



Population biology of *Gnathophausia longispina* (Mysidacea: Lophogastrida) from a central North Pacific seamount

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Abstract. Large numbers of the lophogastrid mysid Gnathophausia longispina were discovered in 1984 over Southeast Hancock Seamount on the northern Hawaiian Ridge. Additional specimens were collected from the same area during subsequent surveys in 1985, 1987, and 1988 to obtain new information on the life history of this species. Estimates of growth suggest that G. longispina reaches sexual maturity by its second year. Young are brooded by the female for nearly a year and released in late winter-early spring. It is doubtful if G. longispina live longer than 2 yr or produce more than one brood. Most G. longispina are found within 100 m above the seamount summit. The modal progression of size classes over time indicates that this species is dependent on local processes rather than recruitment from other areas to maintain its populations at the seamount.

Introduction

Many mysid species are characterized by swarming or schooling behaviors which may make them locally very abundant (Mauchline 1980, 1986, Wittmann 1984). Such aggregated distributions have frequently been seen in continental shelf and slope regions and are often attributed to behaviors involved in reproduction, feeding, predator avoidance, or population maintenance within a restricted zone of occurrence (Clutter 1967, 1969, O'Brien 1988, Kaardvedt 1989). Unusual aggregations of some sound scatterers were noted during accoustic observations over a seamount on the northern Hawaiian Ridge in 1984 by the National Marine Fisheries Service, Honolulu Laboratory. Midwater trawls revealed the dominant species in the scattering layer to be the lophogastrid mysid Gnathophausia longispina and the sternoptychid fish Maurolicus muelleri (Boehlert 1988). Despite these collections. little is known about the biology and distribution of G. longispina. The genus Gnathophausia belongs to the suborder Lophogastrida and includes eight species (Mauchline 1980). Four species in the genus are cosmopolitan, one is found only in the Atlantic Ocean, and the others are restricted to the Pacific or Pacific and Indian Oceans. G. longispina is considered to have the most restricted geographical distribution in the Pacific, and has only been taken west of 157° W in the tropical and north temperate regions between $7^{\circ}36'$ S and $31^{\circ}40'$ N (Clarke 1962). It is probably the shallowest-dwelling species in the genus (Clarke 1962).

What little reported information exists on the life history of Gnathophausia longispina is based on a total of fewer than 200 specimens collected from several surveys between the late 1800's and mid-1900's (Clarke 1962, Mauchline 1980). Consequently, information on vertical distribution patterns, size at maturity, and other biological traits of G. longispina is nonexistent or based on only one or a few specimens (Clarke 1962). The present study provides biological information on G. longispina based on a large number of specimens taken over several years from a single seamount in the subtropical North Pacific.

Materials and methods

The study site was Southeast Hancock Seamount (29°48'N: 179°04'E) near the northern edge of the North Pacific central water mass and accompanying subtropical frontal zone (Roden 1984). The flat-topped summit of this seamount is about 2.4 km in diameter (4.5 km²) at a depth of ~260 m; it is the highest of several peaks collectively called Hancock Seamount (Brainard 1986). Bottom depths reach 5200 m approximately 22 km from the summit to produce an average slope along the flanks of 0.22 (Brainard 1986). Water temperatures generally are about 19 to 27°C at the surface. 13 to 15°C at the summit depth. and 4 to 6°C by 750 m depth.

Specimens of Gnathophausia longispina were collected at night during seven cruises of the NOAA ship "Townsend Cromwell" in 1984, 1985, 1987 and 1988. No G. longispina were collected during several daytime tows over the summit. All specimens in this study were collected with a 1.8 m Isaacs-Kidd midwater trawl (IKMT)

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with a 2.9 m² mouth opening. Mesh sizes for the net body and cod end varied among the early cruises: 10 and 0.333 mm (summer 1984), 3 and 3 mm (winter 1985, spring and summer 1987), and 3 and 0.505 mm (subsequent cruises), respectively. Net damage required the use of a replacement 5 mm-mesh net body during the last half of the winter 1988 cruise. All tows in 1984-1985 targeted the seamount-associated sound-scattering layer over the summit (Wilson and Boehlert 1990). Tows during spring 1987 were oblique to depths of 80 to 275 m. However, only two of these tows were deeper than 225 m in areas near the seamount where G. longispina were thought to occur, and thus may have under-sampled large specimens (see "Results"). Tows on subsequent cruises were either horizontal across the summit at nominal depths of 50, 100, 150, and 200 m, or oblique, generally to 250 m depth. The average ship speed during the IKMT tows was 1 to 2 m s⁻¹. Usually, IKMT tows were about 1 h long, although some shorter tows were made during the first three cruises. The volume of water filtered was determined with a calibrated General Oceanics flowmeter. The net depth profile was determined with a Benthos time-depth recorder during all IKMT tows except during the first two cruises, when net depth was estimated by the cosine of surface wire angle and meters of wire out.

