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Marine Molluscs in Nearshore Habitats of the United Arab Emirates: Decadal Changes and Species of Public Health Significance

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ABSTRACT

This paper describes the results of three qualitative surveys of marine molluscs conducted in December 2010 and May 2011 and 2012 in nearshore benthic habitats along the Arabian Gulf and Gulf of Oman coasts of the United Arab Emirates. Findings are compared to historical studies, focusing on extensive surveys from the 1960s and 1970s. Molluscan species of public health significance are identified based on their potential as vectors of algal toxins in light of the recent occurrence of harmful algal blooms (HABs) in the region. Habitats sampled included intertidal sand or gravel beaches, rocks and jetties, sheltered soft-sediment flats and mangroves, and shallow subtidal coral reefs. The present study showed differences in taxonomic composition and decreased species richness of gastropods compared to a previous mollusc survey conducted in the early 1970s, reflecting the probable impacts of extensive, ongoing coastal development activities, although other environmental stressors may play a contributing role. The major habitat change found in the current survey was replacement of natural "rocky" substrates with manmade jetties and breakwaters. Of the 27 live gastropod species collected, 7 predatory or scavenging species were identified as potential biotoxin vectors: *Thais savignyi*, *T. tissoti*, *T. lacera*, *Murex scolopax*, *Nassarius persicus*, *Hexaplex kuesterianu*s and *Rapana* sp. Of the 22 live bivalve species collected, the following 11 suspension-feeders were deemed to be potential vectors of HAB toxins based on their body size and feeding mode: three venerid clams (*Circenita callipyga*, and *Tivela ponderosa* that are consumed locally, and *Amiantis umbonella*), the widespread encrusting rock oyster, *Saccostrea cuccullata*, also consumed locally, two pearl oyster species, *Pinctada* spp., the prickly pen shell *Pinna muricata*, the scallop *Chlamys livida*, the cockle *Acrosterigma lacunosa*, and the facultative suspension-feeding tellinids *Asaphis violascens* and *Hiatula rosea*.

ADDITIONAL INDEX WORDS: distribution, gastropods, bivalves, harmful algal blooms

INTRODUCTION

Coastal development in the United Arab Emirates (UAE) has occurred at a rapid rate for several decades, particularly in the Arabian Gulf (AG) but also along the east coast in the Gulf of Oman (GO) (Sale *et al.*, 2011; Sheppard *et al.*, 2010). Natural coastal habitats have been dredged and filled to provide land for homes, industrial installations, recreational facilities, and other human uses. The scale and rate of coastal development is alarming, and studies of anthropogenic impacts on some natural habitats are underway. Most attention has been focused on the coral reefs in the region, which have been negatively affected by development activities as well as thermal bleaching and harmful algal blooms (HABs) (Bauman *et al.*, 2010; Burt, 2014; Burt *et al*. 2011, Grizzle *et al.*, 2016; Sheppard, 2016). Other ecologically important nearshore habitats such as mangroves which occur on both UAE coasts clearly have been affected by widespread coastal development activities, but their spatial extent and condition have been little studied in recent decades (Moore *et al*., 2015). Similarly, other coastal habitats in the UAE such as seagrasses and pearl oyster reefs, as well as the occurrence of commercially and otherwise important taxonomic groups, including molluscs, in relation to habitat type, have received limited attention to date (EA Abu Dhabi, 2008).

Marine molluscs of the UAE are Indo-Pacific in origin, although their diversity, particularly in the Arabian Gulf, is restricted by extremes in both air and seawater temperature and high salinities (Basson *et al.*, 1977; Bosch *et al.*, 2008). Many molluscan species are important in sustaining production of upper consumers and provide other ecological services in habitats that occur in the region, particularly mangroves, coral reefs, seagrasses and the rocky intertidal (Basson *et al.*, 1977; George, 2005, 2012). There is a substantial literature dealing with the taxonomy of molluscs in the region (Anbiah, 2007; Biggs, 1973; Bosch *et al.*, 1982; Bosch *et al*., 2008; Feulner and Hornby, 2006; George, 2012; Smythe, 1979, 1982; Morris and Morris, 1993). The published literature includes an impressive list of species at least potentially found in coastal waters of the AG and the GO on UAE's east coast. It may be hypothesized that the rapid coastal development occurring in recent decades has affected mollusc populations, but there are no published studies that examine this possibility. The present study aimed to provide a qualitative characterization of UAE's marine mollusc populations by habitat type via sampling in 2010-2012 and an assessment of changes that have occurred since coastal development activities were greatly accelerated due to the rapid population growth experienced in the UAE between the 1960s and 2015, based on analysis of United Nations data.

Massive blooms of the harmful dinoflagellate *Cochlodinium polykrikoides* were documented in the region in 2008 and 2009 that affected > 500 km^2 of the AG coast, and resulted in massive die-offs of molluscs, fish and marine mammals (Al-Azri *et al*., 2012; Richlen *et al.*, 2010), as well as restricted the operation of desalination plants (Villacorte *et al.*, 2015). Several neurotoxic algal species that pose a threat to humans, were also documented in the region: *Gymnodinium catenatum* and *Pyrodinium bahamense var. compressum*, known producers of paralytic shellfish toxins (PSTs), *Karenia mikimotoi* and *Dinophysis caudata* (reviewed by Anderson *et al*., 2011). Harmful algal outbreaks have expanded globally in past decades (Hallegraeff, 1993). They occurred along the coast of Oman (in 2010/2011) and appear to be increasing in frequency in the AG/GO region (Al-Azri et al., 2012). Many mollusc species can readily accumulate phycotoxins while suffering limited adverse effects, and can thus act as the main vectors of these toxins to humans, thereby posing a public health risk (Anderson *et al*., 2001). Although there is no record of toxic shellfish in the region, the present study is preemptive. Suspension-feeding bivalves (*e.g.*, Bricelj and Shumway, 1998), and predatory and scavenging gastropods that feed on them (Shumway, 1995), represent major vectors for HAB toxins. Therefore, although the present study included all bivalves and gastropods encountered, it emphasized species of potential public health significance.

The threat of human consumption of toxic shellfish is amplified in the UAE by the fact that ~65% of the total population lives within 5 km of the coastline (Brook and Dawoud, 2005). Human harvest and consumption of shellfish species is known to occur in some coastal UAE areas, as evidenced by their sale in local markets, but the extent of this activity has not been adequately documented (Carpenter *et al.*, 1997). There is a need to identify those species that have the potential to be harvested and consumed by humans in the UAE in order to anticipate potential public health risks associated with HAB events and develop effective management policies. Additionally, even when they do not threaten human health, HABs can have direct deleterious effects (mass mortalities, recruitment failure, reduced production) on shellfish species (*e.g.,* Bricelj and MacQuarrie, 2007; Rolton *et al*., 2014), fish and other marine fauna (Landsberg, 2002).

