THE BLACK MUREX SNAIL, *HEXAPLEX NIGRITUS* (MOLLUSCA, MURICIDAE), IN THE GULF OF CALIFORNIA, MEXICO: II. GROWTH, LONGEVITY, AND MORPHOLOGICAL VARIATIONS WITH IMPLICATIONS FOR MANAGEMENT OF A RAPIDLY DECLINING FISHERY

*R. Cudney-Bueno and K. Rowell*

**ABSTRACT**

We assessed longevity, seasonal growth variation, age of reproductive maturity, and geographic variations in morphology of the black murex snail, *Hexaplex nigritus* (= *Muricanthus nigritus*) (Philippi, 1845), a heavily harvested species of the Gulf of California, Mexico. Results from mark-recapture, $\delta^{18}O$ in shell carbonate, and 5 yrs of field observations, indicate that *H. nigritus* reach reproductive maturity between 2–3 yrs of age and live to be at least 8 yrs. Maximum growth occurs in the first year and slows down markedly in subsequent years. Seasonally, growth is accelerated during the summer and fall and largely stunted during winter, particularly January-March. Regional variations in morphology exist and have affected fishing practices, resulting in an artificial selection of stocks. We discuss our findings in the context of comparison of this species with other muricid snails and of the management implications for the black murex fishery.

The speed at which many invertebrate fisheries evolve often out-paces our knowledge of the species being harvested (Hobday et al., 2001). There are numerous examples of marine mollusks that have been the target of a rapidly developed fishery lacking proper knowledge on the species’ life history and subsequently leading to their rapid demise, from pearl industries worldwide (Donkin, 1998) to abalones (Hobday et al., 2001) and conch snails (Stoner et al., 1998). Addressing this lag in knowledge in marine invertebrate fisheries is of particular relevance today given increasing evidence of worldwide tendencies to fish down marine food webs (Pauly et al., 1998; Sala et al., 2004). Here, we present basic demographic information for a heavily-exploited mollusk in the Gulf of California, Mexico: the black murex snail, *Hexaplex nigritus* (= *Muricanthus nigritus*) (Philippi, 1845).

*Hexaplex nigritus* is a muricid gastropod endemic to the Gulf of California, Mexico (Poutiers, 1995), that has been subject to intense fishing by commercial divers since the early 1990s largely for the Asian market (López-Reyes, 1992; Cudney-Bueno and Turk-Boyer, 1998). Historically, adult *H. nigritus* inhabited intertidal and subtidal waters (primarily sand and gravel substrate) up to 60 m deep (Poutiers, 1995; Brusca et al., 2004). Today, they are rarely found intertidally (Cudney-Bueno et al., 2008), and fishing has turned to targeting their large subtidal summer breeding aggregations. Targeting breeding aggregations has likely resulted in the observed declines in catch of ~88% (from 600 to 71 mt) in less than a decade (Cudney-Bueno et al., 2008).

Despite the state of the resource, as well as its ecological and economic importance, our knowledge of the species is limited. The lack of basic knowledge of this species puts managers in the situation where they must rely on information from congeners, at best. Given mollusks’ ability to display phenotypic and ontogenic plasticity (Kemp and Bertness, 1984; Jones, 1988), application of other species’ life history information for management of *H. nigritus* can be highly risky (see Radwin and D’Attilio, 1976;
Hobday et al., 2001). Plasticity may also render a need for region-specific management schemes. For instance, fishermen’s local ecological knowledge suggests that there are regional variations in shell morphology of *H. nigritus*, influencing fishing patterns and market value of the species (Cudney-Bueno, 2000). Evidence of these variations, however, is limited to these anecdotal accounts.

We assessed area-specific morphological variations, longevity, age at reproductive maturity, and seasonal growth variations of *H. nigritus* in the northern Gulf of California, Mexico. We used a combination of field (mark-recapture) and laboratory (stable oxygen isotopes, δ18O) approaches, as well as 5 yrs of field observations. The analysis of δ18O profiles has been used successfully in other mollusks (Wefer and Killingley, 1980; Allmon et al., 1992). This method is particularly useful when a rapid estimate of growth is needed (Gurney et al., 2005), such as for a heavily harvested fishery like *H. nigritus*. The daily deposition of shell material makes mollusk shells excellent biological recorders (Goodwin et al., 2001), as variation in the δ18O records the seasonal temperatures (Jones and Quitmyer, 1996). High δ18O values are produced during winter temperatures and low δ18O values represent summer temperatures (Goodwin, 2001). Measuring the growth that occurs between two full seasonal cycles (winter to winter) results in an estimate of annual growth. Coupling the δ18O record (documenting seasonal temperature) with shell growth enables the determination of chronology of growth, validation of annual growth, and back-calculation of individual ages. Such data will inform population demographic models and ultimately allow for better management decisions and a long-term assessment of the species’ conservation status.