Gnathophausia longtspina from all tows were immediately removed from the net and placed in about 4% buffered formaidehyde-scawater solution and later transferred to a 50% isopropanolfreshwater solution during subsequent processing in the laboratory. Specimens from summer 1984 and winter 1985 were only used to determine estimates of size-specific fecundity (i.e., brood size); specimens from later cruises were used to generate these and other biological results.

Carapace length (CL), from the eye to the posterior lateral edge of the carapace, was measured to the nearest 0.1 mm for random subsamples of at least 40 brooding females captured in the summers of 1984 (early July), 1987, and 1988 (late-August), fall 1988, winter 1985, and spring 1987 (only 3 specimens carrying young were caught in spring). For the 1987-1988 cruises, CL was determined for all Gnathophausia longispina from tows with fewer than about 75 specimens, or from a subsample $(n \ge 50 \text{ individuals})$ for larger catches. To facilitate comparisons with other studies. CL and total length (TL) from the hind margin of the eye orbit to the posterior edge of the uropods and telson excluding the setae (Mauchline 1980) were measured for 74 specimens to determine the functional relationship between the two variables. The least-squares regression equation is $TL = 2.09 CL + 3.54 (r^2 = 0.99)$. Measurements of G. longisping for the TL to CL sample and size-specific fecundity estimates were made with vernier calipers. Other CL measurements were made with a dissecting scope that was interfaced to a videodigitizing system (Optical Pattern Recognition System, Biosonics, Inc., Seattle, Washington).

Brooding females (n=181) were grouped into 0.5 mm CL size classes to estimate size-specific fecundity (i.e., brood size). Counts included Stage I "egg-like" embryos. Stage II "eyeless" embryos. and Stage III "eyed" embryos, as defined by Mauchline (1980). Within each size class, the female with the greatest number of young within the marsupium was considered the best estimate of that size-specific fecundity. Justification for this assumption was the presence of many loose embryos of G. longispina in our samples. indicating that the young were often released from the marsupium upon capture and sample fixation. Only 22% (n = 232) of the brooding females (marsupium fully developed) actually carried young. based on samples from a subset of seven representative tows. Other mysids have been reported to release their young upon capture (Clutter 1967, Childress and Price 1978, Mauchline 1980, Carleton and Hamner 1989). Thus, maximum fecundity within each size interval was regressed on size by using weights equal to the interval sample size.

The CL and stage of sexual maturity for specimens possessing secondary sexual characters were recorded from deep (maximum net depth. ≥ 225 m) and shallow (≤ 125 m) tows during the summers of 1987 and 1988 and all spring 1987 tows. Brooding remales were considered to comprise Mauchline's (1980) Categories e-g; namely, mature females with (1) fully developed marsupium not yet



Fig. 1. Gnathophausia longispina. Vertical nighttime distribution over Southeast Hancock Seamount: data pooled from summer 1987 and summer, winter, and fall 1988. Number of tows is shown at end of each bar

Table 1. Cruises to Southeast Hancock Seamount, total number of Gnathophausia longispina caught, and number of tows in which species was present (n)

Cruise	Dates	Total catch	Positive tows (n)
Summer 1984	07 July - 30 July		
Winter 1985	30 Jan. ~25 Feb.	831	12
Spring 1987	11 Apr28 Apr.	751	11
Summer 1987	08 Aug25 Aug.	1 173	18
Winter 1988	12 Jan 30 Jan.	861	7
Summer 1988	13 July -21 Aug.	4 203	18
Fall 1988	26 Oct08 Nov.	2 0 5 9	15

filled with young, (2) ovigerous, and (3) "empty" females. Although the latter two categories were reasonably distinct, the former was not [as Mauchline (1980) also reported], and may have resulted in the inclusion of a few immature specimens. Likewise, our classification of males as sexually mature, on the basis of elongation of the spine on the posterior lobe of the pleuron of the second abdominal segment (Clarke 1962), is probably not perfect for smaller specimens, but was considered useful in the absence of any histological data on reproductive stages.