METHODS

The study included the major nearshore habitats on both UAE coasts, particularly intertidal areas, and mainly consisted of qualitative sampling methods. The aim was to encounter and sample as many species as possible, but focusing on taxa that might be consumed by humans and thus pose public health risks if affected by HABs.

Study Area and Major Habitats

The two coasts of the UAE, the Arabian Gulf (AG) and the Gulf of Oman (GO) (Figure 1), have very different characteristics. The former, extending 650 km, is relatively shallow (<80 m in most areas) and its benthic fauna is adapted to extreme seasonal fluctuations in environmental parameters, particularly temperature and salinity (Riegl and Purkis, 2012; Sheppard *et al.*, 1992). Temperatures of inshore waters range from tropical summer conditions (June to September), i.e. >35ºC, to temperate conditions during the winter (December to March), i.e., 11-12ºC (Foster *et al.*, 2012; Sheppard *et al*., 1992). Oceanic water with salinity averaging ~36.5 enters the AG through the Strait of Hormuz and increases to >40 as it flows westward (Riegl and Purkis, 2012). In the present study salinities of 47.6 were measured in mangroves in Abu Dhabi. Tides in the AG are complex with solar/lunar tidal, wind, and density-driven components; tidal range varies from 1 to 4 m (Riegl and Purkis, 2012). As a result of the relatively harsh environmental conditions, many species that occur at similar latitudes in the Pacific, do not occur in this region. Some of the adaptive strategies developed by molluscs to tolerate the harsh environmental conditions present in intertidal UAE lagoons have been described by Feulner and Hornby (2006). The southern AG along the UAE coast is characterized by a gently shelving coastline with numerous inshore and nearshore islands. The coastline along the GO covers only 90 km and the fauna of shallow waters is more diverse than that in the AG due to the less harsh environmental conditions. Salinities of nearshore waters typically fluctuate around 37 and water temperatures vary seasonally between 20 and 32ºC (Reynolds, 1993; Wang et al., 2013). Tides in the UAE portion of the GO do not exceed 3 m (Admiralty Tide Charts).

The current study included four major coastal habitats in the UAE: exposed sand and/or gravel beaches, natural rock or manmade rock jetties and breakwaters, mangroves and soft-sediment tidal flats, and coral reefs (Figure 2). All are in intertidal to shallow subtidal waters, except coral reefs which are only subtidal.

Exposed sand and/or gravel beaches. There are extensive intertidal sandy beaches along both coasts, interspersed with pebble to cobble-size material in some locales (Figure 2A, B, F). Most are exposed to some amount of long-fetch wind waves and thus represent dynamic environments characterized by unstable sands. In some areas, extensive gravel deposits occur and are sporadically exposed and buried by moving sand (Basson *et al*., 1977).

Natural rock, and manmade jetties and breakwaters. Intertidal rock outcrops occur throughout the AG and extend into shallow subtidal waters (Basson *et al*., 1977; see Riegl and Purkis, 2012 for geomorphological features of these natural "hardground ridges"). Unfortunately, the rapid coastal development occurring throughout the region has resulted in destruction of these natural rocky bottoms in many areas along with their associated live corals and other species (Sheppard *et al*., 2010, 2012). Yet the manmade jetties and breakwaters typically fronting the widespread dredge and fill projects are on the increase (Figure 2B, C), providing hard substrate for colonization by epibenthic plants and animals (Burt *et al*., 2009, 2012). Most collections from intertidal hard substrates were made on jetties and breakwaters constructed of natural rock from the region or concrete, and included sites in six of the seven emirates.

Mangroves and soft-sediment tidal flats. There are extensive soft-sediment intertidal flats behind barrier beaches in many areas (Figure 2D; Basson *et al*., 1977); many are associated with mangroves (Figure 2G, I) and/or seagrasses (Figure 2E). Sediment types in this habitat range from soft muds with high clay content to firm sands consisting largely of carbonate particles of biogenic origin (Basson *et al*., 1977). Mangrove-dominated habitats in the UAE range from areas with only sparse cover by small trees (Figure 2I) to densely forested areas with some trees exceeding 5 m in height (Figure 2G; Moore *et al*., 2015). The only mangrove species known to occur in the UAE is *Avicennia marina*, a eurythermal, euryhaline species (Basson *et al*., 1977; Sheppard *et al*., 1992). Early mangrove mapping efforts in the UAE (*e.g*., Saenger *et al*., 2004) have been recently updated by Moore *et al*. (2015). Three species of seagrasses occur in the region: *Halodule uninervis* (the dominant species), *Halophila ovalis* and *Halophila stipulacea* (Phillips, 2003). Seagrass beds occur widely in the shallow waters of the AG, to water depths of ~15 m (Basson *et al*., 1977; Phillips, 2003).

Coral reefs. These (Figure 2H) occur along both coasts of the UAE (Grizzle *et al*., 2016; Spalding *et al*., 2001). However, elevated sea temperatures in 1996, 1998, 2002 and 2010 resulted in substantial loss and degradation of coral reefs throughout the region from which there has only been limited recovery (Burt *et al*., 2008, 2011). Abu Dhabi waters were extensively mapped from 2005-2007, and a map of live as well as mostly dead coral reefs has been published (EWS-WWF, 2008). Living shallow-water coral reefs in all other emirates were recently mapped (Grizzle *et al*., 2016).

Sampling Protocol

The overall aim of the present study was to sample as many of the above-described habitats as practical, and to include sites in all seven UAE emirates and on both coasts. Sampling was conducted during three field surveys: December 11 - 17, 2010, May 13 - 17, 2011, and May 13 - 30, 2012. A total of 40 sites were visited, and all observations were made during daylight hours. It is recognized that this might underestimate the abundance and distribution of nocturnal organisms, where nocturnal habit limits their exposure to desiccation during the day. At each site, general environmental conditions (habitat type, wave exposure, tidal height, water depth) were recorded and water salinity and temperature were measured using a handheld YSI Model 85 meter. Latitude/longitude coordinates were determined using a hand-held Garmin Model 76 GPS unit (Appendix A). Photographs including some underwater images were taken to document habitat conditions and life habit mode of some species.

Molluscs were mainly sampled qualitatively using a hand rake, spade and other hand tools by wading in the intertidal zone; some sites (*e.g.*, coral reefs) were visited by boat and involved SCUBA diving and snorkeling in subtidal waters. A few quantitative samples focusing mainly on the taxa with potential to accumulate phycotoxins and pose a public health risk, were made at some sites on intertidal hard substrates (mainly jetties) and soft sediments surrounding mangroves. These were conducted by making direct counts of molluscs in quadrats taken on hard substrates or photographic quadrats in some cases, and excavating five to ten 0.1 m^2 (or 0.05 m^2 in cases where densities were high) quadrats to a depth of 10 cm in soft sediments. In these, samples were washed on a 2 mm mesh sieve (note that 2 mm represents the approximate size of the smallest molluscs that were sampled during the present study), and all molluscs retained were identified and counted.

