INTRODUCTION

Worldwide, there are numerous examples of fisheries that have collapsed and the economic consequences that such collapses have caused. Over the past two decades the molluscan fisheries throughout the world have expanded dramatically as the market for such species has increased. The result has been intensive exploitation of the prized species and a subsequent decline of regional and local populations. Scallops, which are of great economic value, provide a good example. The scallop genera of most commercial interest are Pecten, Placopecten, Patinopecten, Aequipecten, Argopecten, and Chlamys (Quayle & Newkirk 1989). They have supported important fisheries in Alaska, Oregon, Florida, Peru, Chile, Mexico, and Tasmania, but the fisheries in, not all, most of these areas have collapsed because of overexploitation and lack of management practices and timely mandatory regulations (Wolff & Alarcon 1993, Foster 1997, Robinson 1997, Marelli et al. 1999, Santamaria et al. 1999, Department of Primary Industries, Water & Environment 2004).

In the eastern Pacific, the exploitation of only two species of Argopecten still persists, Argopecten ventricosus (Sowerby II 1842) from Mexico to Ecuador, and Argopecten purpuratus (Lamarck 1819), which is found in Peru and Chile. For many decades A. purpuratus sustained a diving fishery in Independence Bay (Peru) and Tongoy Bay (Chile). Overfishing caused the closure of the fishery in both bays, and fishermen reported densities as low as 0.1 ind/m² (Wolff & Alarcon 1993). After the depletion of stocks in Chile, Japanese mariculture techniques were used to bolster the stock of A. purpuratus, which has helped in the recovery of the natural banks (Aguilar & Stotz 2000, Stotz 2000). Management (temporal bans, quotas, restocking) of the natural banks in Tongoy Bay by fishermen has helped the population there to recover and has demonstrated a potential for sustained exploitation (Aguilar & Stotz 2000). In Mexico, especially in Baja California Sur, A. ventricosus once supported an important fishery. It yielded 5,531 t (metric tonnes) of fresh meat in 1989, but after 1991 several large fluctuations in landings occurred. In 1993, the population was severely depleted, and the fishery was closed in 1994 (Santamaria et al. 1999). As a result, an effort to enhance the A. ventricosus stock in this area via mariculture has become very important.

The A. ventricosus fishery in Panama has experienced similar problems: the scallop fishery developed for many years until it collapsed at the end of the 1980s possibly because of over-exploitation, although other factors cannot be ruled out, for example variable environmental factors impacting such populations, which naturally have a short life span (Villalaz & Gomez 1997). The first official records show that in the 1960s “several boats harvested about 300 t of scallops annually,” but there were no further reports until 1975 (Arosemena & Martinez 1986, cited in Villalaz & Gomez 1997). In 1975 and 1976, a total of 6.9 t and 143 t of scallop meat, respectively, were exported, with a value of 351,026 US dollars (Villalaz & Gomez 1997). Again, no reasonably reliable records were available until the fishery was fully reinitiated in 1982, when it was reported that “26 t of scallop meat were harvested,” followed by a decline in exports to 3.9 t and 1.5 t during 1983 and 1984 respectively (USDOC 1977 cited in Villalaz & Gomez 1997). Reports indicate that in Panama scallop fisheries reached their maximum point during the years 1985 to 1986; 4.1 t of scallop meat were exported in 1985 and the amount increased to an unprecedented 2050 t in just six months during 1986, worth 10 million US dollars (Anonymous 1987). Panamanian government publications of fishery production/export statistics between 1981 and 2003 (Dirección General de Recursos Marinos 1994, 2004) demonstrate a similar pattern although not all data appear to be consistent when comparisons are made of these various published reports. Some inconsistencies may arise.
from the different data recorded and reported (e.g., harvest, landings and exports). Caution is therefore required in any attempt to reconstruct and interpret the historical trends of actual in situ scallop population abundance over these decades. Villalaz & Gomez (1997) provide the most complete account of the fishery in Panama and this is summarized later. During the heyday of this fishery in the mid 1980s, the areas from Veracruz to Farallon along the northwest mainland coast of the Gulf of Panama were targeted, and scallops were harvested at depths of 3–20 m using commercial shrimp vessels (>30 m long) and small artisanal boats (<5 m long). The small boats could harvest half a bushel in 20 min or 20 bushel in one day (equivalent to 136 kg of meat). Shrimp vessels sold the scallops to large companies that processed the product near the mainland port of Puerto Vacamonte (~70 km northwest off from Las Perlas), whereas small boats landed the scallops at beaches and local small ports where shuckers cleaned them and packed the adductor muscle in bags to a weight of 3.5 Kg. The scallop meat was sold by middlemen to exporting companies at a price of $6.30/kg, and the meat was shipped to major scallop markets in the United States (Villalaz & Gomez 1997).

