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Biology of the Wavy Top Turban *Megastraea undosa* (Wood, 1828) from Southern California, and the Baja California Peninsula (Turbinidae)

Paul M. Tuskes and Ann M. Tuskes
3808 Sioux Ave. San Diego, California 92117, tuskes@aol.com

ABSTRACT *Megastraea undosa* (Wood, 1828) and *M. turbanica* (Dall, 1910) constitute a notable fishery in Baja California, México and a much smaller fishery in southern California, USA. The *in situ* diet of *M. undosa* includes over 30 genera of marine algae. New data from southern California are presented and compared to research from México. Information regarding the habitat of early age classes, change in shell shape with age, growth rates, longevity, and muscle weight vs. basal diameter are presented. California State Fish and Wildlife data for commercial landings of *Megastraea* for the past 23 years indicate 75 % of the catch has been taken off San Diego, California. Among *M. undosa* with basal diameters of 90 mm or greater, approximately 15.5 % of the gross weight is edible muscle.

KEY WORDS *Megastraea,* diet, longevity, depth, commercial catch

INTRODUCTION

Within the gastropod family Turbinidae, McLean, 1970 assigned *Astraea undosa* (Wood, 1828) and *A. turbanica* Dall, 1910 to a new subgenus *Megastraea.* That decision was based on shell size, pattern of radial ridges, the heavy fibrous periostracum, and the uniquely ribbed-calcareous operculum. In Marine Shells of Southern California*,* 2nd edition McLean (1978) continued to use *Astraea* as the genus and *Megastraea* as the subgenus for *A. undosa*; *Astraea turbanica* appears to have been outside the scope of that publication. Hickman & McLean (1990) revised the superfamily Trochacea (now Trochoidae) and *Megastraea* as a subgenus of *Astraea* was retained. It is not clear when or by whom *Megastraea* was elevated to a full genus, but *Megastraea* was used by California Fish and Wildlife (Taniguchi & Rogers-Bennett, 2001). Williams *et al*. (2008) reviewed the molecular genetics of the Turbinidae, Trochidae, and Trochoidea, and those results indicate that both *Megastraea* and *Pomaulax* from the Pacific coast of North American are distinct from *Astraea/Lithopoma* of the western Atlantic.

The goals of this paper are to: (1) examine both the depth and habitat of *M. undosa,* (2) review extensive life history information published primarily in México, (3) present new information from California regarding age and growth, (4) provide initial data on the relationship between shell size, age and muscle weight, and (5) present a brief review of the commercial fishery for *Megastraea* in both southern California and the Baja peninsula of México. Other observations and data are presented.

Although *M. undosa* and *M. turbanica* are similar in general appearance, these two species are easily identified by their profile and opercula. Both have a prominent peripheral undulating radial cord with regularly spaced nodules. *Megastraea undosa* has one such cord with the suture immediately below, thus the shell is conical and typically only the radial cord is projecting (Figures 1a-b). Some *M. undosa* may have an enlarged nodule at the base of each

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axial ribs (Figures 4 & 5) but do not fuse to form a solid second radial cord. *Megastraea turbanica* has two undulating radial cords with an imperforation between, both of which are equally prominent on the early whorls. On later whorls, the suture is often on the shoulder of the lower cord making it appear diminutive compared to the upper cord. The prominent constriction between the two cords gives the profile a rough and slightly bulbus appearance The axial ribs of *M. turbanica* are solid, less numerous, and often twice as wide as those of *M. undosa* (Figures 8a & b).

The calcareous operculum of both species has three strong ridges on the outer surface. The operculum of *M. undosa* is elongated, the length to width ratio (L:W) average of 1.25; the ridges of the operculum are somewhat parallel until they meet near the apex; all three ridges have a rough texture (Figure 1c). The operculum of *M. turbanica* is more oval with an average L:W ratio of 1.45; the upper opercular ridge is rough, while the two lower ridges are typically smooth, and they fold as they approach the apex (Figure 8c). Both species of *Megastraea* are harvested commercially for their meat, and the authors have observed the polished shells sold in shops from Europe to Australia.