Specimens from each taxon were stored in labeled plastic bags and returned to the laboratory for processing. The presence of empty shells (*i.e*., dead specimens) was noted and specimens were also brought back to the laboratory for identification, but only live taxa are reported herein. Representative shells of all live species collected were retained to establish a reference collection, and for positive identification. Upon return to the laboratory, all specimens were frozen for at least one day. After thawing, soft tissues were removed and the shells cleaned and dried for storage. Bosch *et al.* (1982, 2008) were the major keys used for identification, and the taxonomy of Bosch *et al.* (2008) was followed herein. However, the taxonomic nomenclature was updated based on the World Registry of Marine Species (WoRMS; http://marinespecies.org) in Table 1. Duplicate reference collections have been deposited at the Marine Environment Research Centre-MOEW, Umm Al Quwain, UAE, and at the Jackson Estuarine Laboratory, University of New Hampshire (UNH), USA. All three surveys were conducted as a collaborative effort involving scientists from the UAE MOEW, and the municipalities of Dubai and Abu Dhabi.

RESULTS

The results of the study were interpreted in the context of current conditions in UAE's coastal waters, how current conditions compare to similar previous studies conducted in the 1960s and 1970s, and implications with respect to HABs.

Present Study

A total of 49 live mollusc species were collected during the present study, including 27 gastropods and 22 bivalves (Table 1). Considering only those sites where live molluscs were collected (none were collected at five of the 40 sites, and two of the numbered sites were skipped; Table 1 lists 33 sites), species richness varied widely ranging from 2 to 19 species per site. All the sites that did not yield any live molluscs were sandy beaches, and were in industrial areas or on the east coast where the 2009 HAB event reportedly caused widespread mollusc and fish dieoffs. The sites with highest species richness were man-made breakwaters or jetties, and coral reefs. Although each of the four major habitat types sampled had a distinctive assemblage of species, three species were widespread and common in at least two habitats (Table 2): the Venus clam *Circenita callipyga*, pearl oyster *Pinctada radiata*, and rock oyster *Saccostrea cuccullata*. All three are suspension-feeding bivalves capable of accumulating HAB toxins, and are discussed individually below in the section on species of public health significance. Most of the more common species in each habitat (Table 2) are of public health significance because they potentially accumulate HAB toxins and are known to be consumed by humans.

As expected, there were notable differences between the molluscan assemblages when comparing sites in the Arabian Gulf (Sites 7 – 43) and east coast (Gulf of Oman [GO]; Sites 1 – 4b) (Table 1). The mean number of species (± standard error, SE) per site was 6.0 (± 0.65) at the 28 AG sites compared to 4.6 (±1.03) at the five GO sites (Table 1). Although these data might suggest that species richness was greater in the AG, it should be noted that >20 species represented only by dead shells were collected at one site on the east coast of GO during the 2010 visit. Additionally, this region of the GO reportedly had not recovered from extensive die-offs of molluscs during HAB events that occurred in 2009. Nonetheless, adults of four species were collected only on the east coast: the horse mussel *Modiolus auriculatus*, the black-lipped pearl oyster *Pinctada margaritifera*, the jewel box *Chama douvillei*, and the purple clam *Asaphis violascens*. Overall, these data indicate differences in molluscan assemblages between the two coasts, but disparity in the number of sites visited (5 vs. 28 in the GO and AG, respectively) and the recent HAB events on the east coast preclude making definitive comparisons.

When considering only sites in the AG, there was a strong trend of decreasing species richness proceeding from the northeast to the southwest, *i.e.*, moving away from the Strait of Hormuz and further into the AG (Figure 1). The eleven sites from Ras Al Khaimah and Umm Al Quwain had a combined total of 20 gastropod and 13 bivalve species, compared to 10 gastropod and 5 bivalve species from the eight sites in Dubai and Abu Dhabi (Table 1). A similar geographic pattern of decreasing densities was also reflected in the quantitative data collected for the rock oyster, *Saccostrea cuccullata* (see data below). These trends reflect the increasingly harsh conditions in water temperature and salinity moving from northeast to southwest in the AG, as noted in the Methods section.

Changes in the Arabian Gulf's Nearshore Molluscan Fauna Since the 1960s and 1970s

Bosch *et al.* (2008) provides extensive taxonomic information, but no data on collection sites or details on distribution patterns or times of collection sufficient to allow comparisons to data from the present study. Biggs (1973) provides extensive data on molluscan surveys in Abu Dhabi made by multiple investigators between 1961 and 1965, and included over 100 collection sites. He listed 34 species of live gastropods and 41 live bivalve species, compared to 27 gastropod and 18 bivalve species from AG sites visited in the present study. These numbers suggest a large (56%) reduction in species richness for bivalves, but it is important to note that the present study involved only about 1/3 the number of sites reported by Biggs (1973). There were only 10 species common to both studies, suggesting there have been substantial changes in species composition. Precise station locations were not given in Biggs (1973), so site-by-site comparisons to the present data (latitude/longitude coordinates of sites surveyed in the present study are shown in Appendix A) were not possible.

Smythe (1979), however, provided data that allowed a more robust comparison to the present study. She reported on two surveys conducted between December 1971 and August 1973 that included nearshore habitats (*i.e.*, a total of 38 sites, compared to a total of 28 sites in the AG in the present study) in all six emirates east of Abu Dhabi, including many near those sampled in this study. Smythe (1979) provided minimal information on sampling methods, but did provide an extensive dataset that allowed compilation of taxonomic lists by sampling site of all species represented by live specimens. This enabled comparison of results from an overall perspective as well as on an emirate-by-emirate basis (Figure 3). Although the historical comparison is limited due to the qualitative design of both the past and present studies and other possible differences (*e.g.*, sampling effort at each site), some useful observations can be made.

Smythe (1979) reported a total of 46 gastropod and 48 bivalve species, considering only those collected alive, compared to 27 gastropod and 18 bivalve species in the current study considering only sites in the AG (Figure 3). The combined list from both studies included 121 species, with only 17 common to both studies. These data also (see earlier comparison to Biggs 1973) strongly suggest that the overall molluscan species composition has changed, and suggest that species richness has decreased in the region at least for gastropods (Figure 3). However, when assessment is made on a habitat basis, the most commonly encountered species showed some overlap in rocky substrates and soft-sediment flats, the two habitat types that were well represented in both studies (Table 2). An emirate-by-emirate comparison based on the mean number of species per site illustrates the differences in gastropod species richness between the present study and Smythe (1979), as noted above. Both datasets show the same general geographic trends (Figure 3) overall, and as already noted above for the present study, there was a general decreasing trend in species richness from the northeast (Umm Al Quwain) to the southwest (Dubai and Abu Dhabi). Finally, one major change that should be noted is that nearly all “rock” habitat sites in the current study were man-made jetties or breakwaters, while Smythe’s were natural rock outcrops.