The boom of the scallop fishery in the Pacific during the mid 1980s brought new factories and more financial investment to Panama. The fishery became an important industry that created more than 35,000 new jobs, providing income to 70% of fishermen who were otherwise unemployed (Gaceta Financiera 1986, Anonymous 1987, Villalaz & Gomez 1997). During the months of February and March, when shrimping was banned, many shrimp vessels harvested scallops. During this period of intensive harvest, conflicts between small-scale, local village fishermen and commercial vessels intensified; the former claimed that scallop-harvest areas were being depleted by the larger commercial shrimp boats. As a result, the Government of Panama belatedly enforced some regulations to maintain the continuity of the scallop fishery (Gaceta Oficial 1987). Decree No. 6 (February 3, 1987) and created transitory measures situated in the Gulf of Panama in the Pacific Ocean (Fig. 1). The Study Area collapse of the fishery in Las Perlas Archipelago.

A. ventricosus have recovered to any noticeable extent after the imported mainly from South America, because fishing the grounds in Las Perlas Archipelago. Seventeen years after the Oficial 1987). Unfortunately, Decree No. 6 excluded the fishing areas within 4.5 km of the coast, from Farallon to Veracruz, and these areas were designated exclusively for small boats (Gaceta Oficial 1987). Unfortunately, Decree No. 6 excluded the fishing grounds in Las Perlas Archipelago. Seventeen years after the decree and the collapse of the local fishery, scallops are not longer cost-effective in Panama.

The goal of this study was to determine if populations of A. ventricosus have recovered to any noticeable extent after the collapse of the fishery in Las Perlas Archipelago.

**MATERIALS AND METHODS**

**Study Area**

We conducted our study in Las Perlas Archipelago, which is situated in the Gulf of Panama in the Pacific Ocean (Fig. 1). The boundaries of our study area, which had an approximate area of 150,000 ha, were 8°11’31”N, 8°40’16”N, 78°46’22”W, and 78°08’40”W. Las Perlas Archipelago can be divided in two general regions: the southern area, which contains the 3 largest islands (Del Rey, San Jose, and Pedro Gonzalez) and other smaller islands; and the northern part, which has the majority of the small islands including Contadora, Saboga, Pacheca, Mogo-Mogo.

The Gulf of Panama is periodically affected by two major environmental events: a seasonal wind-driven upwelling and an increase in water temperature caused by periodic El Niño Southern Oscillation (ENSO) events (D’Croz & Robertson 1997). Every year, upwelling occurs during the dry season from January to April when northerly winds displace nutrient poor coastal waters, which are then replaced by deeper cold (15°C to 20°C) and nutrient rich waters, increasing phytoplankton blooms and coastal productivity (D’Croz et al. 1991). Also, ENSO warming events are often followed by extensive cooling events or La Niña, marked by thermocline shoaling and upwelling with temperatures below 14°C (Enfield 2001, Glynn et al. 2001). Salinity during the dry season usually ranges from 32%o to 35%o. During the rainy season, between May and December, the Gulf of Panama has warm, low salinity (<30%), nutrient poor waters (D’Croz et al. 1991). During ENSO events, water temperatures can be as warm as 30°C to 31°C (D’Croz et al. 2001). Annual gross production rate ranges from 255–280 gC/m² (Forsberg 1969).

**Anecdotal Survey and Historical Data**

We collected anecdotal data about the local scallop stock by interviewing fishermen and government officials. We carried out informal interviews from May 15 to May 30, 2004 in all nine fishing communities within the Las Perlas Archipelago to determine the sites where A. ventricosus was locally exploited approximately two decades ago, particularly from the villages of San Miguel and Martin Perez in Isla Del Rey, and from the Contadora, Saboga, Casaya, and Pedro Gonzalez Islands (Fig. 1). Priority was given to fishermen older than 35 y who would have been young men during the years of scallop exploitation. We interviewed 157 fishermen, half of whom affirmed that they had been part of the scallop fishery in the 1980s. We also examined historical statistics for A. ventricosus fishery production (exports) from published government reports (Dirección General de Recursos Marinos 1994, 2004) but it should be noted that these data are for the whole of Panama and not solely data from Las Perlas Archipelago specifically. Interpretation of data trends from these different sources needs therefore to be carried out with caution.