**Materials and Methods**

We collected *H. nigritus* shells from four fishing zones located off the coast of Puerto Peñasco, Sonora, Mexico, in the northern Gulf of California (Fig. 1): La Cholla, Sandy Beach, Los Tanques-Conchas, and San Jorge Island. Fieldwork took place in years 1999–2001 and 2003–2004, between May and August when the species reproduces. During this time, we participated in fishing trips with commercial divers and obtained random samples of their catches by “scooping” specimens with 11-L buckets (n = 792 snails from 20 distinct *H. nigritus* breeding aggregations).

**Shell Morphology.**—We tested the null hypothesis that there are no variations in snail morphology between fishing zones. We recorded total length (TL, measured from apex to anterior tip of siphon canal), aperture length (AL, measured from tip of aperture notch to posterior tip of siphonal canal), and total wet weight (WW) (Fig. 2). We calculated the length/weight and length/aperture ratios, compared these ratios across zones using a one-way ANOVA framework, and performed a Tukey’s HSD multiple comparison test to determine pairwise relationships. We then plotted TL by WW of all snails and obtained the best length-weight equation fit via regression. Using an ANCOVA framework, we tested the null hypotheses that TL-WW and TL-AL relationships did not vary across the various zones. Prior to our analysis, we examined the data for homogeneity of variance, excessive skewness, and outliers.

**Growth, Longevity, and Age of Reproductive Maturity.**—We used two means to estimate growth: mark-recapture data and stable oxygen isotope ratios. We marked 180 breeding adults from San Jorge Island in July 2003. We weighed each snail (wet weight, WW), and measured its total length (TL) and the distance from the tip of the marked spine to the tip of the newest spine (SL). We attached stainless steel (0.5 cm) number tags to the largest spine on the second-to-last or third-to-last most posterior varix (thickness-dependent) of each snail (Fig. 2). Tags were secured with zip ties that laced through a drilled hole on the spine. In July...
2004, 31 of the 180 tagged snails were recaptured, weighed (WW₂), measured (TL₂), and any new varices were counted. We also measured whorl growth (WG), defined as the distance from the edge of the tip of the most posterior and last (newest) spine found in 2003 with the edge of the tip of the newest spine developed since snails were tagged (1 yr whorl growth). We plotted the difference in total length (ΔTL = TL₂ − TL₁), whorl growth (ΔWG = WG₂ − WG₁) and wet weight (ΔWW = WW₂ − WW₁) and tested for variations in relation to TL₁ using a regression framework.

We used δ¹⁸O profiles as a tool to reconstruct maximum age for *H. nigritus* and determine age of reproductive maturity. We obtained δ¹⁸O profiles along the axis of growth for shells from La Cholla. Because of the expense of analyzing δ¹⁸O in carbonate, our sample size was limited to two specimens sampled in detail: Specimen Ch01—the smallest reproductive individual we observed depositing an egg mass, 93 mm TL, and specimen Ch02, one of the largest and heaviest specimens we found in 5 yrs of work, 180 mm TL.

We cut both specimens in sections parallel to each whorl suture (perpendicular to growth increments) and only sampled the shell between the exterior/exposed portion and the interior cavity of the snail to avoid contamination from other calcareous material (Fig. 3). In a previous study of the larger specimen (Ch02), the last three varices of the body whorl were sampled and estimated to represent 2 yrs of growth (Todd-Pearson et al., 2005). We sampled the remainder of this specimen's body whorl to obtain a complete series of samples representative of the entire body whorl growth (Fig. 3). Because much of the oldest portion of the shell (the spire, posterior of the body whorl) was burrowed and reworked, we were unable to sample the
rest of this specimen. However, for the smaller individual (representative of approximately the same width and size class for which we were unable to sample on Ch02), the entire shell was sampled, giving us a good estimate of growth during these earliest stages (Fig. 3A–D). Even though the shell of the large specimen had some burrowing, it was chosen because it was by far the largest specimen observed while still being relatively uninfested. We also felt that it was important to use this specimen since it had been sampled in an earlier study by the same authors and others (Todd-Pearson et al., 2005), therefore being consistent and building on existent information.