Molluscs of Potential Public Health Significance as Vectors of HAB Toxins

A total of 7 gastropod and 11 bivalve species that could potentially pose a threat to public health were collected during the present study (see highlighted species in Table 1; Figures 4 - 6). Most were found on both coasts, and thus the public health implications discussed herein apply to all UAE's coastal waters. All 18 species are known to be capable of accumulating paralytic shellfish toxins (PSTs) at levels exceeding the action level for harvesting closures in other parts of the world (see Discussion). Four were widespread and/or found in a diversity of habitats, and warrant further mention here.

Thais savignyi (dog whelk). This carnivorous snail was one of the most commonly encountered gastropods throughout the study area (Figure 4A; Table 1, Appendix A), mainly occurring on hard substrates. Although no quantitative data were obtained due to its very patchy distribution, there was no apparent geographic trend in overall densities. Live specimens were collected at a total of 10 sites (mainly breakwaters) in the AG from Ras Al Khaimah to Dubai (Table 1A). *Thais savignyi* was also much more common than its congeners *T. tissoti* (Figure 4E; collected at five sites) and *T. lacera* (Figure 4C; found only at site 15).

Saccostrea cuccullata. The rock or hooded oyster was widely distributed on both coasts (Table 1), occupying a distinct zone in the high- and mid-intertidal on hard substrates (Figure 5H, I) and among mangrove roots as well as in small clusters scattered across the intertidal soft-sediment flats (Figure 5J). Replicated quadrat counts were made on breakwaters at two sites (7 and 34) in Umm Al Quwain and two sites (35 and 36) in Dubai; mean densities (± SE) ranged from 4.2 m^{-2} (± 0.97) in Dubai to 29.4 m^{-2} (± 2.77) in Umm Al Quwain. Maximum densities of ~500 m^{-2} were recorded when the species occurred at 100% cover on rock jetties at Umm Al Quwain. Although these were the only quantitative data obtained, estimates of relative abundances confirmed the same pattern of decreasing densities moving southwestward along the AG coast from Umm Al Quwain to Abu Dhabi. Rock oysters typically occupied most of the surface area of rocks on breakwaters in Ras Al Khaimah and Umm Al Quwain, but decreased in coverage from Ajman to Abu Dhabi. This trend most likely reflects the generally more stressful environmental conditions (higher salinities and water temperatures) moving southwestward in the AG, but could also be related to the age of the breakwaters themselves.

Circenita callipyga (Venus clam). This venerid clam was collected from a total of 13 sites and on both coasts (Table 1; Figure 6E). It was also commonly found in fish markets (Figure 6F).

Quantitative data were obtained from two sites: a sheltered sand beach in Ras Al Khaimah (site 39) where it occurred at a mean density (± SE) of 1.8 individuals m^{-2} (± 0.65, n = 5), and among mangroves in Ajman (site 38) where only small juveniles occurred at a density of 49.6 individuals m^{-2} (± 9.37, n = 5). Although replicates were insufficient to provide meaningful densities, a maximum of 20 individuals were raked from one 0.1 m^2 quadrat taken on an exposed cobble beach in the GO (Site 2). Clearly, *C. callipyga* is widespread in the region, and it can be found at relatively high densities.

The pearl oyster, *Pinctada radiata*, was collected at 13 sites, and occurred on a variety of hard substrates (Tables 1 and 2; Figures 5B, C, D, F). In contrast, its congener *P. margaritifera* (Figure 5A) was only collected at two sites (Table 1). It should be noted, however, that although all adult pearl oysters were identified as *P. radiata*, large numbers of juveniles were observed at several AG sites (*e.g.* Figure 5C, D, E, F) that were not identified at the species level. Indeed, the vast majority of pearl oysters collected were juveniles, suggesting that *Pinctada* spp. populations are probably substantial but that mainly juveniles occur in nearshore water.

DISCUSSION

Although the present study focused on molluscs with public health significance, it yielded data sufficient to compare to recent previous studies in the region as well as historical research conducted in the 1960s and 1970s before the ongoing rapid coastal development began.

Recent studies

Reviews by George (2005, 2012) list 95 gastropod and 68 bivalve species from the Arabian Gulf in UAE waters. There are no recent studies that expand this list to include species found on UAE’s east coast. However, substantially more taxa would likely be added as the literature describing all molluscs reported from eastern Arabia (AG and GO) lists approximately 1,200 species (Bosch *et al.*, 2008). Although the total species list of 49 taxa reported herein represents only a small portion of the previously reported molluscs, the present study was restricted geographically and only included shallow-water habitats. Few recent studies (conducted since the 1990s) provide data to compare with the current study, and all focused on a single habitat type, were restricted to a relatively small area, or differed otherwise from the present study.

Morris and Morris (1993) sampled two intertidal sandflat areas (one in Fujairah), and reported a total of 14 species, including four new species which they named and described. Only five of the taxa they reported were found in the present study. In their review of the literature on molluscs found in UAE's coastal lagoons in the AG and GO, Feulner and Hornby (2006) listed 25 gastropod and 24 bivalve species; 16 of these were found in the present study. Yekta *et al*. (2012) listed 43 gastropod species and 25 bivalve species from qualitative sampling of intertidal habitats in the northeastern AG near the Strait of Hormuz in 2010 and 2011; 19 of the species they listed were found in the present study. Anbiah (2007) reported 7 gastropod and 7 bivalve species from a limited collection in shallow waters of Abu Dhabi; all 7 bivalves but only 2 of the gastropod species were found in the present study. Overall, this cursory comparison among qualitative studies that have been done recently shows considerable similarity in species richness, but also striking differences in the species encountered. This suggests that much more work is needed to fully characterize the current diversity of marine molluscs in UAE's coastal waters.

The most definitive geographic trend found in data from the present study when considering only sites in the AG was a general decrease in molluscan species richness, and population densities for which data were collected, proceeding southwestward away from the Strait of Hormuz into the AG. The same trend has been documented for corals, the most-studied group in the region, and the cause is typically attributed to the associated gradient in increasingly harsh environmental conditions (reviewed briefly in Grizzle *et al*., 2016). Moreover, the present study only sampled a few sites in western Abu Dhabi representing limited habitat diversity. Additional studies of the molluscan fauna are thus particularly needed in the western portions of the Abu Dhabi emirate.

Three species of oysters that were widespread on both UAE coasts, and were reported in most of the recent studies mentioned above, warrant further discussion with respect to their ecological importance. The rock oyster, *Saccostrea cuccullata*, occurs throughout the region, including the northwestern-most areas of the Gulf in Kuwait (Al Bakri *et al.*, 1997), sometimes forming (with barnacles) a visually distinctive zone on hard substrates in the mid-intertidal (Figure 2J) (Basson *et al.,*1977; Bosch *et al.*, 1982; Bosch *et al.,* 2008; Feulner and Hornby, 2006; Morris and Morris, 1993). As mentioned above, however, the present study indicated decreasing densities moving southwesteward into the AG (this species was not collected in Abu Dhabi). It is noteworthy that *S. cuccullata* also commonly occurs in small clusters on soft sediments, particularly among mangroves (Figure 5J). This widespread and locally abundant oyster provides important habitat for other species in the intertidal zone on both coasts, as well as food for humans (see below).