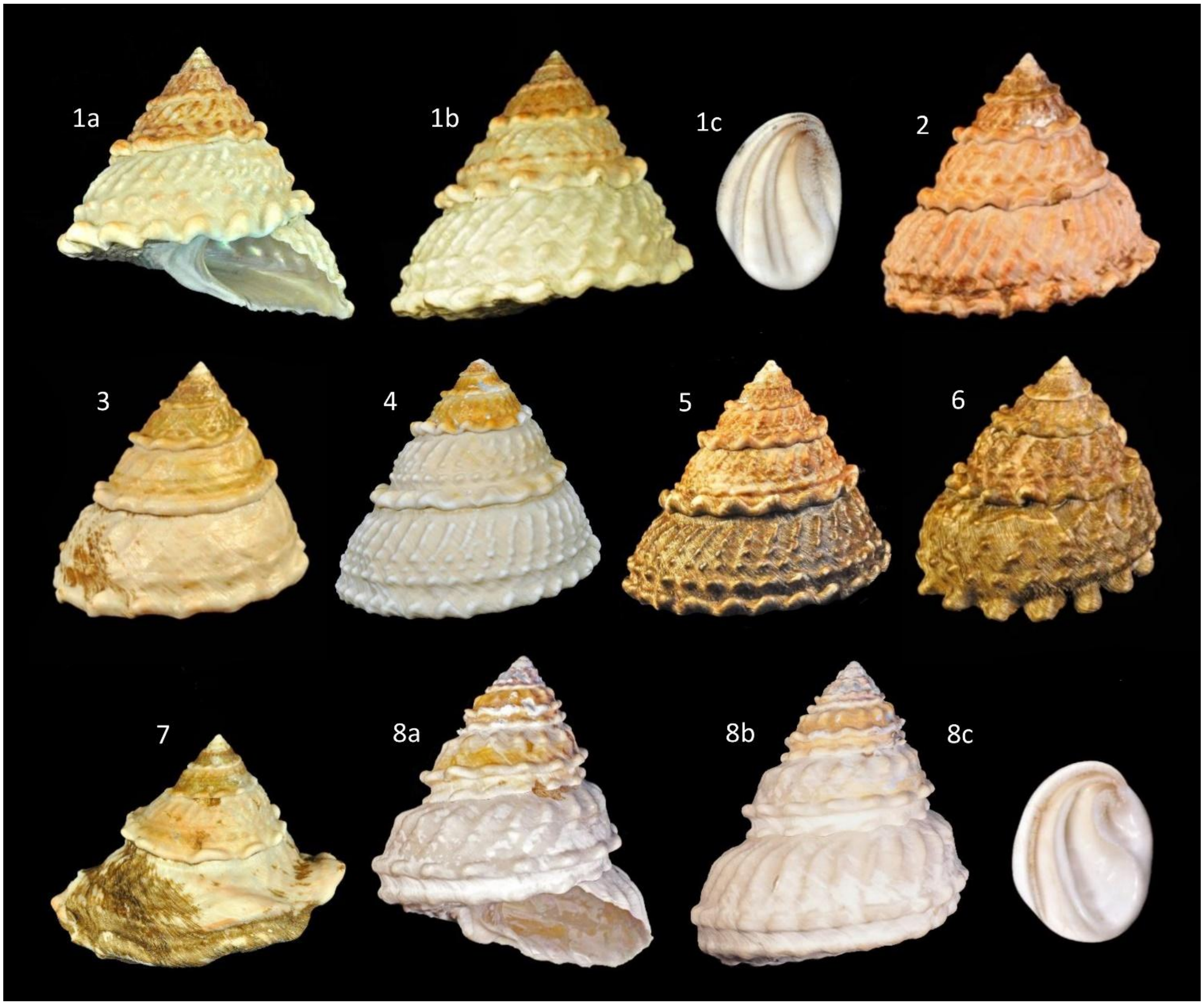
The most northern record for *M. undosa*, is Avila Beach, just north of Shell Beach, San Luis Obispo Co. California, Alf (2019). The current expected range remains from Point Conception (34°27’04N-120°28’16W), Santa Barbara Co., California, south to the area of Punta Pequeña which forms the headlands of Bahía Scorpion (26°13’52 N-112°.29’29 W) and the community of San Juanico, Baja California Sur, México (BCS). San Juanico is in the transitional zone between the temperate California Marine Province and the tropical Panamic Marine Province.

Martone & Micheli (2012) cited Morris *et al.* (1980) indicating that *M. undosa* occurs further south to Bahía Magdalena in BCS, that location is incorrect. Abbott & Haderlie (1980) *in* Morris *et al.* (1980), stated the southern record for this species [at that time] was Isla Asuncion, which is approximately 350 Km NW of Bahia Magdalena. The type locality of *M. turbanica* is from the area of Bahía Magdalena, BCS (Dall, 1910) and may have been the source of confusion. The type specimen of *M. undosa* was illustrated by Wood (1828), with the type locality listed only as California.

Because the apex of large *Megastraea* shells may be eroded, the height of those shells can only be estimated. The most reliable measurement of size is the basal diameter (BD) and is the standard regulatory measurement in México. The term ‘mature’ is applied to large shells in age class 10 or greater. The distinction is made because sexual maturity may occur as early as age class 5, at which time the basal diameter may be only half that of a mature shell. Initially, *M. turbanica* was to be included in this paper, but sufficient numbers of various age classes for a meaningful statistical comparison with *M. undosa* have not been found, but will be the subject of a future paper.

Abbreviations

AE = Assimilation Efficiency
Avg = Average
BC = Baja California, México
BCS = Baja California Sur, México
BD = Basal Diameter of shell
CA = California
H/W = Height to Width ratio
OP = Operculum
STD = Standard Deviation



Figures 1-8: 1a-1b. *M. undosa*, basal diameter 110 mm, height 112 mm, typical phenotype with strong undulating radial cord. **1c.** External operculum, length 45.5 mm. *M. undosa* range of variation (**2-5**): **2.** Pink, with strong axial ribs extending to radial cord. **3.** Yellow-cream, axial nodes and ribs absent, radial cords with reduced undulation **4.** Typical form, Isla Guadalupe, BC, México. **5.** Typical form with periostricum and some free nodes in axial ribs. **6 & 7.** Unique aberations. **6.** Nodules of radial cord of final whorl enlarged and oriented down vs horizontal, with heavy periostricum. **7.** Shell with projection on opposite sides, radial cord present but simple. **8a-b**. *M. turbanica,* basal diameter 137 mm, height 153 mm. **8c**. External operculum, length 59.6 mm.

METHODS

Megastraea were collected while SCUBA diving in Mission Bay, Point Loma and La Jolla, San Diego, CA. The series of *Megastraea* measured from Isla Guadalupe, BC, were harvested commercially and purchased at the island approximately 30 years ago.

San Diego shells were cleaned with a wire brush and then a scraper to remove surface debris such as algae, barnacles, tunicates*, Crepidula,* tube worms and then placed in plastic bags and frozen. After two days shells were thawed, and excess liquid removed by loosening the foot, so that trapped water and mucus could drain. An identification number, in pencil, was assigned to the shell and corresponding operculum and information recorded as follows (1) basal diameter (BD), (2) shell height, (3) gross weight, (4) weight of the cleaned foot, minus the operculum, (5) operculum length and (6) number of growth increments on the operculum, and distance between each increment. When comparing *M. undosa* growth between Mission Bay and La Jolla, a one tailed *t*-test, was used to evaluate both opercular length and basal diameter.

Two methods were attempted to estimate age based on research in México. (1) External annual growth lines on the shells required carefully cleaned and the shell bleached in order to reveal growth patterns on the shell. That method was both time consuming, and growth lines were often lacking. (2) An alternative method utilized a dissecting scope to count and measure distance between growth rings on the operculum proved to be reliable and reproducible. The rings of the operculum was the method used in this study. Data from both locations was maintained separately.

