/female mating pairs as found in studies on other species of garden eels (Fricke 1969, Tyler and Smith 1992, Kakizaki et al. 2015). Herald (1970) found that *Taenioconger digueti* was spaced 1–2 ft (30–60 cm) apart. That same study found that the male-female paired burrows were between 6.1 and 20 cm apart, whereas the male-male distance was between 86 and 140 cm. The minimum distance between *G. hawaiiensis* burrows was reported as 5.5 cm (Randall and Chess 1979), a value that overlaps with our data.

Density estimates from our study (~2.4 to 38.7 eels m^{-2}) generally exceed those reported for this and other species of garden eels. Randall and Chess (1979) estimated the density of *G. hawaiiensis* to be ~0.92 eels m^{-2}. Density estimates of other species of garden eels ranged from 1 to 15 eels m^{-2} (Fricke 1969, 1970, Clark 1971, Clark et al. 1990, Robison and Lancraft 1984). Most of these studies sampled only in one area of the colonies. Our depth-stratified sampling indicates that density within a bed is largely dependent on depth and position (e.g., edge versus center).

Analysis of size structure suggests that individual eel size varied with depth and position within colonies. The beds at Crystal Cove and Puakō Bay were continuous along the shore for at least 100 m. Qualitative observations indicated bed length perpendicular to shore (shallow to deeper limits) varied with location and slope. These attributes, plus within-bed variation in density, make it impossible to calculate colony size without more extensive sampling.

Age and Growth

We estimate that *G. hawaiiensis* lives at least 6 yr. However, our estimates of age must be considered preliminary, even though the growth increments were quite discernible and counts repeatable. Age verification or validation has been possible in only a few growth studies of eels. In one such study, Hood et al. (1988) used marginal increment analysis and back-calculations to estimate ~13 yr classes for *Conger oceanicus*. In our case, the only corroborative information was in burrow diameters (as a proxy for eel size). With all depths and sites combined, three modes were apparent (see Figure 3), which generally agrees with the age classes we would expect from our size at age information.

The growth parameters resulting from the two approaches used to fit the von Bertalanffy growth function (i.e., t_0 allowed to vary versus t_0 anchored at 0) were quite different, but one appears to provide more reasonable growth coefficients. In the case in which t_0 was allowed to vary, the resulting L_∞ was almost twice that of the largest observed individual and was thus deemed to be unreliable. The t_0 value was very low, indicating either a poor fit or a very prolonged leptocephalus stage, resulting in ambiguous growth zones in the center of the otoliths. The growth coefficient ($K = 0.09$) was low but reasonable. In the case in which t_0 was anchored at 0, the L_∞ (600 mm TL) is closer to the known maximum size of 686 mm (this study), and the growth coefficient high ($K = 0.69$), indicating that *G. hawaiiensis* is fast growing, with maximum size reached within ~4 yr. The only verified leptocephalus larva of *G. hawaiiensis* was 47 mm and appeared to be close to its maximum length (P. Castle, pers. comm.). This coincides with the length at 0–1 yr of age on the growth curve in Figure 3. Insufficient sampling in the yr 0 and 6+ age classes limits the estimation of our growth curves. For this and other reasons, we believe the second approach is more reasonable but that more age and growth work needs to be done.

Our K value ($K = 0.69$) appears to be reasonable. From a survey of 175 fish stocks, Pauly (1980) reported a geometric mean K of 0.33; 44 of these stocks had K values larger than the 0.6. Further analysis of his data indicates that elongate, tropical forms had considerably higher K values. Most studies of eel growth are from distantly-related species, such as *Anguilla* spp. (Ogden 1970, Moriarty and Steinmetz 1979, Deelder 1981, Moriarty 1983, Helfman et al. 1984*a*,*b*) and *Conger oceanicus* (Hood et al. 1988, Fahay 1993), and do not provide K values, so it is difficult to compare growth parameters.