Two species of pearl oysters were collected in the present study, *Pinctada radiat*a and *P. margaritifera*, but most specimens were juveniles and could only be identified as *Pinctada* spp. The present study documented that pearl oysters are widespread in UAE's coastal waters, yet much remains to be learned about their current status. Many species of oysters occur in dense "beds" or "reefs" that provide important ecosystem services in coastal waters worldwide (Beck *et al*., 2011). Pearl oysters in the AG have historically occurred nearshore in dense aggregations on both hard and soft sediments as juveniles, but were found mainly on firm substrates offshore as adults (Basson *et al*., 1977; Al-Khayat and Al-Ansi, 2008) in the southwestern AG (see Figure 1 in Carter, 2005). Pearl oyster larvae appear to preferentially settle on seagrass and macroalgae in shallow waters in late spring in the AG, where the juveniles remain until they attain ~5 mm in shell height (Basson *et al*., 1977). The presence of large numbers of juveniles (*Pinctada* spp.) were documented at many AG sites in the present study (Figure 5F), but very few and only small adults were recorded. In the fall, juveniles are apparently carried into deeper offshore waters where they form permanent subtidal reefs. This movement during their early life history is similar to that of blue mussels, *Mytilus edulis* (Bayne, 1964; Grizzle *et al*., 1996; Seed, 1976), and likely explains why small juveniles (typically <20 mm), rather than adults, were most commonly found in the present study which focused on nearshore waters.

Before the development of pearl oyster culture techniques in the early 1900s, fishing/diving for wild oysters supported a global pearl industry which was the mainstay of the regional economy between the 18th and mid-20th centuries (Al Bowardi and Hellyer, 2005; Bondad-Reantaso *et al*., 2007; Landman *et al*., 2001; Sharabati, 1981). Some natural pearl harvest is ongoing in the western Gulf in Kuwait (Landman *et al*., 2001), but the reefs that historically occurred throughout much of the southwestern AG (see Figure 1 in Carter, 2005) have not been harvested in modern times. Recent studies in nearby Qatar indicate, however, that many of these historical reefs likely persist, even if at low population densities (Al-Khayat and Al-Ansi, 2008; Smyth *et al*., 2016). Thus, pearl oysters represent a major unknown with respect to the molluscan fauna and the overall ecology of UAE's Arabian Gulf waters. Beck *et al.* (2011) did not include the AG in their review of the global decline in oysters because no data were available from the region (Mike Beck, The Nature Conservancy, pers. comm., August 8, 2016). Thus, although the current extent of pearl oyster reef habitat in the UAE is essentially unknown, observations from the present study of widespread abundance of juveniles strongly suggest that abundant populations still exist in offshore waters. Characterization of the distribution and size of pearl oyster reefs in the AG is sorely needed.

Changes in the Arabian Gulf's Nearshore Molluscan Fauna Since the 1960s and 1970s

Data from AG sites sampled in the present study were compared with studies conducted in the 1960s and 70s, before extensive coastal development in the region, particularly those of Biggs (1973) and Smythe (1979). There have been substantial losses of coastal habitats and alterations of the UAE coastline since the 1970s (Sheppard and Price, 1991; Sheppard *et al*., 2010; Van Lavieren *et al*., 2011). Coral reefs, the most-studied of UAE's coastal habitats, have suffered substantial reductions in taxonomic richness and other metrics indicating degraded conditions over the past three decades (Burt *et al*., 2011; Riegl *et al*., 2012; Sheppard, 2016). However, this degradation has coincided with climate change (AlSarmi and Washington, 2011) and HAB occurrences, thus confounding the assessment of the impacts of urbanization. Furthermore, it has been argued that the spatial extent of UAE's coral reefs has not been adequately assessed ─ particularly reefs in water depths >10 m, the approximate maximum depth for mapping with satellite imagery ─ making quantification of areal losses problematic (Grizzle *et al*., 2016). Despite these uncertainties, UAE's natural coastal habitats have been markedly altered.

Biggs (1973) and Smythe (1979) describe qualitative surveys of the molluscs in nearshore habitats along UAE's Arabian Gulf coast conducted in the 1960s and 1970s, respectively. The most striking difference in findings from the present study compared to both these earlier studies was the small number of species found in all three: only 10 (= 22% of the present total) species were found in the present study and Biggs's (1973), and 17 (= 38% of the present total) in the present study and Smythe's (1979). Additionally, when assessed on a site-by-site basis, Smythe collected an average of 8.3 species per site compared to 5.8 species per site in the present study. Two important comparisons, however, indicated some similarities. Several of the commonly collected species in two (rocky areas, and intertidal soft-sediment flats) of the major habitats were the same (Table 2), and the overall pattern of decreasing species richness from northeast to southwest in the AG agreed with previous findings (Figure 3). Overall, these data suggest that there have been substantial changes in species composition and a decrease in species richness of molluscan communities in the nearshore waters of UAE's Arabian Gulf coast since the 1970s. We caution, however, that potential differences and limitations in sampling effort and methods, differences in site locations, and perhaps other factors preclude making statistical comparisons and thus strong inferences.

An important difference between the present study and Smythe (1979) was in the kinds of "rocky" substrates documented. Most of the hard substrate sites in the latter study were natural rock outcrops extending from the land into the coastal waters on both UAE coasts and "hardground ridges" that are widespread in the AG (Basson *et al*., 1977; see Riegl and Purkis, 2012 for geomorphological features of the hardground ridges). The rapid coastal development occurring throughout the region has resulted in destruction of these natural rocky bottoms in many areas along with their associated species (Sheppard *et al*., 2010, 2012). In contrast, rock jetties and breakwaters were the *only* hard substrate commonly observed and sampled in the present study. This difference clearly reflects trends not only in UAE's coastal waters but in urban areas globally (Airoldi *et al*., 2005; Burt *et al*., 2012). Burt *et al*. (2010) documented substantial differences in the abundance of bivalves (although they did not list species) on rock breakwaters in Dubai, with overall abundances negatively correlated to breakwater age and algal cover. Although there is an extensive literature focusing on successional patterns in "fouling communities" that develop on man-made substrates in coastal waters (Greene and Grizzle, 2006; Nicoletti *et al*., 2007; Osman and Whitlatch, 2004; Sale *et al*., 2011), and breakwaters are typically rapidly colonized by a wide diversity of invertebrate and fish species resulting in diverse biotic communities (Burt *et al*., 2012), much remains to be known about their broader ecological role. It has been hypothesized that breakwaters may serve as effective "walls" for the capture of coral larvae drifting along coastal areas, thereby concentrating settlers on these habitats compared to natural reefs in open waters (Grizzle *et al*., 2016). Additionally, biotic communities associated with breakwaters are elevated above the bottom and perhaps more resilient to wind-driven sediments along the seafloor (Burt *et al*., 2010), perhaps partly explaining the high cover of coral on these structures. For the molluscan fauna, it seems quite likely that these manmade structures function as temporary habitat for pearl oysters, as discussed earlier. However, there may well be differences in the physical characteristics of manmade structures made from quarried rocks compared to natural hardgrounds that would affect molluscan communities. In any case, data from the present study indicate that even though "rocky" habitat in the shallow coastal waters of the UAE is mostly comprised of manmade jetties and breakwaters, the associated mollusc communities are similar to those on natural rocks in the 1970s (Table 2).

