THE BLACK MUREX SNAIL, *HEXAPLEX NIGRITUS* (MOLLUSCA, MURICIDAE), IN THE GULF OF CALIFORNIA, MEXICO: I. REPRODUCTIVE ECOLOGY AND BREEDING AGGREGATIONS

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ABSTRACT

We studied the reproductive ecology and behavior of the black murex snail, *Hexaplex nigritus* (Philippi, 1845), a species heavily harvested in the Gulf of California, Mexico. We found that *H. nigritus* is dioacious and highly gregarious, capable of forming breeding aggregations with a biomass of 3 mt. Snails aggregated in subtidal waters between April and September, laying egg masses on shells of male and female conspecifics. Egg masses on any one snail could be from multiple females and contain an average of 285 capsules. Eggs incubated in capsules for 18–31 d, at which time they hatched as veliger larvae (mean = 3603; 95% CI = 3382–3825 larvae per capsule). Seventy-four percent of aggregations formed adjacent to or within 25 m of a rocky, coquina (beach rock) or mussel bed reef. While aggregated, snails ceased feeding but preyed on at least 10 species of mollusks prior and after aggregating. During winter, snails buried in the sand and emerged in early spring to feed. Breeding aggregations formed on or near (< 20 m) sites used the preceding year, suggesting fidelity to reproductive sites. The species' reproductive behavior has facilitated the removal of much of the reproductive biomass and juveniles newly settled within aggregation sites, likely causing a rapid decline in harvestable stocks. We discuss the implications of our findings in the context of biology and ecology of muricid snails and management and conservation of *H. nigritus*.

The black murex snail, *Hexaplex nigritus* (= *Muricanthus nigritus*) (Philippi, 1845), is a muricid gastropod endemic to the Gulf of California, Mexico (Poutiers, 1995) that has been subject to intense fishing since the early 1990s (López-Reyes, 1992; Cudney-Bueno and Turk-Boyer, 1998). Adults are found in intertidal and subtidal waters living primarily on sand and gravel bottoms in waters down to 60 m deep (Poutiers, 1995; Brusca et al., 2004). Like other muricids, *H. nigritus* is a predator occupying an important niche in food webs of subtidal benthic communities (Paine, 1966), preying upon various species of mollusks (Keen, 1971; Brusca, 1973).

Other than these brief findings, our knowledge on the biology and ecology of *H. nigritus* is scant [see Barber (1961) and D'Asaro (1991) for brief observations on reproduction]. A better understanding of its reproductive life history is particularly needed as the species has been heavily fished during reproduction when it forms large breeding aggregations (Cudney-Bueno, 2000). Harvestable stocks have declined rapidly, from 600 to 71 mt in only 7 yrs and a decrease of 30% in catch per unit of effort (Cudney-Bueno, 2007).

In this paper, we identify key aspects of the reproductive ecology and behavior of black murex. Specifically, we describe (1) formation and habitat of breeding aggregations, (2) fidelity to reproductive sites, (3) sex ratios of breeding aggregations, (4) egg laying and hatching, and (5) reproductive output of individuals. We also describe behavior before and after reproduction, and provide observations on feeding and predation. Our findings extend our knowledge on the family Muricidae and provide information critical for management of the black murex fishery in the Gulf of California.

Materials and Methods

Study Site.—Between 1999 and 2004, we completed fieldwork near Puerto Peñasco, Sonora, Mexico, the largest fishing town for *H. nigritus* (Cudney-Bueno, 2007). We collected data on aggregations within four distinct fishing zones located near Puerto Peñasco: La Cholla, Sandy Beach, Los Tanques-Conchas, and San Jorge Island (Fig. 1).

Formation of Breeding Aggregations and Site Fidelity.—We participated in 53 fishing trips during snail fishing season (May–August), to assess (1) timing, location, size of breeding aggregations, and habitat where aggregations were formed, and (2) fidelity to reproductive sites and snail behavior before, during, and after the formation of breeding aggregations. We dove with fishermen to locate aggregations. We defined an aggregation as a group of at least 10 snails adjacent to each other, engaged in reproductive behavior, and separated by at least 10 m from another aggregation. Once found, we recorded depth, temperature, and approximated the size of the aggregation by measuring its width and length. We also qualitatively described the aggregation habitat and searched for non-aggregated snails within a 25 m radius.