As part of a different study, underwater transects were conducted off Isla Coronado del Norte, BC, México. The effort was a pilot study focused on evaluating methods, statistics, and resources for a larger effort to evaluate gastropod diversity and richness in similar habitats and depths on a north-south gradient. The target areas had similar rock habitat and the depth averaged 14-16 m. Each transect was 20 m^2 and scored by two divers. Ten transects were conducted at each site and no rocks were turned, nor were animals collected.

RESULTS

Annual opercular growth rings provide an estimate of age, which was correlated with opercular length for each age class (Table 1). The operculum length of similar age classes from Mission Bay and La Jolla varied slightly, but insignificantly (*t*-test P <0.05). At age class 12, the average OP length for these two locations varied by only 0.5 mm. The sample size from Mission Bay was 140 specimens, and 62 specimens from La Jolla. The La Jolla sample was less, because six age classes were not present (Table 2).

Age class data for each specimen was then correlated with its BD to generate a chart allowing an estimate of age based upon a single BD measurement (Table 2). Except for age class 11, there was no significant difference in BD between *M. undosa* from Mission Bay and La Jolla. Age class 11 from Mission Bay was significantly smaller (P> 0.001) than specimens of the same age from La Jolla.

Data in Table 3 indicates that *M. undosa* from Isla Guadalupe, BC does not represent a dwarf population as suggested by Alf (2019). The general shape of the shells is consistent with those from San Diego. Graph 1 documents the change in shell shape as *M. undosa* continues to grow. Graph 2 presents the correlation between edible muscle (grams) associated with varying basal diameters of *M. undosa*.

DISCUSSION

Growth – Size – Age: The best measure of shell size is the basal diameter, as notable erosion of the apex may occur among large specimens. In México the BD, not the height of the shell, is used to determine the minimum legal size for harvest. Two methods have been used to determine age: growth lines on the operculum and growth lines on the shell (Cupul-Magana & Torres-Moye, 1996, Gluyas-Millán *et al.*, 2000, Marton & Micheli, 2012). In San Diego, the level of certainty using annual growth marks on the external shell surface proved to be unsatisfactory. Determination of

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age based on opercular (OP) growth lines was productive and reproducible, but some subjectivity is still involved. By counting opercular rings and measuring the distances between intervals, growth history information for prior years can be obtained. As a result, age class 12 could yield a dozen OP growth lines, and one basal diameter measurement.

Typically, not all individuals in the same age class grow at a similar rate. Snails that grow faster or slower, may have a BD that overlaps early or later age classes. Based on annual opercular growth lines for the San Diego area, it is estimated that 7 % of the sample may be improperly assigned (+/– 1 year) when using BD data (Table 2) as a measure of age. The error is most likely to occur in age classes with greater standard deviation in BD. On the positive side, using localized BD data that has been correlated with age does not require additional animals to be sacrificed when estimating the age of an individual or the age class structure of the population. As a result, the measurements of BD can be recorded easily while underwater or on land, and the age estimated (Table 2). The data in Table 2 is relevant to the San Diego area where 75 % of *Megastraea* have been commercially collected in California.

Research on the Baja California Peninsula has demonstrated the need for localized data regarding age class charts, due to variation in growth rates in different fishery management zones. Most studies have dealt with the primary fishing grounds in BC and BCS, and provide comparative data. The following authors estimated the average BD for age class 12 at their study sites: Martone & Micheli (2012) Bahía Tortugas 109 mm and Punta Abreojos 121 mm; Cupul-Magana & Torres-Moye (1996) Bahía de Todos Santos 80 mm; Gluyas-Millán *et al.* (2000) five locations 122.4-128.9 mm (not all locations contained age class 12); Gluyas-Millán *et al.* (1999) Bahía Tortugas 105 mm. None of these authors reported *M. undosa* older than age class 12. The variability reported above may be influenced by water temperature, habitat quality, availability of food, population density, and other biotic and abiotic factors that influence the habitat quality, which in turn, may promote or retard growth. In addition, excessive commercial harvest has also been shown to impact both size and age class structure of a population Rodríguez-Valencia *et al*. (2002).

With one exception, no notable difference in BD was found between the shallow waters of outer Mission Bay and the deeper waters off La Jolla (Table 2). The exception being age class 11; those individuals from Mission Bay were significantly smaller (5.5 mm) than those from La Jolla ($P > 0.001$) (n=26). The reason for the variance in age class 11 is unknown. The length of the OP for age class 11 at both locations were similar and did not reflect the difference in BD. At age class 12, the average BD was not statistically different between the two locations (Table 2).

There was a clear preponderance of larger snails, age classes 11-14 found off-shore, while early age class shells were rarely observed. As such, when evaluating BD, the sample size for ages 1-6, from La Jolla were not sufficient for statistical analysis with Mission Bay. The reverse was true for Mission Bay as age class 12 was uncommon, while all early age classes were commonly found (Table 2).

Isla Guadalupe is an isolated location approximately 255 km off the west coast of BC, México. The authors had the opportunity to examine and measure 29 commercially collected shells from the island. The average BD, height, and shell shape (height/BD ratio) fell within the range of shells from San Diego

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(Table 3). All of the Guadalupe shells were over the legal limit of 90 mm BD and were purchased on the island, in the past. Alf (2019) incorrectly reported the Isla Guadalupe population to being dwarf, not exceeding 80 mm in BD.

The arrangement of the axial pattern and radial cord of *M. undosa* from Isla Guadalupe is not unique, as similar patterns are found in Mission Bay, La Jolla, and Point Loma. Chance (1958) indicated the shells from Isla Guadalupe were "apparently more variable than on the mainland". Of the 29 shells examined by the authors the range of variability appeared similar to that observed in southern California and Baja California. Isla Guadalupe is isolated, but isolation alone is not a criterion for a new species or subspecies. Haupt *et al.* (2013) suggest that *M. undosa* recolonized the northern portion of its current range after the last period of glaciation. The extent of gene flow between the mainland and the island is not known.