Feeding Habits and Internal Morphology

Our results on the zooplanktivorous feeding habits of *G. hawaiiensis* are similar to those for other species of garden eels. Many authors have indicated that garden eels face into the current to feed (Fricke 1970, Clark 1971, 1974) and use their eyes and small mouths to feed on plankton (Rosenblatt 1967, Smith 1989, De Shepper et al. 2007). Randall and Chess (1979) found *G. hawaiiensis* stomachs to contain calanoid, cyclopoid, and harpacticoid copepods; eggs; amphipods; radiolarians; ostracods; pteropods; euphausiids; mysids; and tanaids. Likewise, other studies (Beebe 1938, Herald 1970) found small zooplankton in garden eel guts and sometimes both in their guts and in adjacent plankton samples (Robison and Lancraft 1984). Our study also found that *G. hawaiiensis* stomach contents contained considerable overlap with plankton samples. These results suggest that *G. hawaiiensis* is not especially selective, except for some taxa, such as gastropod larvae and eggs.

The alimentary morphology of this eel suggests that particles ingested are retained and processed by the posteriad rugae in the esophagus. In addition, as proposed by Smith (1989) in his discussion of the relationship between the stomach and intestine, the buccal cavity appears to be expandable, thus adapted for receiving a large influx of water (containing prey items), and the pharyngeal grooves appear to be useful in creating suction.

Behavioral Observations and Co-Occuring Species

Hawaiian garden eels were found with similar macroinvertebrates and fishes everywhere they were observed, likely due to similar habits and habitat requirements. However, no obvious interactions were observed between eels and other members of this sand-bottom community. Clark (1971, 1974) noted that *G. sillneri* in the Red Sea co-occurred with the sand diver *Trichonotus nikii*, the razorfishes *Hemipteronotus niger* and *H. pavo*, and the wormfish (family Microdesmidae) *Gunnellichthys monostigma*. Likewise, Hawaiian garden eels co-occurred with razorfishes and a wormfish. All of these fishes are capable of plunging into the sand like an arrow, staying close to the surface. The ophichthid, lizard fish, and ulua have not been previously observed near garden eel colonies. Ophichthids burrow in the sediment (McCosker 2002), but the lizard fish is epibenthic. The ulua may only have been attracted by sediment disturbance from diving activity.

Diatom rings suggest that eels may cause local nutrient enrichment and perhaps stabilization of the substrate around their burrows. It is possible that organic matter contributed by the eels to the surrounding sediment through feces and other excretions has a fertilizing effect on the diatoms, much in the way that planktivorous damselfishes (*Chromis* spp.) contribute to the productivity of both temperate and tropical reef systems (Bray et al. 1981, Geesey et al. 1984, Bray et al. 1988).

Because of their burrow habitats and nocturnal inactivity, garden eels appear to be relatively secure from predation. They do not appear to leave their burrows except possibly to spawn, though Kakizaki et al. (2015) recently found that *Gorgasia preclara* and *Heteroconger hassi* did not leave burrows to spawn in an aquarium. Large predators cannot easily approach burrowing animals, which can quickly retreat into their burrow (Smith 1989). Large stingrays have been reported to feed on them (Clark 1971), and in the Gulf of California, Herald (1970) suggested that *Dasyatis dipterurus* might be a predator on *Taenioconger digueti*. However, no gut content analyses support that claim. More information is necessary to fully understand the ecological role of garden eels in tropical food webs.

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Literature Cited

Beebe, W. 1938. Zaca venture. Harcourt, Brace, and Co., New York.

Bohlke, J. 1957. On the occurrence of garden eels in the western Atlantic, with a synopsis of the Heterocongrinae. Proc. Acad. Nat. Sci. Phila. 109:58–79.

Bohlke, J., and J. E. Randall. 1981. Four new garden eels (Congridae, Heterocongrinae) from the Pacific and Indian Oceans. Bull. Mar. Sci. 31:366–382.

Bray, R. N., A. C. Miller, and G. G. Geesey. 1981. The fish connection: A trophic link between planktonic and rocky reef communities. Science (Washington, D.C.) 214:204–205.