To assess snail fidelity to reproductive sites and behavior before, during, and after reproduction, in summer 2000 we set a colored concrete block in the center of three breeding aggregations (one each from Los Tanques-Conchas, Sandy Beach, and San Jorge Island), and color-marked between 50–100 snails from each aggregation. We returned to these sites in summer 2001, 2002, and 2003 to see if aggregations had formed near blocks, and we searched
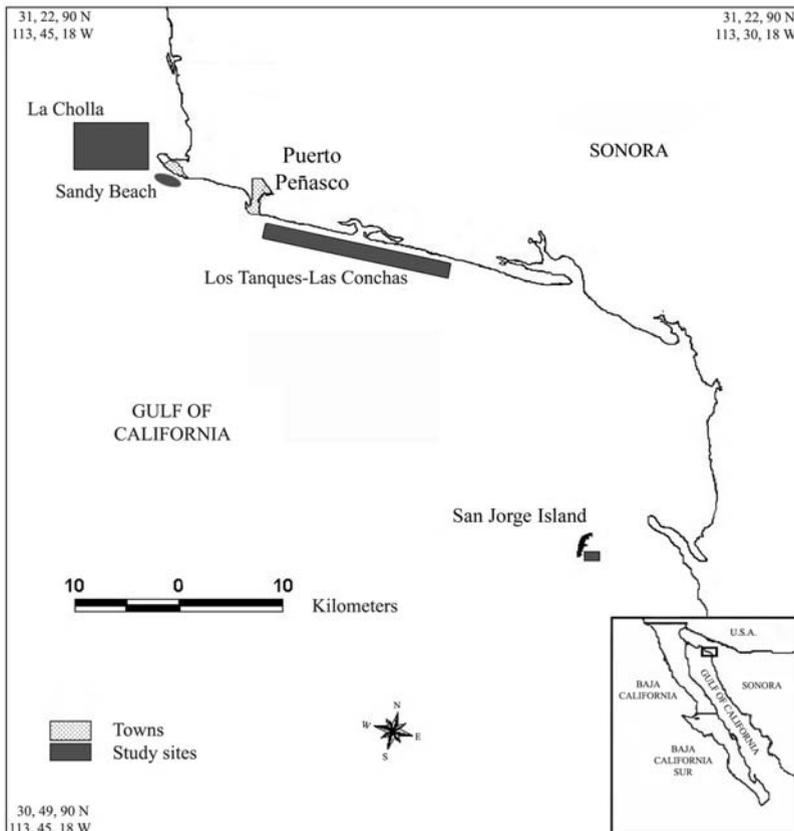

Figure 1. Study area and collecting sites of *Hexaplex nigritus* aggregations in the northern Gulf of California, Mexico.

for marked snails within a 20 m radius. In addition, we worked with local fishermen to set aside a temporary refuge around San Jorge Island, allowing us to follow the entire formation of breeding aggregations without disturbance of fishing activities. In July 2003, we marked 180 breeding adults from San Jorge Island, and set a concrete block in the middle of the aggregation (see Cudney-Bueno and Rowell, 2008). We returned to this site every 2 mo for 1 yr after the snails were tagged. During each visit, we swam around the concrete block at 5, 10, 15, and 20 m intervals, noted whether snails were feeding, mating, or buried in the sand, their direction of movement (moving away/towards the concrete block), and recorded the number of marked snails. After searching within the 20 m circular plot, four divers searched haphazardly for other breeding aggregations and marked snails up to approximately 50 m away from the plot, each diver heading in one of four directions (N, S, E, or W). Throughout this year, hourly temperature readings were recorded by an underwater thermometer (HOBO™) anchored to the concrete block at the aggregation site.

Sex Ratio of Breeding Aggregations.—We swam along two aggregations in La Cholla and obtained a haphazard sample of snails from each aggregation. We returned snails to a local laboratory, sexed each individual snail, and evaluated the sex ratio of both samples using a Pearson χ^2 test.

Egg Laying and Hatching.—We maintained 47 live snails in aquaria, feeding them live venus clams, *Chione* spp. and mussels, *Modiolus capax* (Conrad, 1837). We placed between 5–10 snails in 75- and 189-L aquariums (approximating similar densities of one 350 g snail per 15 L) filled with seawater and maintained ambient water temperature at 28.0–29.0 °C and salinity at 37–38. Throughout these 2 mo, at least once per day we made between 0.5–1.0 hr observations of the behavior of snails, specifically recording if and where (e.g., on other snails, the bottom, or the glass) snails were laying egg capsules. When egg-laying occurred, we recorded its duration and counted the total number of egg capsules laid. We defined an egg-laying event as a snail depositing an egg mass of > 10 capsules with ≤ 24 hrs interruption between each capsule laid. We chose these numbers based on field observations and preliminary laboratory analysis. Harvested snails rarely had anything less than 10 capsules on their shells, and a snail laying an egg mass in the aquarium never laid a capsule in > 10 hrs.

We monitored egg masses laid in the aquaria throughout their development until individual capsules began hatching. We recorded the incubation time, which was defined as days of incubation from the first day a snail began laying an egg mass to the first hatching day. To determine the developmental stage at which offspring hatch from the capsules, we maintained 30 ready-to-hatch capsules in small 20 ml vials with seawater at 28.0–29.0 °C and salinity 37–38. Once hatched, we took a 1 ml sample and observed the embryos under a 10× dissecting microscope.