We obtained and analyzed all samples of shell material following well-established procedures (see Krantz et al., 1987; Jones and Quitmyer, 1996; Goodwinn et al., 2001). Oxygen isotope ratios in carbonate values are expressed relative to the Vienna Pee Dee Belemnite (VPDB) standard (Grossman and Ku, 1986). Shell carbonate was analyzed at the Stable Isotope Laboratory of the Department of Geosciences, University of Arizona, using a Finnigan MAT 252 mass spectrometer equipped with a Kiel-III automated carbonate sampling device. Standardization of oxygen isotope ratios was based on normalization to published ratios of NBS19 and NBS 18. Analytical error was ± 0.1‰.

We plotted the isotopic profiles of each snail in relation to distance from protoconch/apex (cm). Distance was measured between each sample and summed to get the accumulated growth of the snail (distance from the protoconch associated with δ18O values should not be confused with the TL measurement). Using this method we also assessed the relative growth during colder (winter-spring) compared to warmer (summer-fall) months. Little or no differences in seasonal growth are represented by a relatively consistent sinusoid curve in the δ18O profile, with crests mirroring valleys in length, but if sharp peaks in the crest or valley
Figure 3. Cross sections of *Hexaplex nigritus* specimens sampled for δ¹⁸O analyses. Carbonate sample points are marked in black. Illustrations A–D are for the smallest specimen sampled (specimen Ch01), with (A) being the apex/protoconch, (B) oldest whorl, (C) second whorl, and (D) most recent whorl (body whorl). (E) Cross section of the body whorl of the largest *H. nigritus* specimen sampled (specimen Ch02). Arrows indicate the direction of growth and area sampled in this study. The last three varices of the body whorl of this specimen were sampled in a previous study (Todd-Pearson et al., 2005) and are indicated with a vertical line. Scale units in cm.
are present, these represent slowed growth or a hiatus in growth (Wefer and Killingley, 1980; Goodwin et al., 2001).

Results

When pooling TL and WW measurement data of all reproductive snails sampled, we found a power equation fit for the increase of weight as a function of increased TL ($R^2 = 0.77$, $P < 0.0001$) (Fig. 4). However, length-weight and length-aperture ratios varied between the various zones (TL/WW: 1-way ANOVA $F_{3,731} = 107.15$, $P < 0.0001$; TL/AL: 1-way ANOVA $F_{3,236} = 40.81$, $P < 0.0001$) (Table 1). In general, snails from Los Tanques-Conchas were smaller than snails from all other zones. They also tended to have greater buildup of calcareous material, often covering the spines, making them duller and less conspicuous. Snails from La Cholla and San Jorge, in contrast, tended to have thinner shells, even though, on average, they were considerably larger than those of Los Tanques-Conchas (Table 1). We also found marked differences across zones in the length-weight relationship (ANCOVA effect test for zone $F_{3,731} = 11.13$; $P < 0.0001$; Fig. 5). However, we did not find any site differences in the length-aperture relationship (ANCOVA effect test for zone $F_{3,236} = 0.379$, $P = 0.768$).

The recaptured individuals ($n = 31$), revealed a relationship between snail size and growth rate of adult (reproductive) snails. Total length and whorl growth rates decreased as a function of increased snail size ($R^2 = 0.29$, $P = 0.0048$; $R^2 = 0.27$, $P = 0.013$; Fig. 6, respectively). We observed a similar pattern for wet weight gain ($R^2 = 0.22$, $P = 0.015$; Fig. 7). The data also showed considerable variation in TL growth in 1 yr, ranging from no growth to 29.6 mm. Similarly, $\Delta WG$ and $\Delta WW$ were quite variable (0–34.6 mm and 0–340 g, respectively). Half of the snails added 1 spine/varix along the body whorl while the other 50% did not add any.
Table 1. Mean length and weight, length/weight and length/aperture ratios of reproductive *Hexaplex nigritus* from four areas of the northern Gulf of California, Mexico. TL = Total length; AL = Aperture length; WW = Wet weight.