**Scallop Trawling Survey**

To obtain quantitative data, we performed beam trawl surveys. Small local traditional boats were used for shallow water (<20 m) surveys, and a research vessel was used to trawl in deeper areas. Once the fishery sites were identified, a field survey using the artisanal trawling method was carried out in June 2004 (Fig. 1). We used a replicate of the type of trawl used in the fishery (0.823 m long × 0.304 m width; 1-m-long net with 2.5 cm sized mesh). The boat used for the survey was a 6-m long motorboat, the same type that fishermen of the area use every day for fishing. Two fishermen who had been active members of the scallop fishery in the 1980s acted as guides to point out the
areas where scallops had been fished. We sampled a total of 39 sites that ranged in depth from 6–23 m. At each station, we trawled at approximately 3.5 km/h for a period of 15–20 min or until the weight of the net lowered boat speed, indicating that the net was full. The samples were sorted for living animals, including any recruits attached to relic shells, and when a scallop was found, the height and length of its shell were measured using calipers.

The “artisanal” survey covered only the shallow areas of the 1980s fishery grounds. On three additional expeditions, we searched for deeper populations of A. ventricosus within the archipelago and in areas previously exploited by commercial shrimp vessels. In September 2000, we sampled 57 stations using a larger trawl device (0.76 m long X 0.46 m wide; 1.2-m-long net with ~2.5 cm sized mesh) at depths ranging from 15–90 m, for a period of approximately 10 min at each station. During April 2004, we surveyed 74 stations using the same method, and in August 2004 we sampled 20 stations (Fig. 1). In all, we haphazardly sampled a total of 183 trawling stations.

Sea Surface Temperature

To assess the potential effects of changes in seasonal or ENSO hydrographic events on the recruitment of scallop populations, we examined weekly mean sea surface temperature (SST) anomalies from January 1982 to June 2004, based on data obtained from the Integrated Global Ocean Services System (IGOSS). We averaged the temperature data from two 1 X 1 degree quadrants for the northern part of the Gulf of Panama, between 8° to 9° North latitude and 78° to 80° West longitude, encompassing the archipelago (see insert in Fig. 1). Temperature measurements were blended from ship, buoy, and bias-corrected satellite data (sensu Reynolds & Smith 1994).

RESULTS

Anecdotal Survey and Historical Data

The fishermen interviewed on the Panamanian islands of Isla Del Rey, Contadora, Saboga, Casaya, and Pedro Gonzalez Islands identified A. ventricosus’s major fishery grounds to be mostly in the islands and islets of Del Rey, Bayoneta, Casaya, Pedro Gonzalez, Gibraleon, Churra-Churra, Saboga, Bolaño, Contadora, Boyarena, Mogo-Mogo, Buen Nombre, Aposentro, Membrillo, Vivero, Santa Catalina, La Esmeralda, and Bartolome. Most of these areas are situated on the west side of Las Perlas Archipelago (Fig. 1).

Anecdotal information about the scallop market in the archipelago (not the whole Gulf of Panama) during the 1980s was obtained from interviews with fishermen and confirmed
that extensive exploitation of the scallop population in Las Perlas Archipelago occurred during 1985, 1986, and 1987. After 1987, the number of scallops in the archipelago decreased, and by 1989 the resource completely disappeared (according to the fishermen). Some fishermen indicated that exploitation occurred for a period of seven years, whereas others suggested a bonanza for only 2-3 y. They also pointed out that the scallop fishery in the archipelago began on the western side of Isla Del Rey, and from there it expanded to Pedro Gonzalez Island and the rest of the archipelago.

According to the fishermen, scallop fisheries brought a period of wealth and great development to the archipelago, and people from different areas of the country came to work in the scallop fishery. Scallops were collected using small motorboats (6 and 10 m in length) equipped with one or two trawling nets pulled by hand. Each boat could harvest approximately 8-20 bushels of scallops per day, which could yield approximately 54-136 kg of scallop meat, depending on the size of the boat, the number of traw nets used, and the number of hauls per day. Scallop meat from the archipelago was sold at about $1.00 per 0.5 kg to intermediaries, who in turn sold it to exporting companies at a price of $2.00 per 0.5 kg. Fishermen indicated that most of the scallop meat was sent to the United States. Scallops shuckers in the archipelago were paid approximately $0.50 per 0.5 kg.

At times, the scallop catch was so high that not enough shuckers were available to clean them all, and the catch putrefied and had to be thrown back into the sea. It was the opinion of the fishermen from the archipelago that this problem began when the shrimp boats became part of the business. According to the fishermen, the shrimp boats were bigger with larger nets, and no limits on amount of catch and scallop size were observed.