To assess egg laying and reproductive output in the natural environment, we sampled snails from fishermen's catches at the beginning and end of the 1999 fishing season by randomly "scooping" specimens with 11-L buckets. We ensured each sample came from one breeding aggregation by participating in the fishing trip and collecting the sample once the aggregation was found. We determined if there was any variation in number of capsules laid on aggregated snails through time. Samples contained snails with and without egg cases. For snails with egg cases, we counted all capsules on each snail and then compared the mean number of capsules per snail across time for each collecting zone. We analyzed Los Tanques-Conchas data with a Students *t*-test (two sampling periods in 1999). For La Cholla (three sampling periods in 1999) we used a 1-way ANOVA framework and performed a Tukey's HSD multiple comparison test to determine pairwise relationships.

We determined if there was any effect of the sex of snails on deposition of egg capsules by analyzing the same snails that were used to assess sex ratios of breeding aggregations and registering presence and absence of egg masses on male and female snails. We calculated percentage of presence/absence of egg masses for males and females and tested both sexes for marginal homogeneity with a Pearson χ^2 test.

Finally, we determined if egg masses were laid on substrates other than snails. We searched for other substrates with egg masses within 25 m of the perimeters of the aggregations. We also haphazardly searched along the border of the Los Tanques-Las Conchas rocky reefs and around San Jorge Island, covering a combined transect approximately 6 km long, and consulted key fishermen regarding past and/or present experiences of finding egg masses on substrates other than snails.

Determining Reproductive Output.—We determined: (1) the relationship between snail length and capsule length, and (2) the relationship between egg capsule length and number of offspring produced. We collected 84 snails from three aggregations and two egg capsules from each parent snail as they were laid. We measured snail total length (TL) and length of each pair of capsules, calculating an average capsule length (CL) for each snail [Measurements of capsules laid in aquaria showed minimal variance in the CL laid by a snail. Obtaining two samples per snail was only meant to make our analyses more conservative]. Using a linear regression framework, we evaluated the null hypothesis that there was no relationship between snail size and CL.

To determine the relationship between CL and number of offspring produced, we collected ready-to-hatch individual egg capsules from aggregations in La Cholla, Los Tanques-Las Conchas, and San Jorge Island. We collected one capsule from individual carrying snails found within a given aggregation as separate as possible from each other to minimize the possibility of obtaining egg capsules laid by the same snail. We then took length measurements of each capsule (Fig. 2), cut it open, and emptied its contents into a vial with seawater, assuring a total volume of 10 ml. Immediately after stirring, we took a 1 ml sample from the middle of the water column and counted the embryos under a 10× dissecting microscope. We used a 1:10 conversion to calculate the number of embryos contained in each capsule and evaluated the null hypothesis that there was no relationship between capsule size and number of embryos using a linear regression framework.
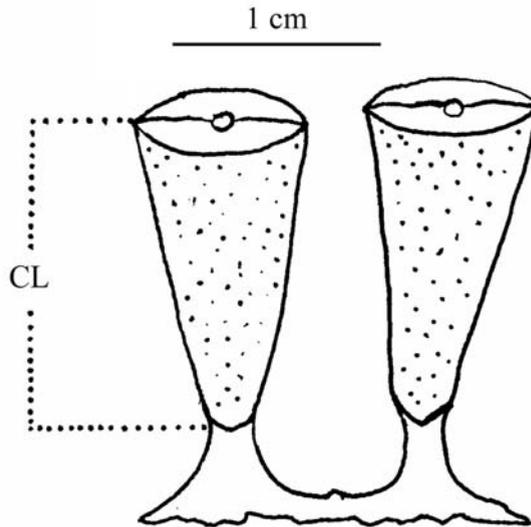

Figure 2. Length measurement and depiction of *Hexaplex nigritus* capsules with larvae (Illustration: T. Ash-Cudney).
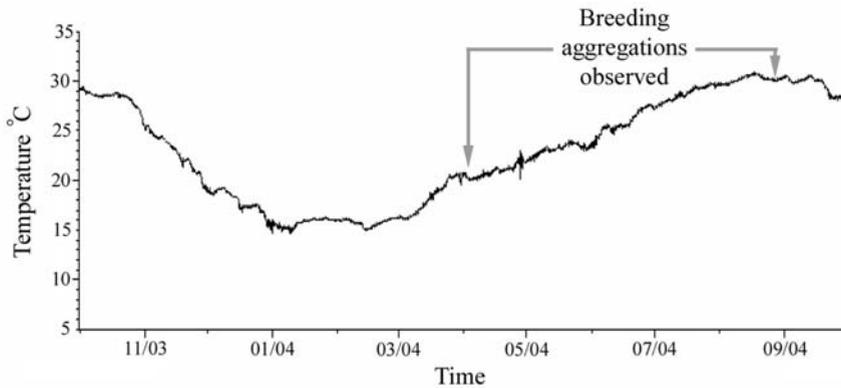
Figure 3. Annual subtidal water temperature cycle in San Jorge Island and period (arrows) when *Hexaplex nigritus* were observed forming breeding aggregations throughout the study region. Temperature readings were made hourly at a breeding aggregation site (12 m depth).