Results

A total of 11 107 Gnathophausia longispina were taken in IKMT sampling over Southeast Hancock Seamount during the course of the study (Table 1). Tows were not suitably stratified to produce abundance estimates for G. longispina at the seamount, but did demonstrate their patchy distribution over the summit. For example, Lloyd's (1967) index of patchiness (L) was 3.8 based on oblique summit IKMT tows. Catches from all tows ranged from 0 to 784 individuals per 10^4 m³ of water filtered.

Catches of *Gnathophausia longispina* from horizontal tows were greatest below 100 m depth (i.e., within ~ 100 m above the summit; Fig. 1). A total of only four specimens in eight tows (two tows per cruise) were taken at the 50 m depth interval. Vertical distribution patterns were similar among cruises.

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Fig. 2. Gnathophausia longispina. Size composition, as a function of month, regardless of year of collection. During summer 1988, tows were made in mid-July and again in mid-August. August samples from 1987 and 1988, which were similar, were combined. Seven vertical lines indicate modal lengths of presumed instar stages (see "Results"). Number of brooding females (filled bars) within each size class is shown for April

The 3439 specimens of Gnathophausia longispina comprising the carapace length sample ranged from 3.7 (spring 1987) to 14.7 mm CL (male and female specimen, summer 1988). Length-frequency plots from each cruise were bimodal (Fig. 2). When plots were arranged by month without regard to year of collection, progression of the smaller mode to larger sizes was clearly apparent over time (Fig. 2). However, no similar increase was observed for the larger mode, which remained around 11.5 mm CL regardless of season.

When the bimodal length data from the summer of 1987 and 1988 cruises were combined and plotted as a function of depth, relatively greater numbers of small individuals were found at shallow depths (Kolmogorov-Smirnov test, P < 0.001; Fig. 3). Thus, the population



Fig. 3. Gnathophausia longispina. Size composition as a function of depth, for pooled data from summer of 1987 and 1988. Plots based on data from (a) tows <125 m depth (n = 128 individuals) and (b) oblique tows from surface to >225 m depth ($n \approx 1.045$ individuals). Number of brooding females within each size class is shown by filled bars



Fig. 4. Gnathophausia longispina. Maximum number of embryos in marsupium as function of carapace length. Fitted regression line was weighted by sample size (see "Results"); numbers above data points are sample sizes. •: Brood size of single specimen reported in Clarke (1962) (plotted for comparison only and not used in regression analysis)

size-composition of *Gnathophausia longispina* from the nominal 0 to 250 m depth comprised about equal numbers in the two dominant length modes of ~ 6.5 and 11.5 mm CL (Fig. 3 b), whereas relatively few large specimens occurred above 125 m depth (Fig. 3a). No trends in size with depth were observed during spring 1987 and winter and fall 1988 (data not shown). The sex ratio of those specimens from the summers of 1987 and 1988 with developed secondary sexual characteristics was 3.3 females: 1 male.

Among the 0.5 mm CL categories, the maximum number of brooding embryos increased with size of the ovigerous female and equaled 7 to 16 (Fig. 4). Size classes contained 6 to 57 brooding females. A simple linear relationship between maximum fecundity (F) and CL of the



Fig. 5. Gnathophausia longispina. Percent carrying Stage I, II, and III embryos from early summer (July 1984), late summer (August 1987 and 1988), fall (October-November 1988), and winter (January-February 1985). Only three females carrying embryos were captured during spring (April 1987); these are not included

brooding female was considered most descriptive. The fitted regression equation was $F = 1.928 \cdot CL - 11.784$ ($r^2 = 0.70$). The smallest *Gnathophausia longispina* actually brooding embryos was 10.1 mm CL (3 Stage I embryos, summer 1984), and the largest was 14.0 mm CL (16 Stage I embryos, summer 1987). The smallest male with a slightly elongated pleural spine on the second abdominal segment was 8.4 mm CL (spring 1987), although most specimens were at least 10 mm CL (mean CL = 11.2 mm, SD = 1.19, n = 136).