Species of Potential Public Health Significance

As noted, the occurrence of HABs in UAE's coastal waters provided the incentive for the present project. Thus, a major focus of this study was on those mollucs that can concentrate HAB-produced toxins and are of public health significance because they are potentially consumed by humans, although the UAE population appears to be characterized by limited consumption of local molluscs. Low-volume recreational fisheries for clams in intertidal mudflats are mostly conducted by Asian expatriates (Edwin M. Grandcourt, Abu Dhabi Environment Agency, pers. comm., October 31, 2017). Changes in human demographics, however, can result in changes in global seafood consumption patterns. In this context, expatriates currently comprise most (≥80%) of the UAE population and although their numbers increased by a factor of 2.6 between 2005 and 2015 alone, South Asians have remained the dominant group among expatriates to date (United Nations data source). It is difficult to predict how this could change in the future.

Gastropods

Gastropod species that pose a potential public health risk in UAE waters (Table 1) are all large carnivores that feed on other live molluscs, or are scavengers that feed on dead or moribund molluscs. This is the case with dog whelks, *Nassarius* spp. (Shumway, 1995) such as *N. persicus* (Figure 4C) that can attain up to 25 mm in the UAE. *Nassarius* spp. are known to accumulate up to 18,990 mouse units (MU) 100 g^{-1} soft tissues [3,780 µg saxitoxin equivalents (STXeq) 100 g^{-1} based on a conversion factor of 0.2 µg STXeq MU^{-1}] in mainland China where they cause human fatalities (Chen and Gu, 1993). Note that the regulatory level for shellfish closures worldwide is 80 µg STXeq 100 g^{-1}. The carnivorous dog whelk *Thais savignyi* (maximum size = 60 mm) is also listed in Carpenter *et al.* (1997) as a potential food item for populations in the UAE, and was the most commonly occurring carnivorous gastropod found in the present study. Its prevalence, size and feeding mode make it the gastropod that poses the greatest public health risk in the event of a toxic bloom in the region. The whelk *Thais lima* from the Pacific US accumulated maximum PSP toxicities of 180 MU 100 g^{-1}, and the rapa whelk, *Rapana rapiformis*, can accumulate the related neurotoxin, tetrodotoxin (TTX), attaining a maximum level of 140 MU 100 g^{-1} (reviewed by

Shumway, 1995). The kusters murex or comb shell, *Hexaplex kuesterianus*, (Figure 4F; maximum size = 90 mm) was presumably a major source of food in the UAE and Oman in historic and prehistoric periods, based on findings in middens (Durante and Tozi, 1977). Murex or rock snails, *Murex* spp., and *Rapana* spp. (Figure 4D and E, respectively) can also act as vectors of dinoflagellate toxins (reviewed by Shumway, 1995 and Marcaillou *et al.*, 2009, respectively). The Persian conch or cone shell, *Strombus persicus*, is a large (up to 50-75 mm) edible species that was once harvested along the coast of Oman (AlMali, 1999), but *Strombus* spp. are primarily herbivorous, grazing on macroalgae, detritus and epiphytic algae in seagrass habitat (Randall, 1964). It is thus unclear whether they can act as a vector of algal toxins to humans or are affected directly by these toxins.

Bivalves

Given that bivalves are primary consumers, filter large volumes of water, and are generally sedentary, they provide early warning of HAB toxins and are ideal candidates for biotoxin monitoring programs. Screening of bivalves, including scallops, oysters, mussels and clams, for contaminants (heavy metals and organic pesticides) is an ongoing activity under the shore sampling program of the Regional Organization for the Protection of the Marine Environment (ROPME) in partnership with the International Atomic Energy Agency (IAEA) (Lindén *et al.*, 1990). The PST-producing dinoflagellates *Pyrodinium bahamense* and *Gymnodinium catenatum* have been reported in the survey region at relatively high densities ($9.2x10^4$ and $6x10^3$ cells L^{-1}, respectively) (Anderson *et al.*, 2011). It is therefore of interest to determine the potential risk of local shellfish species for accumulation of PSTs.

Among bivalves, pearl oysters are important to consider in the context of HABs as both species of *Pinctada* appear to have considerable potential for development as fisheries and/or aquaculture species both for their meats and pearl production. The black lip pearl oyster, *P. margaritifera,* and rayed pearl oyster, *P. radiata* (Family: Pteridae) have a potentially edible adductor muscle and were cited as consumed by Arab and expatriate populations in the UAE by Carpenter *et al*. (1997). The largest of the two species, *P. margaritifera* (up to 300 mm in shell size) produces a large adductor muscle, whereas *P. radiata* attains a smaller maximum size of 150 mm. Human harvest of *Pinctada* spp. still occurs in some coastal UAE areas although this activity is not well documented at present. Although the adductor muscle of a number of bivalve species is typically free of PSTs, thus allowing marketing of this organ in PSP-affected areas, toxicity levels exceeding the regulatory level have at times been reported in scallop (Pectinidae) adductor muscle during severe PSP outbreaks (reviewed by Bricelj and Shumway, 1998).

Hooded oysters (*Saccostrea cuccullata*) (Family: Ostreidae), that can attain 85 mm in shell height, are consumed in the UAE. Evidence of their human harvest is based on the widespread occurrence of only the lower valve still cemented to the substrate. This was observed in several areas in Dubai and Ajman (Figure 5I), and local officials indicated they are harvested by some individuals although the extent is unknown. Two venerid clam species, *Circenita callipyga* and *Tivela ponderosa* (maximum size = 55 mm and 85 mm, respectively) were found at fish markets (Figure 6F and G), and *C. callipyga* was abundant on many intertidal beaches and sand flats on both coasts. No live *T. ponderosa*, however, were collected in field surveys in the present study. Additionally, the scallop *Chlamys livida* (Figure 6A) was abundant on coral reefs on both coasts. The cockle *Acrosterigma lacunosa* (Figure 6B; maximum size = 60 mm) is listed as probably edible in the UAE by Gardner (2005), but this information is based on archaeological records and may not be relevant today. All these species are suspension-feeders and thus capable of concentrating HAB toxins and becoming vectors of HAB poisoning. Another common suspension-feeding bivalve species occurring intertidally or in shallow subtidal waters and likely to be widely distributed on both coasts includes the prickly pen shell (*Pinna muricata*, maximum size = 300 mm; Figure 5G), which is listed by Carpenter *et al*. (1997) as a potential food item in the UAE. Other *Pinna* spp. (*P. pectinata* and *P. attenuata*) are known to accumulate high levels of PSTs, exceeding 3,000 MU 100 g^{-1}, in Guangdong, southern China (Lin *et al*., 1993, reviewed by Anderson *et al*., 2001). The large venerid clam, *Amiantis* (now *Callista*) *umbonella* (Figure 6H; maximum SL = 80 mm), is also potentially edible in the UAE.