RESULTS

FORMATION OF BREEDING AGGREGATIONS AND SITE FIDELITY.—Breeding aggregations formed from early April through September. Between April and June, aggregations were found closer to shore in shallow waters (≤ 15 m deep). We located aggregations in waters with temperatures of 22–31 °C (Fig. 3) and depths of 4–25 m. Sixty percent of aggregations were between 100–200 m^2. The largest aggregation was in La Cholla, covering an area of approximately 900 m^2 and providing a total fishing catch of 3 mt after having harvested the entire aggregation. We estimate that this aggregation contained between 5400–5800 snails based on the average weight of 533 g/snail reported for that area (Cudney-Bueno and Rowell, 2008).

In San Jorge Island, where we observed a breeding aggregation site for an entire year, an aggregation of 120 m^2 formed and dispersed completely in a period of 40–60 d. The aggregation grew throughout the season but reproduction began early in its formation. As the season progressed, new snails were recruited into the aggregation and old ones began leaving after copulation and egg-laying. Breeding snails did not feed, but in the months immediately preceding (April–May) and following the formation of the aggregation (September–November), snails preyed primarily on mussels (*M. capax*) from an adjacent mussel bed, leaving conspicuous trails of open shells. As the water temperature dropped, it became increasingly difficult to locate snails, and those found were usually buried, exposing only part of their spines.

Of the 42 aggregations we located, 30 were within the fishing zone of La Cholla. In addition, 78.5% formed on broken and complete mollusk shells, rhodoliths, other encrusting coralline algae, and large grain sand (Fig. 4A,B). All other aggregations were found on sandy bottoms, which dominate in the study area, and 73.8% in areas adjacent or within 25 m of a rocky, coquina (beach rock) or mussel bed reef. Towards the end of the breeding season of *H. nigritus* (July through August) aggregations of another muricid snail, the pink-mouthed murex, *Phylonotus erythrostomus* (Swainson, 1831), were found adjacent and sometimes intermingled with those of black murex. Contrary to *H. nigritus* aggregations which are extended in area yet only comprise
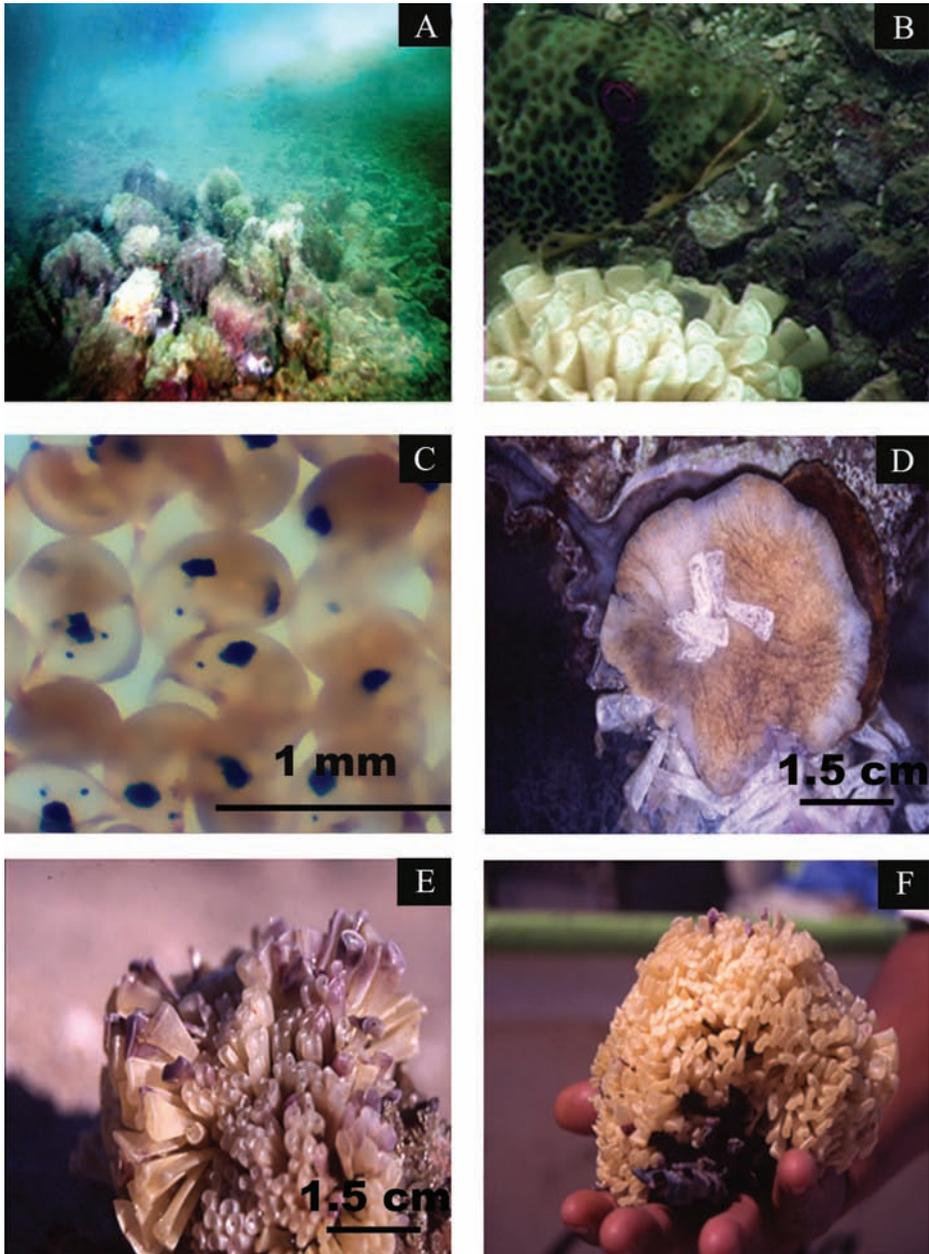
Figure 4. Breeding aggregations, egg capsules, and larvae of *Hexaplex nigritus*. (A) Portion of a breeding aggregation with numerous egg masses laid on top of conspecific snails; (B) a spotted sand bass, *Paralabrax maculatofasciatus*, next to a *H. nigritus* egg mass and over typical *H. nigritus* breeding aggregation habitat comprised of broken shells, sand, and calcareous algae/rhodoliths; (C) veliger larvae; (D) female with foot extended while laying egg capsules on glass of aquarium. Individual eggs within the egg capsules can be observed; (E) variations in egg cases laid by different snails; (F) egg mass of > 1000 capsules. Photo credits: (A, D, E, F) R. Cudney-Bueno; (B) J. Rupnow; (C) D. Moon.