Development of Gnathophausia longispina embryos through Stages I-III takes about 7 to 9 mo. with parturition occurring in late winter-early spring. Embryos from ovigerous G. longispina were typically in the same developmental stage during any given season (Fig. 5). During early summer (July 1984), 90% of the females with young carried Stage I embryos. By late summer (August of 1987 and 1988), females with young carried either Stage I (54%) or Stage II (46%) embryos. By fall, 95% of the females with young carried Stage II embryos, and by winter (1985), 76% carried Stage III embryos. During spring (April 1987), only three females carried young: two at Stage III (11.5 and 12.9 mm CL) and one at Stage I (12.3 mm CL). Thus, most brooding females were carrving Stage I embryos in July and probably released young between February and April.

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The sizes of the Stage I or Stage III embryos did not appear to differ with the size of the brooding female. The mean diameter of Stage I embryos from a small (10.1 mm CL) brooding female was 2.4 mm (SD 0.07, n=3) and from a large (13.8 mm CL) brooding female was 2.3 mm (SD 0.14, n=11). Mean body length (from base of eyestalk) of Stage III embryos from three small (≤ 11.0 mm CL) brooding females was 7.8 mm (SD 0.81, n=7) and from the three large (≥ 12.9 mm CL) females was 7.9 (SD 0.85, n=15).

Discussion

A large population of Gnathophausia longispina is a persistent feature associated with Southeast Hancock Seamount. The occurrence of large numbers of G. longispina at different stages of development, during various seasons, and among different years (Table 1, Fig. 2) suggest that development of all growth stages regularly occurs at the seamount. The patchy distribution of G. longispina in our samples is probably related to aggregating behavior, which has been linked with population retention in other mysids (O'Brien 1988). Euphausiid patchiness is greater near shallow topography (L=5.0) than in the open ocean (L=2.6), but this is probably related to disruption of the normal pattern of distribution by current-topography interactions or predation (Genin et al. 1988).

Recruitment of Gnathophausia longispina to the seamount probably depends on local processes rather than immigration, as no other large aggregations of G. longispina have been reported along the southern Emperor-northern Hawaiian Ridge (SE-NHR). G. longisping were not taken during a survey we conducted over four other seamounts along the SE-NHR in 1988 (summer). Although G. longisping were reported farther south off the main Hawaiian Islands as early as the late 1800's (Clarke 1962), a recent study (Reid et al. 1991) around the islands found maximum catches of less than \sim 7 individuals per 10⁴ m³ of water filtered. Population maintenance of seamount-associated species such as G_{i} longisping probably relies on various physical and biological mechanisms, and their aggregating behaviour may play an important role, as in other mysids (Clutter 1969, O'Brien 1988, Kaartvedt 1989).

An analysis of the length-frequency histograms provides the first estimates of growth for *Gnathophausia longispina* over intermediate instar stages. The temporal progression of the smaller length mode in the size-frequency histograms among seasons suggests that modal lengths may represent successive instars and can thus provide estimates of growth over these stages (Fig. 2). Although a wide variation in molt factor and synchronized breeding could produce a similar temporal progression of modal length, the narrow size ranges observed within seasons suggest that modal lengths probably represent different instar stages. Similarly discrete size classes in *G. ingens* have been verified as different instar stages (Childress and Price 1978). Thus, we tentatively refer to each size class in the length distribution as representing a particular instar stage. Based on the vertical lines fitted by eye to the length data in Fig. 2 to identify modal positions of the various presumed instars, seven instar stages are probably represented in the data. The bimodal size-frequency data from July presumably represent three instar stages (Fig. 2). Assuming the percentage increase in CL with size to be roughly constant, the smaller length-frequency mode in July is about equally composed of two instars: a younger instar stage centered at a modal length of ~5.5 mm CL, and an older instar at ~6.5 mm CL.

Reduction in growth with the onset of sexual maturity is common in crustaceans (Somerton 1980), and probably occurs in Gnathophausia longispina. The length mode at 11.5 mm CL (Fig. 2) probably represents the instar stage at sexual maturity, and possibly a terminal molt, since it persists as the largest mode in the data and generally defines the length range of brooding females (Fig. 3). Non-brooding individuals composed nearly the entire 10.3 mm CL length mode, which preceded the 11.5 mm CL mode, and was present in April (Fig. 2). (Insufficient sampling effort below the 225 m depth interval during April probably resulted in the relatively small number of specimens within the 10.3 mm CL size class.) The size distribution of the fecundity sample (mean 11.8 mm CL; Fig. 4) was similar to the 11.5 mm CL modal size distribution in the length samples (Fig. 2); this also suggests that production of young occurs at the latter instar stage.

