A Review of Queen Conch (*Strombus gigas*) Life-history

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Introduction

The queen conch, *Strombus gigas* L., occurs throughout the Caribbean and into the Gulf of Mexico, south Florida, the Bahamas, and Bermuda. The conch fishery was once the second most valuable in the greater Caribbean region (Berg and Olsen, 1989) with an estimated 1992 harvest value of U.S. $30 million (Appeldoorn and Rodriguez, 1994). A steady decline of the species resulted in conch being listed as commercially threatened by the Convention on the International Trade in Endangered Species (CITES) in 1985 (Wells et al., 1985). Declines in conch abundance persisted causing CITES in 1992 to downgrade the status of queen conch to a listing in Appendix II, which requires signatory nations to manage conch stocks closely, and to monitor exports carefully to prevent extinction of the species. Many nations now have strict regulations regarding harvest of conch, designed to preserve their stocks.

As recognized at the Queen Conch Stock Assessment and Management Workshop (CFMC/CFRAMP, 1999), queen conch have a number of life history traits that make the use of assessment methodologies designed for finfish assessment problematic. Growth of conch (shell length) is deterministic and soft tissue weight is constant in older individuals. Conch cannot be accurately aged. Conch morphology is highly plastic and may be quite variable among populations separated over short spatial scales. Also, reproduction in conch is characterized by multiple spawning events over many months and little information exists regarding larval transport among populations. A review of queen conch life history is presented here.

Taxonomy

Queen conch, *Strombus gigas*, are prosobranch mesogastropods in the Family Strombidae. Members of this Family usually have thick, heavy shells with conical spires that may be ornamented. In addition, shells of species in this Family often have a wing-like, broad lip with an anterior notch (the "stromboid notch"). The stromboid notch is particularly conspicuous in the genus *Strombus*. Six species of *Strombus* occur in the greater Caribbean region. Queen conch is the largest of those.

Distribution and Habitat

Queen conch occur throughout the Caribbean from the Orinoco River in Venezuela into the southern Gulf of Mexico, in the nearshore waters of the Caribbean islands to south Florida and Bermuda. Usually, conch are found in discrete aggregations that may include hundreds of thousands of individuals. Conch are found in shallow, clear water of oceanic or near-oceanic salinities at depths generally less than 75 meters and most often in water less than 30 meters deep. Conch are likely limited to that depth range by limits in seagrass and algae cover. Seagrass meadows, coral rubble, algal plains, and sandy substrates are the preferred habitat.

Growth

Conch growth, as measured by shell length (tip of the spire to anterior edge of the shell), is deterministic. Maximum shell length is attained at sexual maturity and corresponds with the formation of the flared lip of the shell. Shell length may decrease in older individuals due to erosion of the shell. Shell thickness, including thickness of the shell lip, increases with age. Interior volume of the shell decreases with age such that very old individuals have significantly smaller body size (CFMC/CFRAMP, 1999). Lip thickness has been used to age adult conch, at least relatively (Appeldoorn, 1988a; CFMC/CFRAMP, 1999).

Deterministic growth may affect estimates of juvenile growth, age, and mortality (CFMC/CFRAMP, 1999). Length-frequency analysis of large juveniles may be misleading because mean size of the largest juveniles will be less than the true mean size of the largest juvenile size class because as juveniles begin to mature and cease growth, new smaller juveniles enter the largest juvenile size class affecting the mean size. Relative numbers of large juveniles decrease with a concomitant increase in the relative number of adults. Growth of additional juveniles into the largest size class will change the shape of the frequency mode and increase the variance of growth estimates. L_∞ will likewise be affected (CFMC/CFRAMP, 1999).