one layer of individuals, *P. erythrostomus* aggregations consisted of large mounds, up to 2.5 m tall and 15 m in circumference, covering one single colonial egg mass.

Of the 180 snails tagged in San Jorge Island in summer 2003, we located 31 snails in summer 2004, all aggregated within 10 m of the original aggregation location. We did not find tagged snails in another aggregation located 35 m away. Similarly, for the three consecutive years that we monitored the breeding aggregation sites in Sandy Beach, Los Tanques, and San Jorge Island marked in 2000, we observed aggregations forming on or within 20 m of locations used in previous years. We also found marked snails in these aggregations after the first year, with a minimum recapture success of 10% at Sandy Beach and a maximum of 22% at San Jorge Island.

Sex Ratios of Breeding Aggregations.—The percentage of male:female snails was 56%:44%, respectively, for the first sampling period (La Cholla, June 23 1999: n = 36) and 50%:50% for the second sampling period (La Cholla, July 5 1999: n = 32). The percentage of males and females of both samples combined was 53%:47%. In no cases were there significant differences to a 1:1 ratio ($\chi^2 = 0.21$, P = 0.646).

Egg Laying and Hatching.—Nine snails held in aquaria laid 10 egg masses. The number of capsules per egg mass varied from 27 to 337 (mean 137 ± 71, 95% C.I.). Incubation time ranged from 18 to 31 d (mean = 23 ± 4; Table 1) and all capsules released veliger larvae (Fig. 4C).

Eight egg masses were laid on the glass surface of the aquaria (Fig. 4D), and two on top of other snails. Subtidal SCUBA observations revealed the presence of 45 egg masses laid on substrates other than conspecific snails, including loose shells of clams and other snails, small granite boulders, crevices within coquina reefs, and our three permanent concrete marking blocks.

We found no differences when comparing the mean number of capsules per carrying snail for the three sampling periods of La Cholla (1-way ANOVA after square root transformation: $F_{2,57} = 1.7$, P = 0.191), and the two sampling periods from Los Tanques (t-test: P = 0.37). In La Cholla, percentage of male and female snails carrying egg masses was also similar: 63.89% and 65.63%, respectively (n = 68, $\chi^2 = 0.022$, P = 0.881).

It was common to find carrying snails within one aggregation with the majority of the capsules recently laid and others with most of their egg capsules hatched. Like-

Table 1. Egg mass sizes and egg mass laying times for ten *Hexaplex nigritus* snails maintained in aquaria.

	Snail TL (mm)	Snail weight (g)	Capsules laid per egg mass	Days laying	# of capsules laid day^{-1}
	110.2	290	69	3	23
	110.2	290	186	9	21
	118.3	330	337	14	24
	120.4	340	161	2	81
	120.8	290	117	6	20
	122.8	310	27	6	5
	127.2	340	261	8	33
	141.5	440	63	10	6
	146.0	500	62	7	9
	146.0	500	87	1	87
Mean	123.3	363	137	6.6	30.9
SE	4.3	26.7	31.4	1.2	9.2

wise, individual carrying snails often had a patch or patches of recently laid capsules and others of hatched capsules. These patches could easily be identified at a glance by a variation in color, structure, and/or size of the capsules. Some snails had up to four of these patches (Fig. 4E).