Landing statistics obtained from the Panamanian Government (Fig. 2) showed a considerable increase in the scallop’s fishery production during 1986 and 1987 (Direccion General de Recursos Marinos 1992). This information would seem to be the best continuous record available other than isolated historical reports (sensu Villalaz & Gomez 1997), and it confirmed the fishermen’s recollection of the approximate years of intensive scallop exploitation from the archipelago. The record shows a marked decrease in scallop production after 1990; only 1 metric ton of harvested scallops was reported in 1991. After 1992, there were no reports on scallop production until 1998 and 1999 when 3 t and 7 t, respectively, were recorded (Direccion General de Recursos Marinos 1992, Autoridad Maritima de Panamá 1999, Contraloria General de La República 2003). According to unpublished statistics obtained from the Dirección General de Recursos Marinos (2004), no scallop harvest has been reported in the country after 1999.

Scallop Trawling Survey

During the artesanal survey in June 2004, a total of 39 stations were sampled in the former fishery grounds in Las Perlas Archipelago, but no live A. ventricosus were found (Fig. 1). Many relic juvenile scallop shells (approximately 800 individuals) ranging from 0.7-3.5 cm were collected in areas along the western shore of the archipelago at depths between 9 and 23 m in coarse-fine sandy sediment.

In September 2000, 57 deeper sites were surveyed using larger trawl nets and a research vessel. Argopecten ventricosus was found at seven of these stations at depths between 16 and 90 m (Fig. 1). However, only 12 live individuals, approximately 2-3 cm diameter, were found and these came from only two stations (north of San Jose Island and near Puerco Island) (Fig. 1). Of the 74 stations surveyed in April 2004, we found 17 live scallops (1.5-2.5-cm diameter) at 15 of these stations in areas near Vivero Island, Pedro Gonzalez Island, San Jose Island, Galera Island, and the southern peninsula in Del Rey Island, at depths ranging from 10.6-30.2 m (Fig. 1). Finally, out of the 20 trawling stations sampled in August 2004, only one live A. ventricosus (3.01-cm height, 3.26-cm length and 1.27-cm width) was collected from the eastern side of Pacheca Island at 25-m depth (Fig. 1).

Sea Surface Temperature

When we analyzed the weekly average temperature from January 1982 to June 2004 (Fig. 3 top), we found that surface temperature in the archipelago was normally maintained between 26°C and 28°C, although minimum average temperatures as low as 23°C were recorded during the dry season as a consequence of seasonal upwelling or La Niña events (Fig. 3). The maximum average temperature of 30.2°C was recorded during the years 1983, 1997, and 1998, which coincided with El Niño phenomena that took place in the area during these years; these years also show the highest temperature anomalies (+2.5°C). The lowest temperature anomaly of −4°C occurred in 1989 followed by 1985 and 1986 (Fig. 3 bottom).

DISCUSSION

Information obtained from fishermen, export statistics from the Government of Panama, and our intensive trawling surveys
Failed Recovery of a Collapsed Scallop Fishery

Around Las Perlas Archipelago in 2004 generally support the premise that the overexploitation of *A. ventricosus* populations in the 1980s was the principal cause for the collapse of the stocks in Panama, as opposed to any theory suggesting that natural changes reduced the local populations. However, given the inconsistency of some of the data and lack of other supporting data it is difficult to prove this conclusively. It is probable nevertheless that the heavy exploitation of a species with a short life span is responsible for the lack of recovery of the scallop fishery, as was the case for the same species in other areas of the Gulf of Panama (Farallon & Veracruz, Villalaz & Gomez 1997). It would seem that the scallops were harvested without discrimination of size or age; therefore, no recovery time was available for reproduction, the species was fished beyond its sustainable limit, and not enough recruitment occurred to maintain the population.

Today, almost two decades after the collapse of the scallop fishery in the archipelago, the population shows no signs of recovery. Our intensive trawling surveys suggest that little successful or sustained recruitment has occurred in the archipelago. Marelli et al. (1999) reported that in low-density populations of *A. irradians* in Florida, recruitment is likely to fail because low fertilization success may act against recovery. They suggested that natural recovery may take a decade or more and enhancement efforts may be necessary to restore the stock. The causes for the *A. ventricosus* population’s lack of recovery in Panama are certainly speculative; we suggest that, in addition to the previous overfishing pressures, the failure of the *A. ventricosus* population in Las Perlas Archipelago may be related to changes in environmental conditions, lack of suitable available habitats for juveniles, and predation, as suggested by Villalaz (1992) and Villalaz & Gomez (1997).