Growth of Gnathophausia longispina is estimated at about 0.015 mm CL d^{-1} (Table 2) when determined over the period beginning with the earliest instar stage (April, 4.5 mm CL modal length) and ending with the first appearance of the large temporally stationary mode centered at 11.5 mm CL (July: Fig. 2). Growth of sexually mature individuals (11.5 mm CL mode) either slows dramatically or ceases altogether (Fig. 2). Estimates of growth are similar when determined using the first (April) and last (July) instar stages, or those instars separated by shorter time intervals (Table 2).

As is common in many Crustacea (Mauchline 1977) including Gnathophausia ingens (Childress and Price 1978), molt increments for G. longispina – represented by the difference in modal length pairs of successive instars – decreased with an increase in size. Considering the seven length modes (Fig. 2), molt increment (expressed as a percentage of the previous instar CL) was 22% for April– July, 18% for July–August. 15% for August–October. 17% for October–January, 17% for January–April, and 12% for April, and the largest CL mode was in July. For G. ingens, molt increments similarly decreased from about 25% at the second free-living stage to 12% when sexual maturity was reached (Childress and Price 1978).

Although a positive relationship between the number of young in the marsupium and female size is common in shallow-dwelling mysid species, it is less apparent among meso- and bathypelagic species (Mauchline 1973, Wittmann 1984). However, Childress and Price (1983) found a strong relationship between embryo number and size of the brooding parent for *Gnathophausia ingens* when sufficient specimens had been collected. Based on a single brooding female taken near the Equator ($5^{\circ}54'N$; $162^{\circ}05'W$). Clarke (1962) suggested that the number of

Table 2. Gnathophausia longispina. Estimates of growth in carapace length (CL) based on analysis of length-frequency histograms in Fig. 2 (see "Results" for further details). "start" and "end" identify approximate collection dates of the two length samples used to estimate growth. At: number of days between start and end time midpoints: AL: difference between the two modal CLs associated with start and end times. Location of modal CLs of different presumed instar stages are indicated by seven vertical lines in Fig. 2. Entries below dashed line are growth estimates over shorter time intervals that suggest relatively constant growth over these instar stages

Time		Δt	∆L (mm)	Growth
start	end		(1111)	(mint d)
Apr.	July	457	11.5-4.5 7.0	0.015
Apr.	Apr.	365	10.3-4.5 5.8	0.016
Apr.	Jan.	274	8.8-4.5 4.3	0.016
Apr.	July*	92	> 5.5-4.5 1.0	>0.011
			<6.5-4.5 2.0	< 0.022
Aug.	Oct./Nov.	76	7.5-6.5 1.0	0.013
OctNov.	Jan.	77	8.8-7.5 1.3	0.017
Jan.	Apr.	91	10.3-8.8 1.5	0.016
Apr.	July	92	11.5-10.5 1.2	0.013

^a We assumed that the smaller length mode in July (Fig. 2) was composed of two modes (two instar stages) centered at 5.5 and 6.5 mm CL. Thus, *JL* between April and July was intermediate between 1 (5.4 minus 4.5) and 2 (6.5 minus 4.5) mm CL. Likewise, *JL* between July and August (not shown) was probably <1 (6.5 minus 5.5) mm CL, since roughly half of the smaller individuals were already ~6.5 mm CL in July

embryos carried in the marsupium of G. longispina varied little from the 16 "eggs" found in his specimen. Mauchline (1972: Table 4; 1980: Table 3) listed a maximum brood size of 1 for G. longispina.

The number of young Gnathophausia longispina in the marsupium increased with the size of the brooding female (Fig. 4). No G. longispina specimens as large as the brooding female reported by Clarke (1962) have been collected at Southeast Hancock Seamount. However, if our derived relationship between maximum observed fecundity and CL for G. longispina is representative of other geographic locations, then specimens of the size reported by Clarke may carry as many as 21 embryos (versus his observed value of 16 young; Fig. 4). Thus, brood size in G. longispina may range from ~ 7 in small females to as high as 16 (and possibly 21) in large specimens. Given that some growth stages of G. longispina were stratified by depth (Fig. 3) and little sampling occurred within 50 m above the summit or flanks at Southeast Hancock