Bray, R. N., A. C. Miller, S. Johnson, P. R. Krause, D. L. Robertson, and A. M. Westcott. 1988. Ammonium excretion by macroinvertebrates and fishes on a subtidal rocky reef in southern California. Mar. Biol. (Berl.) 100:21–30.

Cailliet, G. M., and J. P. Barry. 1978. Comparison of food array overlap measures useful in fish feeding habit analysis. Pages 67–69 *in* S. Lipovsky and C. Simenstad, eds. Fish food habits studies. Proceedings of the 2nd Pacific Northwest Technical Workshop. Washington Sea Grant, Seattle.

Cailliet, G. M., M. S. Love, and A. W. Ebeling. 1986. Fishes: A field and laboratory manual on their structure, identification, and natural history. Wadsworth Publishing Company, Belmont, California.

Cailliet, G. M., W. D. Smith, H. F. Mollet, and K. J. Goldman. 2006. Age and growth studies of chondrichthyan fishes: The need for consistency in terminology, verification, validation, and growth function fitting. Environ. Biol. Fishes 77:211–228.

Castle, P. H. J., and J. E. Randall. 1999. Revision of Indo-Pacific garden eels (Congridae: Heterocongrinae), with descriptions of five new species. Indo-Pac. Fishes 30:1–52.

Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64:1297–1304.

Clark, E. 1971. The Red Sea garden eel. Bull. Am. Littoral Soc. 7:4–10.

———. 1974. Houdinis of the Red Sea. Int. Wildl. 4:13–17.

Clark, E., J. F. Pohle, and D. C. Shen. 1990. Ecology and population dynamics of garden eels at Râs Mohammed, Red Sea. Natl. Geogr. Res. 6:343–356.

Deelder, C. L. 1981. On the age and growth of cultured eels, *Anguilla anguilla* (Linnaeus, 1758). Aquaculture 26:13–22.

De Schepper, N., B. De Kegel, and D. Adriaens. 2007. Morphological specializations in Heterocongrinae (Anguilliformes: Congridae) related to burrowing and feeding. J. Morphol. 268:343–356.

Fahay, M. P. 1993. The early life history stages of New Jersey's saltwater fishes: Sources of information. Bull. N. J. Acad. Sci. 38:1–16.

Ferry, L. A., and G. M. Cailliet. 1996. Sample size and data analysis: Are we characterizing and comparing diet properly? Pages 70–81 *in* K. D. Shearer and D. D. MacKinlay, eds. Feeding ecology and nutrition in fishes. American Fisheries Society Symposium, San Francisco.

Fishelson, L. 1996. Skin morphology and cytology of marine eels adapted to different lifestyles. Anat. Rec. 246:15–29.

Fowler, A. J. 2009. Age in years from otoliths of adult tropical fish. Pages 55–92 *in* B. S. Green, B. D. Mapstone, G. Carlos, and G. A. Begg, eds. Tropical fish otoliths: Information for assessment, management and ecology. Springer Dordrecht, Heidelberg, London, New York.

Fricke, W. 1969. Biologie et comportement de *Gorgasia sillneri* (Klausewitz) et *Taenioconger hassi* (Klausewitz, Eibesfeldt) (Teleosteen). Zoology Ser. D. 269:1678–1680.

———. 1970. Erste funde junger Rohrenaale von *Gorgasia sillneri* (Klausewitz) und *Taenioconger hassi* (Klausewitz & Eibesfeldt) (Pisces: Apodes: Heterocongridae). Senckenb. Biol. 51:307–310.

Geesey, G. G., G. G. Alexander, R. N. Bray, and A. Miller. 1984. Fish fecal pellets are a source of minerals for inshore reef communities. Mar. Ecol. Prog. Ser. 15:19–25.

Helfman, G. S., E. L. Bozeman, and E. B. Brothers. 1984*a*. Size, age, and sex of American eels in a Georgia river. Trans. Am. Fish. Soc. 113:132–141.