<table>
<thead>
<tr>
<th>Zone</th>
<th>n TL</th>
<th>Mean TL (mm) (95% C.I.)</th>
<th>n WW</th>
<th>Mean WW (g) (95% C.I.)</th>
<th>n TL/WW</th>
<th>Mean TL/WW (95% C.I.)</th>
<th>n TL/AL</th>
<th>Mean TL/AL (mm) (95% C.I.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cholla</td>
<td>283</td>
<td>142.14 (140.7,143.5)</td>
<td>283</td>
<td>533.0 (517.8,548.1)</td>
<td>283</td>
<td>0.29 (0.28,0.30)</td>
<td>95</td>
<td>0.50 (0.49,0.50)</td>
</tr>
<tr>
<td>Sandy Beach</td>
<td>40</td>
<td>114.17 (110.4,117.9)</td>
<td>40</td>
<td>250.12 (209.8,290.4)</td>
<td>40</td>
<td>0.47 (0.44,0.50)</td>
<td>40</td>
<td>0.47 (0.46,0.48)</td>
</tr>
<tr>
<td>Los Tanques-Conchas</td>
<td>198</td>
<td>112.95 (111.2,114.6)</td>
<td>183</td>
<td>280.53 (261.6,299.3)</td>
<td>183</td>
<td>0.42 (0.41,0.43)</td>
<td>72</td>
<td>0.46 (0.45,0.46)</td>
</tr>
<tr>
<td>San Jorge Island</td>
<td>271</td>
<td>133.48 (132.0,134.9)</td>
<td>226</td>
<td>451.49 (434.5,468.4)</td>
<td>226</td>
<td>0.31 (0.30,0.32)</td>
<td>31</td>
<td>0.52 (0.50,0.52)</td>
</tr>
</tbody>
</table>
Isotope profiles of the small reproductive (93 mm TL) individual suggest that it was between 2–3 yrs old, with two distinct peaks (colder water temperatures) and valleys (warmer temperatures) and what appears to be the beginning of a third year of growth (Fig. 8). The larger specimen also exhibited distinct seasonal cycles in the variation of its oxygen isotope profile documenting ~3.5 yrs of growth (Fig. 8). If we add this to the estimated 2.5 yrs represented by the last three varices (Todd-Pearson et al., 2005), it appears that it took 6 yrs for this specimen to complete its last body whorl. Although we were unable to sample the remainder of this large specimen (the spire), the width of that section was equivalent to that of the young reproductive individual we sampled. Given this, we estimate that the lifespan of a black murex snail can be at least 8 yrs.

**Discussion**

**Growth and Morphology.**—We found evidence of geographic variation in snail morphology. In biological terms, these variations could be attributed either to genetic differences (Gould, 1966) or to environmental influences acting on the phenotypic expression of the genotype (Kemp and Bertness, 1984). Although no genetic studies have been conducted on this species, it is very likely that the observed geographic variation in *H. nigritus* shell morphology represents morphological plasticity that is environmentally mediated, as has been shown for other gastropods (Kemp and Bertness, 1984; Berg and Olsen, 1989; Stoner et al., 1998). For instance, maximum size of abalone is determined by both quantity and species composition of local food availability (Breen, 1980), and stunted individuals can retain the potential for adequate...
growth when moved to more favorable habitat (Breen, 1986). Similarly, shell variation among genetically undifferentiated gastropods can be a function of variations in snail growth rates predicted by differences in snail densities in a resource-limited environment (Kemp and Bertness, 1984). Interestingly, the larger individuals in our study came from San Jorge Island and La Cholla, where we observed a higher abundance and density of black murex prey species, such as mussels, *Modiolus capax* (Conrad, 1837), and callista clams, *Megapitaria* spp. (Sowerby, 1835), possibly releasing *H. nigritus* from intraspecific competition.

Some gastropods also can grow more rapidly in agitated water than in quiet water (Hyman, 1967). This has some consistency with our findings. Both San Jorge Island and La Cholla experience intense daily tidal currents, whereas the currents of Los Tanques-Conchas, where stunted individuals are found, are usually mild (Cudney-
Snails from Los Tanques-Conchas also tended to have more silt and calcareous deposits than other snails, and much of the characteristically irregular surface of the species was concealed by these deposits or worn out, suggesting older individuals.