Prior to maturation, growth of juvenile conch can be measured by increase in shell length. Appeldoorn (1990) provided equations describing juvenile conch growth for a population near La Parguera, Puerto Rico (southwest coast) developed from (1) length-frequency analysis and (2) growth-increment data.

$$(1) \qquad L_t = 340(1-e^{-0.437(t-0.462)})$$
$$(2) \qquad L_t = 460(1-e^{-0.25(t-0.244)})$$

Where L=length in millimeters and t=age in years. Although shell length ceases to increase in adult conch, shell lip thickness increases over time (until the shell begins to erode in old adults) and has been used to estimate adult conch growth since maturation. Appeldoorn (1988a) provided the following equation for determining age from maturation in years (t) from lip thickness (LT) measured in millimeters.

$$LT_t = 54.9(1-e^{-0.3706t})$$

Berg (1976) reported von Bertalanffy parameters for conch growth in shell length for animals in St. John and St. Croix, US Virgin Islands.

	L_∞	k	Phi
St. John	260.4	0.516	1.323
St. Croix	241.7	0.420	1.212

Queen conch are often landed after removal from the shell, therefore length/meat weight relationships are particularly important. CFMC/CFRAMP (1999) provided a number of equations illustrating the relationship between weight (meat, tissue, shell) and shell length for juvenile and adult conch and lip thickness of adult conch from La Parguera, Puerto Rico. Their table is reproduced here:

Group	Regression equation Y=a + b(x)	r^2	N	Mean x	Mean y
Meat Weight					
J Log(MW)=	-2.535+3.486 Log(L)	0.926	94	1.838	1.254
A Log(MW)=	-1.510+2.804 Log(L)	0.494	130	2.393	1.392
A Log(MW)=	2.212+0163 Log(LP)	0.274	131	2.394	1.117
A Log(MW)=	-1.357+2.571 Log(L)+0.135 Log(LP)	0.684	130		
A Log(MW+100)=	1.797+0.232 Log(L)	0.354	130	2.101	1.117
Tissue Weight					
J Log(TW)=	-2.286+3.459 Log(L)	0.925	94	2.053	1.254
A Log(TW)=	-1.444+2.928 Log(L)	0.524	130	2.632	1.392
A Log(TW)=	2.469+0.147 Log(LP)	0.214	131	2.633	1.117
A Log(TW)=	-1.294+2.726 Log(L)+0.118 Log(LP)	0.659	130		
A Log(TW+100)=	1.764+0.403 Log(LP)	0.321	130	2.121	1.117
Shell Weight					
J Log(SW)=	-1.786+3.517 Log(L)	0.878	94	2.626	1.254
A Log(SW)=	-0.286+2.530 Log(L)	0.347	130	3.237	1.392
A Log(SW)=	2.952+0.256 Log(LP)	0.579	131	3.237	1.117
A Log(SW)=	0.013+2.129 Log(L)+0.273 Log(LP)	0.822	130		
A Log(SW+100)=	2.793+0.293 Log(L)	0.633	130	3.720	1.117

All weights are in grams, length is in cm, and lip thickness is in mm. N is sample size. Logs are base 10. Meat weight=MW, wet-tissue weight=TW, shell weight=SW, juvenile =J, adult=A, shell length=L, lip thickness=LP. Mean x and y values are provided to permit conversion to y=u+vx where v=b/r and u=(mean y)-v(mean x).

Morphology

Conch shell morphology is highly plastic (Clerveaux et al., 2005) and habitat appears to exert a strong influence on juvenile and adult morphology (Martin-Mora et al., 1995). Food availability and quality differences among areas may be important indirect influences on conch morphology and growth. Appledoorn (1994) found differences in adult shell length among sampled areas in Puerto Rico. Similarly, Stoner and Ray (1996) observed adult shell length and lip thickness differences among sites in the central Bahamas. In addition, the presence of predators also affects juvenile conch growth. Delgado et al. (2002) showed that juvenile conch grew more slowly and had heavier shells when exposed to predators (spiny lobsters) than did conch held in the absence of predators.

The abiotic factors of depth and substrate type have also been implicated as factors affecting conch growth and morphology. With increasing depth, conch were observed to have slower growth (measured as shell length), tighter coiling of the shell resulting in a wider shell, thicker shells, and fewer, longer spines (Alcolado, 1976).

Growth rate is positively correlated with final shell length, where slow growing conch tend to reach smaller final shell lengths than do faster growing conch (Alcolado, 1976). In addition, Alcolado (1976) found that age at maturation was greater for slow growing than for fast growing conch. Area specific growth and maturity presents problems for stock assessments because growth and maturity found in any particular area may not be applied to conch throughout the region of interest.