Tellinids can also accumulate suspended toxic algae as they are facultative suspension-feeders. The tellinid purple clam *Hiatula rosea* (Figure 6D) was collected in the present study; *Hiatula* (= Soletellina) *diphos* can accumulate high levels of PSTs, up to 9,000 µg STXeq 100 g^{-1} whole tissues, with most of the toxin concentrated in the viscera (Hwang *et al*. 1990). The tellinid *Asaphis violascens* (Figure 6C; maximum shell length, SL = 60 mm) is harvested for food in the Pacific (Paulay, 2000) and was therefore included as one that poses a potential public health risk.

Although oysters generally attain lower PSP levels than other bivalves (mussels, scallops and clams), *S. cuccullata* attains comparable toxicity maxima to the European oyster *O. edulis* (~1,300 μg STXeq 100g^{-1}), and intermediate levels between the Pacific oyster *Crassostrea gigas* and Eastern oyster *C. virginica* (9,929 and 214 μg STXeq 100g^{-1}, respectively) (Bricelj and Shumway, 1998). It can, however, exceed the regulatory level during intense PST outbreaks. Little is known about the capacity of *Pinctada* spp. to accumulate PSTs. A laboratory study found that adults of *P. imbricata* (= *P. fucata*) from Australian waters accumulated PST levels below the regulatory level, but the study was conducted with an *Alexandrium minutum* strain of relatively low cell toxicity (3.3 pg STXeq cell^{-1}; Murray *et al*., 2009). The species identified as potential vectors of algal toxins in the present study should be studied to determine which are consumed by the UAE population as well as which (if any) are exported or imported, and therefore could pose a significant human health risk and would need to be carefully monitored if blooms of PSP-producing species occurred.

If toxic HAB events recur in the region, additional studies will be needed on the human harvesting, marketing and consumption patterns for those molluscs of public health significance. This information is needed to design an effective Marine Biotoxin Monitoring Program, as well as a National Shellfish Sanitation Program, both of which are required to develop a UAE Red Tide/HAB Monitoring and Management Program. It is well established that there are major (100-fold) differences in the capacity of different bivalve suspension-feeding species to feed on and thereby accumulate algal toxins, and in the capacity to eliminate or metabolize toxins (e.g., Bricelj and Shumway, 1998; Anderson *et al*., 2001 for PSTs; Mafra, 2010a, b for domoic acid). Accordingly, management of algal toxins by species has been implemented in other parts of the world (Anderson *et al*., 2001). For effective management it is also important to determine the anatomical compartmentalization of toxins for individual species, as some edible tissues may be toxin-free and may be marketed even during toxic blooms. Harvesting of shellfish for human consumption is possible even in areas affected by HABs if toxin accumulation is only seasonal and monitoring ensures that toxin levels in marketed product remain below the regulatory action level at the time of harvest.

Cochlodinium polykrikoides, the HAB species that resulted in intense and prolonged blooms in the AG and GO in 2008/2009, and prompted the current study, is ichthyotoxic. It is also known to be lethal to larvae of bay scallops, *Argopecten irradians*, oysters, *C. virginica*, and northern quahogs, *Mercenaria mercenaria,* on the US mid-Atlantic coast at densities of 2x10^{3} cells ml^{-1} (Tang and Gobler, 2009). It is not known, however, whether the massive mortalities of molluscs associated with the 2008/09 *Cochlodinium* red tide were due to toxic effects, or low dissolved oxygen from bloom decomposition. The bloom also resulted in massive dieoffs of fish and marine mammals in affected areas (Richlen *et al*., 2010), where *C. polykrikoides* attained densities $\geq 5 \times 10^3$ cells ml^{-1} (Anderson et al. 2011). Therefore, this HAB species may pose a threat to shellfish populations in the UAE even if it is not known to pose a threat to human health.

The impacts of HABs on survival, recruitment and growth of molluscs vary by species and mode of action of the algal toxins involved (Shumway, 1990). Even within the same genus, some species are more vulnerable to the effects of HABs than others. Therefore, generalizations across taxonomic molluscan groups or across HAB species cannot be made, and studies of toxin kinetics and ecological impacts should be considered on a species- and HAB-specific basis. Finally, although the present study focused on molluscs, the major vectors of algal toxins, it should be recognized that other invertebrates, including tunicates, sea urchins and some crustaceans can also pose a food safety concern, although they are often not considered in global biotoxin monitoring programs (Marcaillou *et al*., 2009).

CONCLUSIONS

The present study characterized the taxonomic richness of marine molluscan faunas in shallow-water habitats on both coasts of the United Arab Emirates. Differences in taxonomic composition and decreased molluscan species richness were found in the AG compared to previous qualitative mollusc surveys conducted 4 to 5 decades ago (Biggs, 1973; Smythe, 1979). These results suggest that the extensive and ongoing coastal development, and perhaps secondarily other environmental changes such as decadal, climate-driven changes and recent HAB events, have negatively affected molluscs. Seven gastropods and eleven bivalves, some of which are known to be consumed by humans in the region (Carpenter *et al.*, 1997), were identified as having potential public health significance because they were shown in other areas to accumulate HAB toxins. Thus, the present study provides the basis for developing management policies on monitoring, harvest and consumption during HAB events, as well as general ecological information. This study also points to the paucity of ecological literature on UAE's marine molluscs. Molluscan studies in general, particularly those that provide quantitative data, are especially needed in three major habitats: coral reefs, pearl oyster reefs, and breakwaters.

Corals are probably the most-studied marine invertebrate taxa in the region, in part because coral reefs have suffered dramatic declines (Burt *et al.*, 2011; Riegl *et al.*, 2012; Sheppard, *et al.* 2012). Although it seems reasonable to assume that molluscs associated with coral reefs have also been affected directly and indirectly due to habitat loss, very little has been published in recent decades on invertebrates on these reefs other than corals. In his comprehensive review of the invertebrates (including molluscs) inhabiting the AG's coral reefs, George (2012) noted the lack of attention in the entire region generally given to the many invertebrate taxa commonly found on coral reefs. Sampling on three coral reefs in the present study documented the comparative molluscan species richness of this habitat, but did not adequately characterize the molluscan communities occurring on coral reefs on both coasts of the UAE (Grizzle *et al.*, 2016). In light of the ongoing and extensive destruction of coral reefs in the region, studies on their associated mollusc and other invertebrate communities are badly needed.