Shell Variation. The shells of *M. undosa* are variable both in shape and color. The small nodes usually coalesce to form a series of diagonal, narrow shallow axial ribs (Figures 1, 2, 4) with a slight enlarged nodule ending just above the undulating radial cord, or may consist of a series of fused and isolated nodes that form axial ribs (Figure 5). The radial cord above the suture is undulated with raised nodules. When the axial ribs are poorly developed or nearly absent (Figure 3) the radial cord may lack notable undulations and minimal nodules.

The shell color of first 3-6 whorls may be pink, cream, white, yellow (Figures 1-4), or orange. By age class 9 (BD 95 mm) the newly deposited shell is usually white. With age, pigments tend to fade but may remain present on the upper most whorls. The coloration is not apparent until the fibrous brown periostracum (Figures 5 & 6) is removed. The number of cords on the base of the shell varies from 2-5 with 98% having 3-4 cords (n = 50).

Two of 140 shells collected in Mission Bay displayed abnormal growth. One shell (Figure 6) had extremely thick periostracum and the nodules on the radial cord of the last whorl were large and oriented down rather than horizontally. As a result, the shell rests on the nodules rather than the ventral surface. A second shell (Figure 7) exhibited large, broadly flattened lobes projecting horizontally from opposite sides of the last whorl.

While taking BD and height measurements of *Megastraea undosa*, it was observed that shell shape gradually changed with growth/age. Initially the BD of the shell is greater than the height (Graph 1). As the shell grows, they may approach an equilateral triangle. Approximately 23% of the shells may become taller than wide.

Depth - Size - Habitat. Off-shore, snails are found on rocky reef that support dozens of algal species, and often large species of kelp. Alf (2019) suggested that *Megastraea undosa* occurs on gravel bottoms near rocks at depths to 10 m and is then replaced by *M. turbanica* where the two species are sympatric. That is not correct. Gravel bottoms are exceedingly uncommon in southern California and Baja California. Further, gravel would be an unsuitable substrate for the attachment of kelp and other macro algae in the open ocean. Off-shore, snails are found on rocky reef, or in Mission Bay on large boulders that line the jetty. Small to mid-sized snails may be observed among eel grass beds where the channel opens into the bay and beyond. *Megastraea undosa* has a diverse diet, and is not dependent on kelp nor limited to a 10 m depth. The authors commonly observe *M. undosa* to 25 m, which is the deepest they typically dive.

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Taniguchi & Rogers-Bennett (2001) of California Fish & Wild Life, reported *M. undosa* at a depth of 82 m (250 ft.). They also discussed a shell with a BD of 150 mm taken at Farnsworth Bank, west of Santa Catalina Island, at a depth of 36.5 m (120 ft). Few *M. undosa* of similar size were located in both the collections of the San Diego Natural History Museum and the Natural History Museum of Los Angeles, but could not be aged, as no opercula were associated with the specimens. A shell in the present study, collected from La Jolla had a BD of 137 mm and an OP length of 56.3 mm, the snail was starting its 14th year, it is likely that a BD of 150 mm is age class 15.

Gluyas-Millán *et al.* (2000) and Cupul-Magana & Torres-Moye (1996) refer to the early stages as being either rare or cryptic as they were infrequently observed at their study cites. In the current study the authors failed to find the early age classes at off-shore La Jolla (Table 2). In Mission Bay age classes 1-5 were common in the outer bay at a depth of 0.5 to 1.5 meters below mean low tide. The juvenile snails are found in protected rocky habitat covered with various species of coralline algae. On the east side of Mariners Basin, early age classes were also common in shallow water associated with beds of eel grass. The early age classes are neither rare, hidden, or cryptic; they were found in a different habitat than snails of the size taken commercially. Schwalm (1973) and Alfaro & Carpenter (1999) also reported finding early age classes in shallow water and noted the general absence of early age classes in deeper water.

Despite dozens of dives over a period of three years off La Jolla the authors failed to find adequate numbers of age class 6 and less for statistical analysis with material from Mission Bay. Those early age classes would have a BD of 25 to 70 mm, and be too large to have been overlooked, especially since they were readily found in the shallows of Mission Bay.

The largest shell measured from Mission Bay had a BD of 121 mm and was age class 12, which is uncommon in the bay, where the vast majority of the shells with a BD greater than 90 mm were age classes 9-11. Off-shore at La Jolla, age classes 9-13 where common resulting in a disproportional number of larger shells (Table 2 & 3) and a larger average BD than the Mission Bay sample for shells equal to or greater than 90 mm BD.

Diet Review. In the *Seaweeds of the Pacific Coast* Mondragon & Mondragon (2003) apply the common name kelp to numerous species of large marine brown algae that may grow greater than 2 m in length. Although many algal species would be considered to be kelp based on that definition, when discussing kelp beds in southern California and Baja California, *Macrocystis pyrifera* (Linnaeus) C. Agardh, 1820 and *Egregia menziesii* (Turner) Areschou, 1876 are typically the dominant components. Kelp beds are not a monoculture, as dozens of additional macro species of red, brown, and green algae are present on the rocky reefs.

Laboratory studies have used various methods to determine feeding hierarchy, with the measure focused on selection and consumption. Limitations of such studies include the number of algal species tested, seasonality and geographical preference. Leighton (1966) conducted early studies regarding the diet of *M. undosa* and other kelp bed mollusks.

Dietary studies have become more sophisticated, both in methods and analysis. Coarse estimates of food value are frequently based on C:N and % Assimilation Efficiency (% AE) which includes C:N. Proximal analysis of algae is far more revealing and includes carbohydrates, lipids, amino acids, protein and, based on the characteristics of the herbivore, estimates of caloric value may be possible (Castro-Gonzalez *et al*. 1994). Schwalm (1973) combined assimilation methods with physiological and respiration studies to develop a model reflecting energy use/allocation by *M. undosa*.

The use of stable isotope analysis can enhance the knowledge of current and past diets and the flow of energy through portions of an ecosystem. Piñón-Gimate *et al*. (2016) compared the diet of *Megastraea undosa* with that of the commonly sympatric giant keyhole limpet *Megathura crenulata* (G.B. Sowerby I, 1825) via stable isotope analysis. As expected, *M. undosa* is primarily an herbivore while *M. crenulata* thought to be an herbivore is in fact, an omnivore.