Reproductive Output.—The mean number of capsules laid on individual carrying snails was 285 ± 57 (95% C.I.) for La Cholla (n = 62), and 421 ± 66 (95% C.I.) for Los Tanques-Conchas (n = 82). However, both La Cholla and Los Tanques-Conchas samples contained snails carrying > 1000 capsules (Fig. 4F). Capsule size increased markedly with parent snail length (R^2 = 0.55, P < 0.0001), and number of larvae increased with capsule length (R^2 = 0.16, P < 0.0001) (Fig. 5). The number of larvae/capsule varied considerably, from 150 (CL of 15 mm) to 20,189 (CL of 21.84 mm) (n = 456), with a mean number of larvae/capsule of 3603 ± 221 (95% C.I.).

Observations on Feeding and Predation.—We observed *H. nigritus* preying on at least 10 species of mollusks, primarily *M. capax*, callista clams, *Megapitaria* spp. (Sowerby, 1835), and *Chione* spp. We never witnessed other species preying on adult *H. nigritus*, but wrasses (*Halichoeres* spp.) and spotted sand bass, *Paralabrax maculatofasciatus* (Steindachner, 1868) were observed biting egg masses on aggregations (Fig. 4B). On one occasion, we found the intestines of a recently poached sea turtle, *Chelonia mydas* (Linnaeus, 1758) 200 km south of Puerto Peñasco filled with hundreds of fresh black murex egg capsules.

Discussion and Conclusions

Formation of Breeding Aggregations.—In the Gulf of California, mollusks may spawn year-round or seasonally (Ceballos-Vázquez et al., 2000). The black murex is an example of the latter, reproducing only during late spring and summer, with reproductive peaks in June and July, similar to that reported for prosobranch snails in other regions (see Saglam and Duzgunes, 2007). This pattern is also consistent with spawning and reproduction of various bivalves in the Gulf of California such as *Spondylus calcifer* (Carpenter, 1857) (Villalejo-Fuerte et al., 2002), *Dosinia ponderosa* (Gray, 1838) (Arreola-Hernández, 1997), and *Chione undatella* (Sowerby, 1835) (Baqueiro and Masso, 1988).

For *H. nigritus*, a rise in temperature could be one factor triggering reproduction and explain why the earliest aggregations were found in shallow warm waters nearshore, and as the season progressed, they were found in deeper waters offshore. Rise of temperature in spring induces spawning in many species of prosobranch mollusks (Hyman, 1967), and spawning has been shown to occur as a result of temperature increase for other mollusks in the Gulf of California (Villalejo-Fuerte et al., 2002). However, timing of reproductive events could also be related to temporal variations in other environmental factors, such as food availability and/or photoperiod (Ceballos-Vázquez et al., 2000).

The black murex snail is highly gregarious during reproduction. We confirmed the presence of an aggregation of 900 m² providing a catch of 3 mt. Interviews with fishermen and local buyers strongly suggest that aggregations used to be even larger during the initial stages of the fishery in the early 1990s, with catches of up to 6 mt sometimes obtained from one aggregation (Cudney-Bueno, 2007). Based on current weight data, catches of this magnitude could comprise up to 12,000 animals (Cudney-Bueno and Rowell, 2008). Although breeding aggregations are reported for other
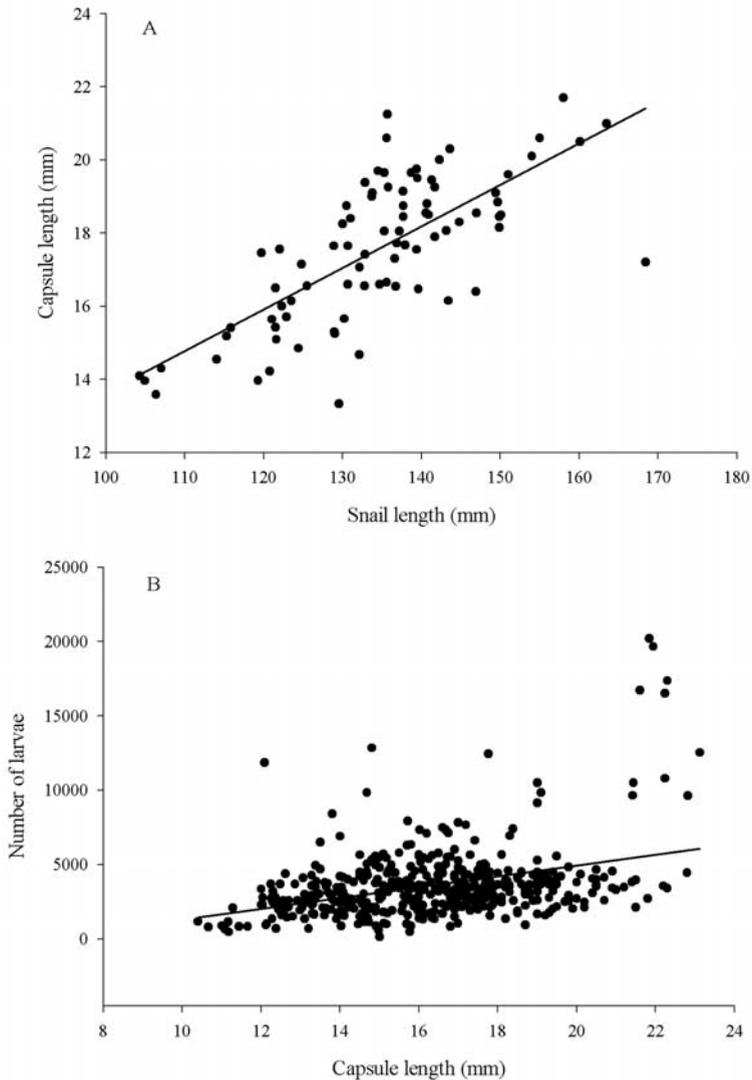
Figure 5. Relationships between (A) snail length and egg capsule length, and (B) egg capsule length and number of larvae for *Hexaplex nigritus* in the northern Gulf of California, Mexico. (A) $y = 0.113x + 2.301$ (n = 84, $R^2 = 0.53$, P < 0.0001); (B) $y = 363.35x – 2320.56$ (n = 456, $R^2 = 0.14$, P < 0.0001).