Another important biogenic reef habitat in the Arabian Gulf is that provided by pearl oysters. Although the present study did not include this habitat because the reefs mainly occur in offshore waters, data herein documented the widespread occurrence of juvenile pearl oysters at many shallow-water sites, including in seagrass beds. These data suggest that extensive pearl oyster reefs may still occur in offshore waters. Pearl production from the AG, including the spatial extent of oyster reefs, was extensively documented historically (see review by Carter, 2005). In stark contrast, the spatial extent of oyster reefs today ─ and the ecosystem services they potentially provide ─ have received scant attention. Pearl oysters and the ecosystem services they provide represent a major unknown with respect to the molluscan fauna and the overall ecology of the AG.

The final major habitat that the present study at least preliminarily characterized with respect to mollusc communities is man-made jetties and breakwaters which now exist along much of UAE's Arabian Gulf shorelines replacing historical natural rocky habitats. The current study documented the widespread occurrence of relatively diverse mollusc communities on some breakwaters, but not others, as well as evidence of human harvest of some species (Figure 5I). Burt *et al*. (2012) demonstrated that breakwaters in the AG can be rapidly colonized by diverse assemblages of fish and invertebrates, but they also underscored the fact that there is still much to be learned about how these man-made habitats compare ecologically and otherwise to natural rocky areas. Considering the pace of coastal development in the UAE and the concurrent construction of breakwaters and jetties, studies on their associated ecology in general are badly needed.

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Class Bivalvia	Sites	Class Gastropoda	Sites
Arcidae		**Fissurellidae**	
Barbatia setigera	37	*Diodora rueppellii* (*Diodora ruppellii*)	37
Mytilidae		**Patellidae**	
Brachidontes variabilis	11, 20, 21, 24, 34, 41	*Cellana rota*	7, 15, 18, 26, 34, 35, 36, 37
Modiolus auriculatus	1, 4b	**Trochidae**	
Pteriidae		*Monodonta nebulosa*	7, 17, 25, 26, 31, 33, 43
Pinctada margaritifera (165 mm)	3, 4b	*Clanculus pharaonius*	35, 37
Pinctada radiata (*Pinctada imbricata radiata*) (85 mm)	3, 9, 15, 16, 17, 18, 24, 26,	*Trochus erithreus*	3, 14c, 17, 21, 24, 37
	31, 33, 34, 37, 41	*Trochus* sp.	43
Malleidae		*Osilinus kotschyi* (*Priotrochus kotschyi*)	15
Malvufundus sp.	9, 37	*Umbonium vestiarium*	10
Pinnidae		**Turbinidae**	
Pinna muricata (230 mm)	4b, 9	*Lunella coronata*	7, 10, 20, 21, 27, 31, 33, 37,
Ostreidae			38, 39, 41, 42, 43
Saccostrea cuccullata (*Saccostrea cucullata*) (60 mm)	4a, 7, 10, 14a, 14c, 15, 17, 18,	*Turbo* sp.	37
	26, 31, 34, 35, 36, 37, 39, 40,	**Neritidae**	
	41, 42, 43	*Nerita albicilla*	4a, 7, 17, 37
Pectinidae		*Nerita longii*	7
Chlamys livida (82 mm)	3, 4a, 4b, 9	**Planaxidae**	
Spondylidae		*Planaxis sulcatus*	7, 17, 25, 26, 33, 34, 36, 40, 41
Spondylus sp.	3, 9, 37	**Cerithiidae**	
Carditidae		*Cerithium caeruleum*	37
Beguina gubernaculum	4b, 37	**Potamididae**	
Chamidae		*Cerithidea cingulata* (*Cerithideopsilla cingulata*)	10, 11, 17, 20, 27, 38, 39, 41,
Chama reflexa (*Chama pacifica*)	37		42, 43
Chama douvillei (*Chama pacifica*)	3	*Terebralia palustris*	42
Chama brassica (*Chama chinensis*)	3, 4b, 9, 17, 34	**Vermetidae**	
Chama sp.	37	*Serpulorbis variabilis* (*Thylacodes variabilis*)	11
Cardiidae		**Strombidae**	
Acrosterigma lacunosa (*Vasticardium assimile lacunosum*) (60 mm)	9	*Strombus persicus* (*Conomurex persicus*)	9, 11, 14c, 31, 43
Psammobiidae		**Muricidae**	
Asaphis violascens	1, 2	*Hexaplex kuesterianus* (*Hexaplex rileyi*) (77 mm)	4b, 9, 10, 11, 14a, 14c, 15, 39, 43
Hiatula rosea	11		
Veneridae		*Murex scolopax* (79 mm)	9
Circenita callipyga (43 mm)	1, 2, 10, 16, 20, 21, 24, 25,	*Thais lacera* (*Indothais lacera*) (40 mm)	15
	27, 31, 33, 38, 39	*Thais savignyi* (*Thalessa savignyi*) (42 mm)	4a, 7, 10, 15, 17, 33, 34, 35,
*Tivela ponderosa**			36, 37
Amiantis umbonella (*Callista umbonella*) (49 mm)	39	*Thais tissoti* (*Semiricinula tissoti*) (39 mm)	9, 15, 17, 34, 37
Dosinia alta	27, 38, 41	*Rapana* sp. (35 mm)	11, 15
		Nassariidae	
		Nassarius persicus (16 mm)	31, 39, 41, 43
		Fasciolariidae	
		Fusinus sp.	11
		Chitonidae	
		Acanthopleura vaillantii	4a, 15, 37, 43

*no live specimens collected in the field; found only in fish markets

Intertidal Habitats	Present Study	Smythe (1979)
Sand and/or gravel beach (Sites: 1, 2, 25)	*Asaphis violascens* *Circenita callipyga*	*Monilea obscura*** *Strombus persicus* *Dosinia* spp. *Oliva bulbosa***
Natural rock or rock jetty (Sites: 4a, 7, 15, 16, 17, 18, 26, 31, 33, 34, 35, 36, 37, 40)	*Cellana rota* *Planaxis sulcatus* ***Thais savignyi*** ***Pinctada radiata*** ***Saccostrea cuccullata***	*Planaxis sulcatus* *Turbo coronatus* ***Thais savignyi*** ***Pinctada radiata*** ***Saccostrea cuccullata*** *Brachiodontes variabilis*
Mangroves and soft sediment flats (Sites: 10, 11, 14a, 14c, 20, 21, 24, 27, 38, 39, 41, 42, 43)	*Lunella coronata** ***Cerithidea cingulata*** ***Hexaplex kuesterianus*** *Saccostrea cuccullata* *Circenita callipyga*	*Strombus persicus* ***Cerithidea cingulata*** ***Hexaplex kuesterianus*** *Mitrella* spp.**
Subtidal Habitats		
Coral reefs (Sites: 3, 4b, 9)	*Pinctada margaritifera* *Pinctada radiata* *Pinna muricata* *Chlamys livida* *Spondylus* sp. *Chama brassica*	(not sampled)

* = taxa not reported by Smythe (1979)

** = taxa not found in present study