Cox & Murray (2006) combined current analytical methods with two-choice laboratory experiments to evaluate food value and diet preference. They tested 12 species of algae and found the % AE was lowest among the kelp and highest among other algae such as *Pterocladiella capillacea* (S.G. Gmelin, 1768) Santelices & Hommersand, 1997 and *Halidrys dioica* Gardner, 1913. They pointed out that the selection of kelp such as *M. pyrifera* with a lower % AE by *M. undosa* seemed counter intuitive and discussed possible evolutionary factors that may have contributed to food selection such as chemical defenses or lack thereof.

Aguilar-Rosas *et al.* (1990) studied the diet of *M. undosa* based on analysis of gut content from snails collected at Punta Banda, just south of Ensenada, BC. They identified 17 genera of algae that were consumed, of which 10 were identified to species. In order of consumption from highest to lowest was *Sphacelaria rigidula* Kützing, 1843, *Gelidium pusillum* Collins, 1903, *Jania* sp., and *Corallina* sp. Some seasonality was shown in the consumption of *Cladophora columbiana* Collins, 1903, *Lithothrix aspergillum* (Gray, 1867), and *Polysiphonia eastwoodiae* Setchell & Gardner, 1930. Pronounced seasonality was observed in the remaining species (still in order of utilization) *Pterosiphonia dendroidea* (Montagne) Falkenberg, 1901, *Laurencia* sp., *Herposiphonia tenella* (C. Agardh) Ambron, 1880, *Ceramium* sp., *Lithothamnion californicum* Foslie, 1900, *Centroceras clavulatum* (C. Agardh) Montagne, 1846, *Hincksia mitchelliae* (Harvey) P.C. Silva, 1987, *Callithamnion* sp., *Ulva* sp., and *Enteromorpha* sp.

Recently Mazariegos-Villarreal *et al*. (2017) published the results of *M. undosa* gut analysis at three locations in BCS; the samples were collected periodically over the course of a year. The snails consume 30 genera of algae, one species of vascular plant *Phyllospadix sp*., and various taxa of invertebrates. The diet varied seasonally and by location. Various species of red and brown algae with *Macrocystis*, *Ecklonia,* and *Corallina* was consumed at all locations. Others algal species were eaten less frequently and/or seasonally. They speculated that invertebrates were incidentally consumed as a result of living epiphytically on algae, but noted that consumption of ascidian tunicates may have been purposeful.

Based on gut analysis of field collected animals, Aguilar-Rosas *et al*. (1990) and Mazariegos-Villarreal *et al.* (2017) identified 31 non-overlapping genera of algae consumed by *M. undosa.* There is little doubt that similar studies at other locations, perhaps further north, will identify even more genera in the diet of this species. The broad diet of *M. undosa* allows it to thrive in a wide range of habitats and at depths well beyond the *Macrocystis* kelp forest.

In Mission Bay, large numbers of *M. undosa* were found with BD of less than 55 mm living among calcareous coralline algae which is also consumed by larger snails over a wide range of depths. Based on A/E % data, Mazariegos-Villarreal *et al*. (2017) commented on the low food value of the coralline species. Although it is speculation, is it possible that the snails benefit more from the ingestion of the calcareous structure of the coralline algae than the consumption of the live plant tissue?

Reproduction – Development Review. Gluyas-Millán *et al.* (2000) found the sex ratios were approximately 1:1. Males were slightly larger than females of the same age class and location. They suggested the difference might be attributed to females putting more energy into gonadal development rather than shell development. Cupul-Magana & Torres-Moye (1996), and Schwalm (1973) also reported a sex ratio of approximately 1:1.

Martone & Micheli (2012) evaluated monthly growth rates, age classes and gonad development in two populations in different oceanic environments. Bahia Tortugas (27°678'N -114°919'W) is an area of persistent upwelling, while Punta Abreojos (26°707'N-113°579'W) is further south, with weak upwelling and warmer water. To the north, sexually mature snails had BDs of 50-60 mm while in the south they matured at 60-70 mm BD. After age class three, the mean BD of shells were significantly larger in the south but they reported reduced fecundity in the warmer water. The first notable increase in fecundity over smaller individuals was among snails with a BD of 60-80 mm.

Belmar-Pérez *et al.* (1991) and Belmar-Pérez & Guzmán-del Próo (1992) examined gonadal development of *M. undosa* and found peak reproductive activity occurred from the fall to early spring, but low levels of reproductive activity were reported throughout the year. The extent of reproductive activity varied yearly, and may be influenced by water temperature, depth, and maturity of the snails. Males tended to congregate in breeding clusters prior to the females arriving. The species is a broad-cast spawner. The gonads of the male are ivory in color while those of the females are green to olive (Belmar-Perez *et al.,* 1991, Gluyas-Millán *et al*., 1999).

Guzman *et al*. (2003) spawned *M. undosa* in the laboratory and both described and illustrated the development from the fertilized egg to the juvenile snail at day 70. On day five the pelagic larvae settle out of the water column, but it was not until day 9 that they entered the post larval stage and displayed well developed eyes. Juvenile shell development began at day 30, with shell pigmentation at day 45; they continued to document development to day 70. During their developmental study the water temperature was 17- 20° C. In laboratory studies Catton, 2005 tested the development of eggs at five-degree increments from 10 to 25° C, and found cleavage in the eggs to be abnormal at only the lowest temperature. Development in the fertilized eggs was normal and accelerated at progressively higher temperatures within the parameters of the study.

The length of time in the planktonic stage is an important factor influencing dispersal and connectivity within a geographic area. Higher water temperatures in BCS may shorten developmental time and therefore the duration in the planktonic stage, which in turn may contribute to less connectivity in warmer waters. Haupt *et al.* (2013) reviewed mtDNA patterns from 17 locations along the length of this species' distribution. They found the northern population were genetically more homogeneous, while portions of the southern population were far more genetically diverse with many haplotypes, indicating that gene exchange from south to north, is not robust. They also discussed historic fluctuations in oceanic conditions and how it may influence genetic connectivity and suggest that the reduced genetic variability of the northern population may be the result of founder's effect resulting from reinvasion of the area after the last period of glaciation.