Reproduction

Queen conch are dioecious and fertilization is internal. Both males and females may copulate with multiple individuals over the spawning season. Multiple males may fertilize individual egg masses from a single female (Steiner and Siddall, pers. comm. in CFMC/CFRAMP, 1999). An additional complicating aspect of conch reproduction is the ability of females to store eggs for several weeks (D'Asaro, 1965). Stoner et al.

(1992) found that spawning increased as a linear function of bottom water temperature, but declined during and after the warmest period. They suggest that photoperiod plays an important role in the timing of conch reproduction. Several authors have noted differences in spawning season at various locations throughout the species range.

Females lay demersal egg masses, generally on patches of bare sand, but occasionally in seagrass. Egg production is highly variable both in terms of the number of egg masses spawned each year and the number of eggs per egg mass. Appeldoorn (1993) examined individual female reproduction over a spawning season with conch held at two densities ($0.2/m^2$ and $0.014/m^2$) in enclosures. Food limitation in the higher density treatment negatively affected fecundity such that fewer egg masses were produced and those egg masses contained fewer eggs than egg masses produced in the low density treatment. Females in the low density treatment produced an average of 13.6 egg masses containing an average of 750,000 eggs each (Appeldoorn, 1993). High density treatment females produced and average of 6.7 egg masses of 500,000 eggs. Individual variation was high with on individual producing 25 egg masses, one of which contained 1.5 million eggs. Appeldoorn (1993) reported a significant relationship, for the low density treatment, between female age (determined from lip thickness) and total fecundity:

$$Log_{10}(Fecundity) = 4.157 + 2.012 Log_{10}(Age) \qquad r^2 = 0.672, N = 10$$

An additional equation to describe the relationship between conch age and fecundity was developed by Appeldoorn (1993). He assumed that fecundity was proportional to tissue wet weight and used as a guide the Gompertz function to predict weight from age for the average adult in the La Parguera population. The equation developed,

$$E_t = E_{max}(1 - e^{-K(t-32)})$$

includes fecundity at age t (E_t), average maximum fecundity for an individual (E_{max}), the instantaneous growth constant (K), and the age in years at the onset of maturation (3.2 in La Parguera). By age 6 (2.8 years after the onset of maturation), 95% of the adult conch growth occurs, based upon the tissue growth equation. K was therefore estimated as 1.07 from $t_{.95} = 3/K$.

Stock size may pay an important role in conch reproduction. Appeldoorn (1995) hypothesized that the repeated cycle of copulation and spawning stimulated reproductive a positive feedback relationship and reproductive output is increased. Too small a stock size might disrupt that feedback relationship.

Natural mortality

Conch are estimated to have a longevity of up to 30 years (Glazer, pers. comm..). High predation induced mortality is likely for juvenile conch, but decreases significantly among larger juveniles (Appeldoorn 1988b; Ray et al. 1994). Adult conch are thought to have low rates of natural mortality, however few studies have examined this question.

Appeldoorn (1988b) examined the relationship between age and natural mortality. He derived a relationship between juvenile age and natural mortality and estimated natural mortality for adult conch aged at 4.25 years as M=0.52. Natural mortality of older conch have not been estimated, therefore natural mortality rates for the majority of the lifespan of queen conch are unknown. The age-mortality relationship that Appeldoorn derived was further developed by omitting mortality estimates of small juveniles that were not yet epibenthic and therefore not available to the fishery. The estimate of adult natural mortality was included in fitting the age/mortality relationship with the inverse model of Caddy. This model was believed to be the most appropriate because extrapolated adult survival rates were consistent with the estimated longevity of conch. The age-mortality equation provided by CFMC/CFRAMP (1999) was:

$$M_t = -0.242 + 4.33/t \qquad where\ t = age$$

This equation results in negative values for M with older ages and CFMC/CFRAMP (1999) recommended restricting mortality to a minimum M=0.1. Once M=0.1, natural mortality should be assumed to be constant with older conch.