gastropods (Tompa et al., 1984; D'Asaro, 1986), we are unaware of any gastropod that can form aggregations as large as those of *H. nigritus*.

We observed 42 breeding aggregation sites in 5 yrs of study, the majority in La Cholla. This area is the most heavily fished during snail fishing season, providing over 70% of snail catches (Cudney-Bueno, 2000). Cudney-Bueno (2000) recorded 139 successful snail fishing trips in summer 1999, suggesting that there were at least 139 aggregations present in the vicinity of Puerto Peñasco that year, as our participation in fishing trips showed that fishers harvest the entire aggregation once it is found

and often target more than one aggregation in one day. Similarly, a total catch of 600 mt of snail was reported for La Cholla in 1992 (López-Reyes, 1992). This catch could entail at least 1,125,700 snails and a total breeding aggregation surface area of approximately 36,313 m^2 or 3.63 ha [these calculations are based on current estimates of average snail weight (533 g) and breeding aggregation density (31 snails m^{-2}) for La Cholla [see Cudney-Bueno and Rowell (2008) and Prescott and Cudney-Bueno (in press), respectively]. As far as we know, snail captures anywhere close to these amounts in such a small area (approximately 25 km^2) and short amount of time (3 mo) have not been reported for any other region of the Gulf of California or for any other area in the world.

Our observations on reproduction within breeding aggregations and changes in composition of the aggregation with time are similar to those reported for *Murex fulvescens* (Sowerby, 1834) (D'Asaro, 1986). Individuals of *M. fulvescens* gather in protected areas and begin spawning almost simultaneously, while late arrivals add egg masses on the periphery, on the shells of other spawners, or on previously deposited capsules. This explanation is also consistent with fishermen's observations and their fishing methods. At the beginning of the season, commercial divers usually follow the direction of the siphonal canal of individual snails to lead them towards the aggregation. By the end of the season, they follow on the opposite direction to lead them towards the aggregation the snails are leaving (Cudney-Bueno, 2000). Fishermen also rely on the conspicuous evidence of feeding left by snails immediately preceding the formation of a breeding aggregation or as they begin dispersing from it.

Site Fidelity.—The black murex snail shows some level of fidelity to reproductive sites. Individuals return to the same breeding locations during consecutive years and breeding aggregations form in the same general areas. Communal reproductive behavior in specific areas could have biological and evolutionary advantages. For instance, the location of reproductive sites may be an important factor in determining the dispersal and settlement of planktonic veliger larvae (Stoner et al., 1998). Also, as snails leave the aggregation, they could enhance dispersal of newly settled individuals and their survival by reducing local competition for food. A concurrent study found that 25% of snails had *H. nigritus* protoconchs within the spaces between egg capsules (Prescott, 2006). This suggests that some *H. nigritus* larvae are settling on top of snails and could find protection from predation by remaining above ground and hidden between egg capsules. Whether these newly settled individuals come from the aggregation they have settled on or from distant ones, however, is unknown. In this regard, a better understanding of early life history of *H. nigritus* will be of particular importance for management, as larval duration in the water column may have significant consequences for the dispersal range of *H. nigritus* (see Olson, 1985; Scheltema, 1986).

Egg Laying and Hatching.—We confirmed that embryos of *H. nigritus* hatch as veliger larvae after approximately 23 d of incubation (range 18–31 d). This is consistent with another muricid, the rapa whelk, *Rapana venosa* (Valenciennes, 1846), which incubates embryos that hatch as veliger larvae after 22 d (Saglam and Duzgunes, 2007). On the other hand, for *Hexaplex trunculus* (Linnaeus, 1758), full metamorphosis takes place within the capsule, and juvenile snails are released after 1 mo incubation (Vasconcelos et al., 2004).