———. 1984*b*. Comparison of American eel growth rates from tag returns and length-age analyses. Fish. Bull. 82:519–522.

Herald, E. S. 1970. The garden eels. Saltwat. Aquar. 6:203–206.

Hood, P. B., K. W. Able, and C. B. Grimes. 1988. Biology of the conger eel *Conger oceanicus* in the Mid-Atlantic Bight. I. Distribution, age, growth and reproduction. Mar. Biol. (Berl.) 98:587–596.

Kakizaki, T., K. Kobayashi, T. Nakatsubo, R. Wakiya, S. Watanabe, M. J. Miller, and K. Tsukamoto. 2015. Spawning behavior of garden eels, *Gorgasia preclara* and *Heteroconger hassi* (Heterocongrinae), observed in captivity. Mar. Freshwater Behav. Physiol. 48:359–373.

McCosker, J. E. 2002. Notes on Hawaiian snake eels (Pisces: Ophichthidae), with comments on *Ophichthus bonaparti*. Pac. Sci. 56:23–34.

Miller, M. J., S. Wouthuyzen, T. Ma, J. Aoyama, S. R. Suharti, and Y. Minegishi. 2011. Distribution, diversity, and abundance of garden eel larvae off West Sumatra, Indonesia. Zool. Stud. 50:177–191.

Moreau, J. 1987. Mathematical and biological expression of growth in fishes: Recent trends and further developments. Pages 81–113 *in* R. C. Summerfelt and G. E. Hall, eds. Age and growth of fish. Iowa State University Press, Ames.

Moriarty, C. 1983. Age determination and growth rate of eels, *Anguilla anguilla* (L.). J. Fish Biol. 23:257–264.

Moriarty, C., and B. Steinmetz. 1979. On age determination of eel. Rapports et Proces-verbaux des Réunions. J. Cons. Int. Explor. Mer. 174:70–74.

Ogden, J. C. 1970. Relative abundance, food habits, and age of the American eel, *Anguilla rostrata* (LeSueur) in certain New Jersey streams. T. Am. Fish Soc. 99:54–59.

O'Sullivan, S., C. Moriarty, R. D. FitzGerald, J. Davenport, and M. F. Mulcahy. 2003. Age, growth and reproductive status of the European conger eel, *Conger conger* (L.) in Irish coastal waters. Fish. Res. 64:55–69.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer. 39:175–192.

Randall, J. E., and J. R. Chess. 1979. A new species of garden eel (Congridae: Heterocongrinae) of the genus *Gorgasia* from Hawai'i. Pac. Sci. 33:17–23.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Robison, B. H., and T. M. Lancraft. 1984. *Gorgasia barnesi* (Congridae: Heterocongrinae), a new garden eel from the Banda Sea. Copeia 1984:404–409.

Rosenblatt, R. H. 1967. The osteology of the congrid eel *Gorgasia punctata* and the relationships of the Heterocongrinae. Pac. Sci. 21:91–97.

Smith, D. G. 1989. Family Congridae. Pages 460–558 *in* E. B. Bohlke, ed. Fishes of the western North Atlantic. No. I, Part 9, Vol. 1. Orders Anguilliformes and Saccopharyngiformes. Sears Foundation for Marine Research, New Haven, Connecticut.

Tyler, J. C., and C. L. Smith. 1992. Systematic significance of the burrow form of seven species of garden eels (Congridae: Heterocongrinae). Am. Mus. Novit. 3037:1–13.

Vigliola, L., R. Galzin, M. L. Harmelin-Vivien, F. Mazeas, and B. Salvat. 1996. Les Heterocongrinae (Teleostei: Congridae) de la pente externe de Moorea (Ile de la Societe, Polynesie Francaise): Distribution et biologie. [The Heterocongrinae (Teleostei: Congridae) of the outer slope of Moorea (Society Islands, French Polynesia): Distribution and biology.] [In French.] Cybium 20:379–393.