Stoner and Glazer (1998) investigated natural mortality rate in juvenile queen conch in Florida and the Bahamas. They reported that M varied greatly among seasons, habitats, and conch aggregation density. Estimates of M ranged from 12.0 for small (45mm) conch to 1.0 for large juveniles (175-215mm). At one site, estimates of M varied from 1.0 to 4.0 over a seven year period, however a second site located approximately 35 miles from the first had an average M of 4.71 over time for conch of similar size.

Migration/dispersal

Embryonic development of conch proceeds rapidly, although the duration is temperature dependent. The larval shell develops within 24 hours and the free swimming veliger larvae emerge from the eggs within 72 hours. The queen conch larval phase has been estimated to be less than a month in the wild (Davis, 1994). Hatchery reared larvae usually require 16 to 40 days to become competent and metamorphose (pers. obs.). Both observations suggest the potential for long distance transport by surface currents.

Once conch settle to the benthos, dispersal ability is greatly reduced. In a mosaic of benthic habitats, dispersal will be dependent upon the extent of suitable habitat. Sandt and Stoner (1993) report movement of juvenile conch from unvegetated areas to adjacent seagrass meadows at approximately 35-54 mm shell length. Stoner and Ray (1996) found evidence of migration of juvenile conch from shallow water nursery sites to deeper water areas as the conch matured. In the Bahamas, adult conch were observed to move seasonally from sand plains to hard bottom areas (Stoner and Sandt, 1992). Glazer et al. (2003) tracked adult conch with sonic tags for one year to estimate seasonal movement and home ranges in the Florida Keys. They report home ranges of <1 to approximately 60 hectares with most individuals moving over home ranges of less than eight hectares.

Genetic stock assessment

The population structure of queen conch has been studied by Mitton et al. (1989) and Campton et al. (1992) for populations in Bermuda; the Florida Keys; Bimini, Bahamas; Turks and Caicos Islands; several sites in the Lesser Antilles; and Belize. Both studies compared variation in allozyme allele frequencies among populations and both inferred high levels of gene flow. Mitton et al. (1989) reported that conch populations were not panmictic. Conch in Bermuda were isolated from Caribbean populations and Mitton et al. attributed that isolation to current patterns. Heterogeneity in allele frequencies was observed within some island groups, which the authors suggested also resulted from current patterns. Campton et al. (1992) sampled conch in the Florida Keys for three years, reporting significant spatial and temporal genetic variation although genetic similarity among populations was high. The authors suggest that variation in current patterns and other transport processes (e.g. wind driven currents) may allow for much variation in the source and supply of larvae to any particular location.

Two features of allozyme studies limit their usefulness for fine-scale population structure. First, allozymes tend to be slowly evolving relative to the time-scale of population processes, and typically have low levels of polymorphism. This can result in a low-resolution view of population structure. Second, alleles are scored on a gel as fast, slow, intermediate, etc., using standard electrophoretic techniques, but these alleles cannot be related in a hierarchy or phylogeny based on their mobility. This limits the analytical possibilities of allozyme data. Both technical advances in generating high resolution population genetic markers and analytical advances have been made since the pioneering work of Mitton et al., 1989, and Campton et al., 1992.

Morales (2004) compared partial sequences of the 16S rRNA gene from 13 sites in the Caribbean region, including Puerto Rico. Total sample size was 94 individuals with four to 17 individuals per site. He found

evidence of connectivity among distant locations throughout the region and concluded that gene flow is likely facilitated by larval transport.

Steve Palumbi is currently examining the population genetics of conch from the Florida Keys through the Bahamas and Turks and Caicos Islands. He preliminarily reports some differentiation among populations in the Bahamas (Palumbi, pers. comm..).

Discussion

Many aspects of the life history of queen conch are problematic for traditional stock assessment methods. Deterministic growth, inadequate methods for aging adults, highly variable fecundities are among the problems conch life history characteristics present to successful stock assessment. Magnitude and sources of larval supply are poorly understood. Although population genetic studies have been completed, such studies often address population connectivity on timescales greater than those of interest to stock assessment. Finally, many of the life-history characteristics of queen conch vary over relatively small spatial scales. That particular characteristic of queen conch biology may be the most troublesome for stock assessment.

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