Another explanation for some of these morphological differences could involve variations in fishing pressure, with smaller individuals expected in heavily fished areas. However, this is unlikely since the area that has traditionally been fished the most, La Cholla (Cudney-Bueno et al., 2008), is one of the areas with larger snails. Our analyses also coincide with local knowledge regarding snail quality classification according to zone and size (Cudney-Bueno, 2000). This is not to suggest that fishing activity has had no effect on local populations. Fishermen do mention that they have seen more “newer” snails (those that are cleaner, have less calcareous deposits and a thinner shell) in La Cholla than in previous years (Cudney-Bueno, 2007). In addition, although all of the aggregations were found in subtidal waters, fishermen used to harvest *H. nigritus* intertidally during the lowest tides of spring (Cudney-Bueno, 2000). Poutiers (1995) also reports that *H. nigritus* can be found in intertidal waters, and Paine (1966) distinguished black murex as an apex predator, together with the sun star *Heliaster kubiniji* (Xanthus, 1860), in the intertidal zone of the Upper Gulf of California. These accounts suggest that intense fishing in the 1990s could have removed older individuals from the commercial stock and over-harvested populations found closer to shore.

In terms of growth and longevity, we provide evidence that *H. nigritus* can reach reproductive maturity between 2–3 yrs of age and can live for at least 8 yrs. Our estimation of reproductive maturity is based on detailed isotope sampling of the smallest individual we observed breeding. It is therefore possible that some individuals, not sampled, could be reproducing sooner. However, this is highly unlikely as all of our measurements of individuals harvested (all reproductive individuals from

Figure 7. Relationship between snail size and one year weight gain of *Hexaplex nigritus* in the northern Gulf of California, Mexico (\(\Delta WW = -5.441 \times TL + 836.08\)).
breeding aggregations) revealed larger sizes and we never found smaller specimens in our underwater observations of breeding aggregations. Based on the relationships between size-growth rate and size-weight gain obtained from recaptured individuals in San Jorge Island, we also can say that growth in length of *H. nigritus* slows down as mature individuals become older, adding more shell thickness and overall body mass. Using our growth equations to extrapolate to younger individuals, it appears that *H. nigritus* from San Jorge Island grow rapidly during year one, and their growth slows down markedly after the second or third year, once they reach a length consistent with early reproductive maturity, approximately 85–95 mm (see Fig. 4). Although our recapture data were for individuals that ranged from 123.6 to 150 mm (mature individuals), limiting our predictions of growth of smaller individuals, these estimates are consistent with results obtained through our isotope data and similar to those reported for other large gastropods such as the queen conch, *Strombus gigas* (Linnaeus, 1758) and milk conch, *Strombus costatus* (Gmelin, 1791) (Wefer and Killingley, 1980). In contrast, pink-mouthed-murex, *Phyllonotus erythrostomus* (Swainson, 1831), in the Gulf of California can reach sexual maturity in less than a year (Baqueiro et al., 1983).

The isotopic profiles of both specimens show differences in seasonal growth rates. The wide valleys indicate that these snails grew rapidly during warmer months (April–October), illustrated by more negative δ¹⁸O values. The abrupt "peaks" suggest growth rate is reduced considerably during the colder months, with possibly no growth during the coldest months, January and February. This growth pattern is consistent with that reported by Todd-Pearson et al. (2005) and could be related to the species’ reproductive strategy and behavior in the months preceding and following reproduction. *Hexaplex nigritus* has a distinct seasonal behavior centered
around spawning. In March–May, before reproduction peaks, snails feed extensively on nearby mollusk beds and then cease to feed while aggregated for breeding in the summer months (Cudney-Bueno et al., 2008), a behavior that has also been documented for other muricid snails (Tompa et al., 1984). At this time, much of the stored energy could be allocated to reproduction and growth. Immediately after aggregating, snails disperse and again feed, which also coincides with the time they appear to be growing most. As water temperatures become colder, snails stop feeding and between December and early March they bury in the sand (Cudney-Bueno et al., 2008), possibly accounting for the slowed to no growth in cold months.