Temperature Tolerance. In a laboratory study Diaz *et al.* (2011) determined that at 29.7 °C (85.7° F) 50 % of the *M. undosa* tested could no longer grip the surface with their foot, an LD_{50} was not determined**.** Gluyas-Millán *et al.* (2002) reviewed the impact of an El Niño event (1997-98) in the northern portion of BCS where ocean temperatures reached 27 °C, nearly 4 °C higher than normal. They observed increased mortality among *M. undosa*, a significant decrease in snail biomass, and a 26.5 % reduction in annual catch. They attributed the elevated mortality and reduced biomass to starvation resulting from the loss of the giant kelp *Macrocystis pyrifera.* Considering the diverse diet of this herbivore, many of the other 30 genera of algae they are known to consume must have also been negatively affected. During the 2016 El Niño, surface water temperatures in Mission Bay reached 27 °C. Below three meters the water was 25 °C. Both *M. pyrifera* and *E. menziesii* were temporarily lost in Mission Bay, but increased mortality or other obvious changes in the *M. undosa* population was not observed.

Commercial Fishery. The commercial fishery for *Megastraea* started in BCS in 1980. A report from the Secretary of Agriculture, Livestock, Rural Development, Fisheries and Food (Item 11, *Megastraea*. 2018) summarizes the commercial fisheries of México from 2000-2016. An estimated average of 200 tons of *Megastraea* muscle was harvested in BCS annually; the average catch in BC was approximately 49 tons/year. A decline of the yearly catch began in BCS in 2011 and in BC during 2013. The report does not indicate if the reduced catch was driven by market demand or a depletion of the population. Biologists in México provide recommendations to fishing cooperatives regarding the regional catch. A 20% annual take of the legal sized individuals is the guideline used for annual quotas (Item 11, *Megastraea*. 2018).

The California fishery began in 1992, but initially the catch was placed in the miscellaneous category by California Fish and Wildlife. In 1996 the catch was reported separately as "Snail Top." Table 4 presents California Fish and Wildlife data for the commercial landing of *Megastraea* and price per pound (in shell). The annual value of the harvest in southern California has fluctuated greatly as has the pounds harvested, with record landings from 1998 to 2000. It is likely that competition from the Mexican fishery and market demand combine to make *Megastraea* a marginal fishery in southern California. A summary of the yearly commercial catch in California (Table 4.) indicates approximately 89.6 tons (gross weight) was harvested off southern California between 1996 and 2019; of that 74.8 % (67 tons gross) was harvested off San Diego. California Fish and Wildlife has not updated their on-line commercial catch records since 2019.

California, has no minimum size limit for sport or commercial take. As such, the size (BD) of the snails harvested is unknown. Graph 2 shows the correlation between grams of edible muscle and shell BD for *M. undosa* from San Diego. For snails with a BD of 80 mm or greater the average weight of the edible muscle was 15.5 % of the gross weight (STD 2.12, n = 59). Based on that data, the 67 tons (gross) from the San

Diego area may have yielded approximately 10.5 tons of edible muscle during the past 24 years. Compared to BC and BCS, with a combined average commercial catch of 249 tons of edible muscle annually, the historic catch from southern California is miniscule, but so is the habitat off San Diego.

Although the muscle weight of *M. undosa* and *M. turbanica* are combined in Baja catch data, each species has a different size limit. The minimum legal size for *M. undosa* is a basal diameter of 90 mm, while the minimum BD for *M. turbanica* is 100 mm. In México, the commercial season is closed from November 1st to February 28th (Item 11, *Megastraea*. 2018).

California, has no size limit or closed season for the commercial landings, nor a distinction between either species of *Megastraea*. Management of this low value fishery has not been a priority in California. Strong compliance with the Marine Protected Areas (MPA) and other types of marine conservations areas protects large tracks of habitat off San Diego. Interim regulations were proposed in a 2001 report by the California Fish and Game (Appendix A, 2001) which included a size limit, closed season, and limiting the number of "participants" in the fishery, but no action was taken.

In the recent past, the authors conducted a series of transects off Isla Coronado del Norte, BC. The target areas had similar rock habitat and the depth averaged 14-16 m. At that Island, *M. undosa* has been collected by commercial divers as part of a fishery. All *Megastraea* observed, were typically under 75 mm BD. As such, the population of *Megastraea* must be supported by reproductively active snails far too small to be of value. Martone & Michell (2012) evaluated factors that influence growth and reproduction of *M. undosa* on a regional basis. They found that snails with basal diameters between 60 to 80 mm exhibit the first notable increase in fecundity, over smaller individuals.

Densities in the study area off Coronado del Norte were as follows; *Pomaulax gibberosus* (Dillwyn, 1817) 0.736 m^2, *M. turbanica* 0.186 m^2 and *M. undosa* 0.171 m^2. At Isla San Geronimo, BC, Rodríguez-Valencia *et al*. (2002) surveyed a *Megastraea* population that had been depleted by commercial harvesting. They reported the mean size of *M. undosa* at 60 mm with a density of 0.1 m^2. The mean size of the few *M. turbanica* found was 57 mm with a density of 0.006 m^2. Their study included 101 transects at various depths. They attribute the small mean size and low density to fishing practices.

Knowing the relationship between BD and age, plus the population structure, an estimate of the portion of the population protected from harvest may be made if a minimum size limit is applied. Further, information regarding age-based fecundity allows adjustment to the size limit that may sustain the commercial catch. Unexpected changes in age class distribution may point to years of poor or highly successful recruitment.