Although we observed egg masses laid on substrates other than snails, these were minimal. A large number of egg capsules (> 1000) can be laid on an individual car-

rying snail, and these can be laid at different times and by at least four different females while aggregated. Egg-laying on conspecifics could therefore have evolved as a means for *H. nigritus* to cope with insufficient or lack of unfouled hard substrates for egg mass attachment. Formation of large breeding aggregations could extend the available surface area where egg masses are laid by snails laying eggs on the shells of other carrying snails. Snails were usually found aggregated on sandy or broken shell substrates and close to rocky reefs fouled with algae or other epibionts. Other studies have shown that prosobranch snails requiring unfouled, solid substrata for oviposition have limited choices and can aggregate to spawn on available substrata, including shells of other spawners (D'Asaro, 1986).

Sex Ratios of Breeding Aggregations.—The equal ratio of male to female snails, along with the fact that we did not find snails breeding prior to the formation of aggregations, suggests that breeding mostly takes place while snails are aggregated. However, whether all individuals are aggregating with the purpose of reproducing is not known. Non-spawning females and males have been reported in aggregations of *M. fulvescens* studied in northwest Florida (D'Asaro, 1986). Although there is no sexual dimorphism in *H. nigritus*, we caution that any differential growth between sexes could have biased our collection, which was haphazard. However, this is unlikely, as there is no indication of any type of differential growth between sexes that we are aware of.

Reproductive Output.—The number of embryos per capsule and overall reproductive output of *H. nigritus* is high compared to other muricids (see Vasconcelos, 2004; Saglam and Duzgunes, 2007). For instance, based on our counts, more than 1×10^6 eggs are present in just one egg mass of 300 capsules, compared to a total annual egg production of approximately 4×10^5 eggs for the rapa whelk, *R. venosa* (Saglam and Duzgunes, 2007). It is important to clarify that we focused our efforts on analyzing as many capsules as possible to obtain region-wide trends, which constrained our egg counts (a lengthy process) to one sample per capsule. Future studies obtaining numerous samples from each capsule and calculating averages per capsule could refine our estimations.

We also show that there is a relationship between snail size and capsule size, and capsule length and number of embryos. Both of these findings suggest that larger or older individuals have a higher reproductive output. A relationship between size and/or age and reproductive output has been found in gastropods and other mollusks (see Spight, 1979; Dame, 1996; Saglam and Duzgunes, 2007). Smaller individuals tend to put more effort into somatic growth and older individuals put more effort into reproduction (Dame, 1996). However, younger individuals as a group may contribute as many or more offspring because their numbers are often greater than those of larger individuals in the population (Dame, 1996). This is particularly relevant to fishery-exploited populations, whose size-frequency distributions can be dominated by smaller individuals. It is also important to consider that geographic variation in reproductive output could be present, mediated either by environmental constraints or variations in the genotype.

Management Implications.—Since its beginnings, the black murex fishery has been constrained to late spring and summer months (Cudney-Bueno, 2000). Considering this, our research shows that *H. nigritus* has essentially been harvested as it begins to aggregate, while fully aggregated, and as it begins to disperse. Because ag-

gregations tend to form in the same general areas, these areas can be targeted repeatedly with and among years, leading to a loss of much of the reproductive biomass.

Given the biology and behavior of *H. nigritus*, we suggest that harvest be restricted from May through the end of July as a first step towards a recovery of the fishery. This measure would allow for most individuals to reproduce (Cudney-Bueno, 2000) and would protect inshore populations, which aggregate sooner and are the ones in need of more urgent conservation measures. In 6 yrs of fieldwork we did not find *H. nigritus* in the intertidal zone, even though it was reported as a key intertidal predator in the same region during the 1960s (Paine, 1966). Fishermen also state that the frequency of formation of breeding aggregations close to shore and the overall size of individual aggregations has decreased considerably (Cudney-Bueno, 2007).

Seasonal closures alone, however, may not provide adequate protection and enhancement of overexploited areas. Given that *H. nigritus* reaches reproductive maturity in 2–3 yrs (Cudney-Bueno and Rowell, 2008), areas with low densities that have clear signs of having been over-harvested should be closed for a minimum of 3 yrs to allow for newly settled individuals to reach first reproductive age and reproduce at least once. In addition, population viability analyses of the fishery should be conducted to address long term threats to the species in accordance with various harvesting scenarios.

Finally, management efforts should be coupled with future studies on the species and long-term monitoring of both the fishery as well as of the benthic ecosystem (i.e., epifaunal community, predator-prey interactions) associated with black murex and their breeding aggregations. Black murex aggregations act as temporary reefs in a sand dominated region (Prescott and Cudney-Bueno, in press). We also confirmed the existence of other species feeding on egg capsules, including green turtles (*C. mydas*), wrasses (*Halichoeres* spp.), and spotted sand bass (*P. maculatofasciatus*), and observed the impacts on mussel and clam beds caused by black murex preying before and after formation of breeding aggregations. A better understanding of the species' role in the ecosystem, as well as of its early life history (particularly larval dispersal and post-settlement processes), adult movement patterns, and genetic population structure will be of particular importance to allow for a more comprehensive management and conservation of *H. nigritus* and the subtidal benthic ecosystem of the northern Gulf of California.

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