**Management Implications.**—These first estimates of age, growth, and morphological variations of *H. nigritus* have important implications for management of the black murex fishery. Length-weight and shell variations likely force artificial selection of harvestable stocks. Snail buyers in Puerto Peñasco have consistently avoided buying snails from Los Tanques-Conchas because they obtain a much lower meat yield than snails from other zones since the shell is much heavier in relation to the amount of meat they can commercialize (Cudney-Bueno, 2000). Given evidence of reproductive site fidelity for this species (Cudney-Bueno et al., 2008), it is possible that genetic structure exists and that fishing practices could be exerting more pressure on specific genetic stocks. An assessment of genetic structure within and between breeding aggregations is warranted.

Our results suggest that *H. nigritus* is likely capable of reproducing a minimum of five times in its lifetime, critical information for future population viability analyses of the species and stock recruitment models. We also show that black murex growth is slower than that of the pink-mouthed murex (*P. erythrostomus*). To our knowledge, this is the closest taxonomic relative of *H. nigritus* on which growth studies have been conducted in the Gulf of California. Our results therefore corroborate the risks of using life history information of similar species as proxies for the development of management guidelines.

Given the evidence of site-specific morphological variations and that our sampling was restricted to adults, we caution interpretation of our growth rate and longevity results beyond reproductive *H. nigritus* of the areas of La Cholla and San Jorge Island, where we obtained our specimens for this component of the analysis. Furthermore, our mark-recapture data also showed considerable variation in annual growth rates. This is consistent with results found for other similar species, including topshells (*Trochus niloticus* Linnaeus, 1758), blacklipped abalone (*Haliotis rubra* Leach, 1814), and the whelk *Hexaplex trunculus* Linnaeus, 1758 (see Smith, 1987; Gurney et al., 2005; Vasconcelos, 2006), stressing the need for larger samples sizes and cautious interpretation beyond the specimens studied. Similar shell lengths do not necessarily imply similar ages, especially with larger individuals, as gastropods can show determinate growth (Berg and Olsen, 1989).

We suggest that further studies address growth and age with larger sample sizes from other sites and areas in the Gulf of California and that this information be incorporated to spatially-explicit management approaches. These studies should be coupled with longer-term mark-recapture experiments and more recapture effort at different intervals within a year. Although particularly challenging as young individuals are difficult to find, mark-recapture should ideally span all age classes. This would allow better estimation of intra-specific growth variations, calculation of *k* (von Bertalanffy growth coefficient) and *L*∞ (maximum length), and obtaining von
Bertalanffy growth curves (Bertalanffy, 1938) that could further aid in the development of appropriate management scenarios for the black murex fishery.

Acknowledgments

We thank the divers of the Sociedad Cooperativa Buzos de Puerto Punta Peñasco for their support in the field and knowledge sharing. The Centro Intercultural de Estudios de Desiertos y Océanos (CEDO) provided logistical and financial support throughout this study. We are grateful for the collaboration in the field of O. Hinojosa, O. Morales, J. Rupnow, and R. Prescott. Isotopic lab space was kindly provided by K. W. Flessa and D. L. Dettman, of the Stable Isotope Laboratory of the Geosciences Department at the University of Arizona. Earlier versions of this manuscript were improved by the reviews and editorial comments of P. Raymond, W. Shaw, and R. Steidl. This study was supported by the Tinker Foundation, the David and Lucile Packard Foundation, the Consejo Nacional de Ciencia y Tecnología (CONACYT), the Inter American Foundation, the Wallace Research Foundation, and the Environmental Leadership Program. Research was conducted under permit # DGOPA.04693.150506.1832 from the Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación (SA- GARPA) of Mexico. This is a scientific contribution of the PANGAS Project (www.pangas. arizona.edu) and CEDO.

Literature Cited


DATE ACCEPTED: 2 June, 2008.

Addressees: (R.C.B.) School of Natural Resources, University of Arizona, Biological Sciences East Room #325, Tucson, Arizona 85721 and Centro Intercultural de Estudios de Desiertos y Océanos (CEDO), Apartado Postal #53, Puerto Peñasco, Sonora, Mexico and Institute of Marine Science, University of California at Santa Cruz, Santa Cruz, California 95060 (K.R.) Department of Biology, University of Washington, 528 Kincaid Hall, Box 351800, Seattle, Washington 98115. Corresponding Author: (R.C.B.) Telephone: (831) 239-6370, Fax: (650) 948-2957, E-mail: <cud@ag.arizona.edu>.