Summary

The *in situ* diet of *Megastraea undosa* is known to include at least 30 genera of marine algae. The occurrence of *M. undosa* is not restricted to the presence of giant kelp *Macrocystis pyrifera*. Juveniles age classes are often missing from off-shore surveys. Juveniles are not cryptic or hidden; they are commonly found in shallow water associated with coralline algae on rocks or patches of dense eel grass. Mature *M. undosa* with BD exceeding 130 mm off San Diego are age class 13 or greater. Very large *M. undosa*

are uncommon but, the BD can reach 150 mm and are likely age class 15.

A small commercial fishery has existed in southern California since 1996. Most fishery related research on *Megastraea* has been conducted on the Baja California peninsula, with a focus on diet, growth, and reproduction. In Baja California there are size limits for both species of *Megastraea*, a closed season during part of the reproductive cycle and established annual quotas for the various fishing zones. In California, there is no size limit, closed season or bag limit. Approximately 75 % of the California commercial catch has been taken from San Diego. Approximately 15.5 % of the gross weight (animal and shell) is edible muscle. Shells in the area of San Diego can be aged based on table 2, such data combined with additional sampling can be used to estimate the population structure at different depths and habitat.

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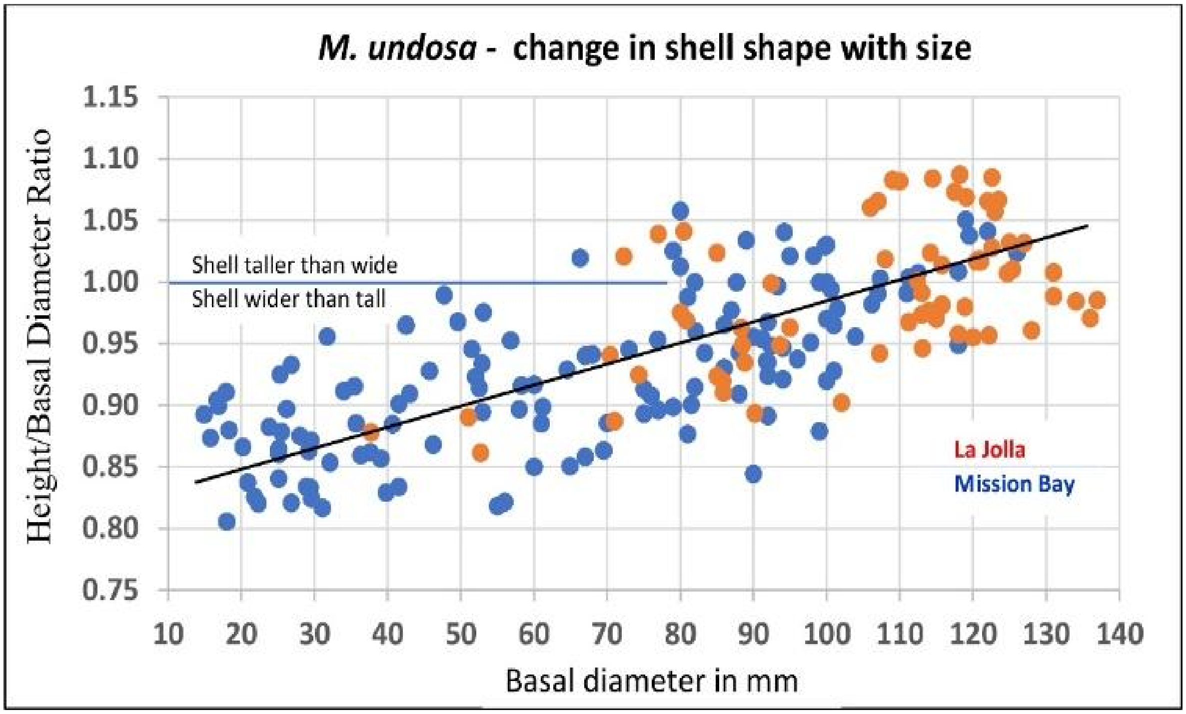
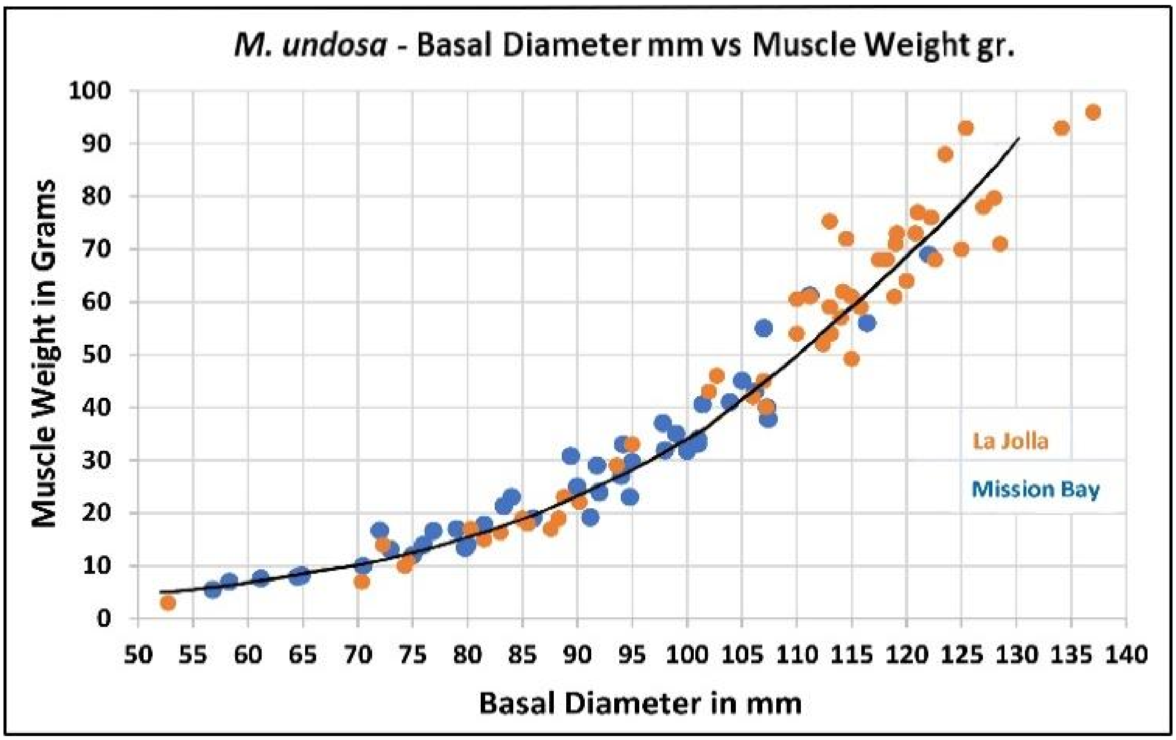


Graph 1. The ratio of height to basal diameter (H/BD). When the ratio is greater than one, the height is greater than width. When the ratio is less than one the shell is wider than the height. Over time the shell of *Megastraea undosa* elongates with age.