Seamount, larger specimens of the size reported by Clarke may concentrate in this region near the seamount. At deeper depths (560 to 640 m) around the Hawaiian Islands (Ortmann 1903), G. longispina have a median CL of 14 mm (range 5 to 17 mm CL from six reported lengths), which exceeds the largest length mode we recorded at Southeast Hancock (Fig. 2) and approaches the larger CL in Clarke (Fig. 4). Two other aspects of the life history of G. longisping reported by Clarke should be revised in view of our data. He reported the minimum size of sexual maturity for female G. longispina, based on the only available specimen, as 17 mm CL (40 mm TL). The smallest female with eggs from our study had a 10 mm CL (24 mm TL). He also reported that G. longispina occur as shallow as 150 m depth. Although most individuals from our study were from this depth or greater, a few were from 50 m.

Evaluation of the results from this present study suggests the following life-history pattern for Gnathophausia longispina. A single brood is produced annually, with young released from the marsupium in late winter-early spring at a size of $\sim 2.1 \text{ mm CL}$ (8 mm TL). In addition to the length data for free-living G. longispina (Fig. 2) and near-term embryos, this pattern is suggested by the nearly synchronous development of embryos among all brooding females over the course of at least 7 mo (Fig. 5). The youngest free-living instars, although not collected in the samples, are likely to be present during the late winter between January and April and undergo two molts [assuming 25% growth increment as reported for G. ingens in Childress and Price (1978) to reach the earliest instar represented in Fig. 2 (i.e., about 4.5 mm CL)]. These first two free-living stages probably occur close to the substrate, where no samples were taken. Although these relatively abundant early stages would easily have passed through the net (particularly that used during spring 1987), we would have expected a few in the fine-mesh cod end if they had been present well above the summit during other times of the year. Growth of the young over the size ranges represented by our samples (Fig. 2) continues throughout the year, with most reaching sexual maturity within 12 to 15 mo after birth at a size of about 11.5 mm CL (Figs. 2 and 3). By late winter or spring, few adults (11.5 mm modal CL, Fig. 2) remain in the population, although increased sampling effort below the 225 m depth is needed to verify this (see "Materials and methods"). Thus, the entire life-span of G. longisping at Southeast Hancock Seamount is about 2 yr.

A decrease in growth with increasing latitude by Gnathophausia longispina may explain the large specimens reported by Ortmann (1903) and Clarke (1962) which were discussed earlier. Alternatively, G. longispina (unlike G. ingens which are semelparous and carry their young at a single instar; Childress and Price 1978) may survive beyond the end of their second year of life to reside at greater depths than were sampled in the present study. This pattern is also suggested by the rather large size range of ovigerous G. longispina at Southeast Hancock Seamount (10 to 14 mm CL). However, no bimodal length distributions of brooding females were observed from April 1987 (Fig. 2), pooled August of 1987 and 1988

(Fig. 3), or size-specific fecundity samples (Fig. 4; distribution not shown), which would indicate the presence of two year-classes. Nevertheless, it is possible that a large reduction in growth accompanying sexual maturity caused CLs of successive instars to coalesce into the unimodal size distribution at 11.5 mm CL (Fig. 2), a situation that has been observed in other crustaceans (e.g. *Gennadas elegans*; Mauchline 1991).

Both Gnathophausia longispina and the deeperdwelling congener G. ingens (Childress and Price 1978, 1983) show similarities in life-history patterns, some of which are characteristic of other meso- and bathypelagic mysids (Mauchline 1991). Larger individuals (e.g. brooding females) typically occur deeper for both species, and brood periods are long - about 17 mo for G. ingens and 7 mo for G. longispina. Although G. longispina are much smaller and thus exhibit about half the absolute growth rate of G. ingens $[0.030 \text{ mm CL } d^{-1} \text{ from Fig. 4 in}]$ Childress and Price (1978)], the relative growth rate (absolute, expressed as percentage of mean CL of population) of G. longispina (0.20% d^{-1}) is about twice that of G. ingens (0.11% d^{-1}). Both species exhibit similar decreases in CL growth increments over their life span, particularly at the stage where sexual maturity is reached. Finally, results of the present work suggest that G. longispina has slightly fewer free-living instar stages than G. ingens (~9 vs 13). Additional sampling closer to the bottom, particularly during late winter-early spring, as well as developmental studies to positively identify different instars of G. longispina, will be helpful to further clarify this aspect of the species' life history, as well as to confirm a 2 yr life span for this species.

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