Graph 2. Edible muscle weight (grs) vs. shell basal diameter (mm) of *M. undosa*. The chart may be used to estimate muscle weight for various size individuals. One once equals 28.4 grams.

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	M. undosa - Mission Bay Operculum Length mm				***M. undosa*** - La Jolla Operculum Length mm				P value
Age	Avg	STD	Range		Avg	STD	Range		P <0.05
1	5.7	0.57	4.7-6.6		6.2	0.71	5.5-7.2		P <0.05
2	9.6	0.76	8.2-10.5		9.7	0.54	8.5-10.6		P <0.05
3	12.7	0.81	11.3-13.8		12.8	0.71	11.2-13.8		P <0.05
4	16.2	1.01	14.1-17.5		16.0	1.32	14.3-19.2		P <0.05
5	19.9	1.32	17.8-22.2		19.6	1.34	18-22.5		P <0.05
6	23.9	1.46	22.4-24.8		23.8	1.54	21.7-26.3		P <0.05
7	27.8	1.35	26-31.3		27.7	1.75	26-30.5		P <0.05
8	32.2	1.06	29-33.4		32.4	1.73	30.5-37		P <0.05
9	35.8	1.15	33.8-38.1		36.6	1.34	36-38		P <0.05
10	39.7	1.80	38-42.2		40.9	2.13	39.7-43.2		P <0.05
11	44.0	1.75	41.5-47		44.2	1.16	44.2-48.3		P <0.05
12	49.9	1.41	49.7-51.9		49.4	1.47	47-51.4		P <0.05
13	--	--			52.9	1.11	51.7-54.7		n/a
14	--	--			56.6	--	56.4		n/a

Table 1. Operculum length vs. Age. There was no significant difference between paired age class data for *Megastraea undosa* from Mission Bay and off-shore La Jolla.

	M. undosa Mission Bay Basal Diameter mm				***M. undosa*** La Jolla Basal Diameter mm				*P* value
Age	Avg	STD	Range		Avg	STD	Range		
1	18.5	2.46	14-22		---	---	---		n/a
2	27.4	2.31	23-32		---	---	---		n/a
3	36.9	3.30	32-42		37.7	---	---		n/a
4	43.8	2.35	42-50		---	---	---		n/a
5	53.7	2.44	47-57		52.7	---	---		n/a
6	60.9	2.91	56-65		---	---	---		n/a
7	72.9	3.39	66-77		73.2	4.28	70-81		*P* <0.05
8	82.1	1.70	79-88		84.5	3.31	80-89		*P* <0.05
9	88.9	2.91	84-92		87.8	2.00	85-91		*P* <0.05
10	96.9	2.53	92-100		99.5	2.64	93-103		*P* <0.05
11	106	3.65	100-112		111.5	3.52	103-115		***P* >0.001**
12	118.9	1.71	116-121		119.8	3.73	113-127		*P* <0.05
13	--	--			128.9	4.89	123-134		n/a
14	--	--			137		137		n/a

Table 2. Age vs. Basal Diameter. *Megastraea undosa,* from Mission Bay and La Jolla. The BD of age class 11 from Mission Bay was significantly smaller than the same age class from La Jolla, yet, at age class 12 the average BD between the two locations varied by only 1.3 mm and was statistically insignificant. n/a = sample size insufficient for statistical analysis.

Table 3	*M. undosa* Mission B	*M. undosa* La Jolla	*M. undosa* Guadalupe*
Avg BD mm STD	104.9 11.0	117.7 9.3	99.19 5.41
BD range for shells > 90 mm	90 - 121	90 - 137	92 - 126
Avg Height mm STD	102.95 14.10	119.0 12.4	103.83 8.44
Height/Base ratio STD	0.97 0.05	1.01 0.05	0.96 0.04
Sample Size	35	44	29

Table 3. Data from shells with the minimum basal diameter of 90 mm (minimum size limit in México) and greater, from San Diego, CA and Isla Guadalupe BC. * Historic commercially collected shells.

Year	Total lbs	SD catch lbs	Price per lb	SD % of catch
1996	721	721	UK	100
1997	3,618	2,907	0.53	80.3
1998	86,956	63,527	0.40	73.0
1999	24,276	22,494	0.40	92.7
2000	26,152	26,148	0.52	99.9
2001	8,743	8,346	0.61	95.5
2002	1,651	1,200	2.02	72.7
2003	774	664	0.69	85.7
2004	8,375	2,171	0.31	25.9
2005	1,213	745	0.45	61.4
2006	370	0	3.47	0.0
2007	475	172	1.10	36.2
2008	362	65	1.17	17.9
2009	588	155	1.26	26.4
2010	572	48	0.98	8.4
2011	990	303	0.88	43.9
2012	981	351	2.95	35.6
2013	830	670	2.57	80.7
2014	903	875	1.77	96.9
2015	4,144	1,668	1.52	40.0
2016	729	356	2.13	48.8
2017	719	146	2.13	19.7
2018	3,008	118	0.49	3.9
2019	2,035	157	1.03	7.8
Total	**179,185**	**134,007**		**74.8%**

Table 4. Summary of annual landings of Wavy Top Turbans (*Megastraea*) in southern California. Gross weight data provided by the California Dept of Wildlife. SD = San Diego. UK = unknown.