Some authors have suggested that temperature might be one of the main factors affecting larval and adult survival, either directly or indirectly. Sicard et al. (1999) reported that the optimum temperature for survival and growth of the *A. ventricosus* juvenile population in Mexico was between 19°C and 22°C. The blended temperature data from the Gulf of Panama (Las Perlas Archipelago) show that water temperature achieved a minimum of 23°C during 1985 and 1986; because these data represent average temperatures, it is probable that minimum temperatures reached 21°C to 22°C at some point. In addition, La Niña events were not clearly distinct in the 22-y record from *in situ* instrumental short-term records showing temperatures lower than 14°C (Glynn et al. 2001). In addition, these low temperatures coincided with the annual upwelling season that brings colder, saltier, and more nutrient rich water to the surface, which allows an increase in the growth of phytoplankton normally enhanced during La Niña years (Enfield 2001, Glynn et al. 2001). According to Villalaz (1992), phytoplankton enrichment and lower temperature could explain in part the high survival rates of scallops in 1986 and the productive scallop fisheries in 1985 and 1986. Based on temperature analysis, similar conditions were recorded in the area in 1989. However, by 1989 onwards scallop production was possibly on the decline caused by overfishing. This suggests that even though conditions were ideal for scallop survival, the scallop population was not able to withstand the rapid and intensive overexploitation of the stock in the archipelago. Drastic changes of temperature have not been reported in the archipelago during the past 20 y, therefore it is unlikely that temperature effects resulted in juvenile mortalities. However, weak upwelling events reported during the years 1998, 1999, and 2000 (D’Croz et al. 2003) may suggest an overall water warming that in turn may affect the scallop population recruitment rate.

Lack of suitable available habitats for juveniles could be another possible cause for juvenile mortality and low recruitment rate. Scallop settlement studies have shown that during their early life stages, scallops settle and attach to submerged vegetation, which allows them to elevate themselves from the bottom and be better protected from predators, thereby decreasing the risk of predation. Such a strategy results in higher scallop recruitment and survival (Arsenault & Himmelman 1996, Ekman 1987, Felix-Pico et al. 1989, Pohle et al. 1991). Santamaria et al. (1999) noted the temporal coincidence of the growth of the annual eelgrass *Zostera* and the appearance of juvenile *A. ventricosus* in Bahia Concepcion, Mexico and suggested the possibility that eelgrass beds could be used as nursery grounds by these scallops. To the best of our knowledge

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**Figure 3.** Time-series data for sea surface temperature (SST) recorded around Las Perlas Archipelago from 1982–2004. The upper plot shows the weekly average for the two quadrants encompassing the northern Gulf of Panama and the bottom plot the SST standardized anomaly.
there are either no small or extensive areas covered by any marine vegetation in the archipelago, and we exclude the possibility that the habitat has changed during the last 20 y. Nevertheless, it is possible that other protective substrates for scallop attachment, such as rhodolith beds, bryozoan colonies, and relic shells, could exist in areas within the area and habitats of the archipelago. However, we observed neither juvenile nor adults along the extensive rhodolith beds surveyed around the northwest shores of Casaya, Gibraleon, and Bayoneta islands.

Predation is another important factor that can affect the survival of juvenile scallops between seeding and harvest. In their predation study, Nadeau & Cliche (1998) found that crabs and several seastar species preyed on the scallop Placopecten magellanicus and were responsible for juvenile scallop mortalities after seeding. In Panama, potential scallop predators include fishes, portunid crabs, gastropods, octopuses, and seastars (Villalaz 1992). Certainly, we have observed healthy and patchy populations of seastars in the area, and octopus support a substantial fishery. Villalaz (1992) and Villalaz & Gomez (1997) suggested the importance of predation but no quantitative studies specifically targeting predation of A. ventricosus have been conducted in the archipelago or other areas of Panama, so the role of predation on the failed recovery of the population remains unknown.

Because no large individuals were found in our study area, it is possible that little natural spawning was occurring in the area and that the larvae that produced the 30 live juveniles collected on our surveys could have come from other areas of the Gulf of Panama, where adult individuals of A. ventricosus have been found. Without further studies, some self-fertilization cannot be ruled out and another possibility is that the larvae of these 30 live juvenile specimens came from an experimental mariculture project that the Ministerio de Desarrollo Agropecuario (MIDA) runs in San Jose Island in the Archipelago de las Perlas.

Our results indicate that once a resource collapses because of overexploitation, its potential for recovery is very limited. Many factors may work synergistically in the maintenance of a species and the recovery process would require a set of specific environmental and physiological conditions. The literature suggests that natural population recovery can take a decade or more, but after almost two decades, no recovery is evident in the Las Perlas Archipelago population of A. ventricosus. Enhancement efforts may be necessary to restore the stock, and Panama is putting efforts into increasing scallop stocks and repopulating natural banks through mariculture techniques. The high success of scallop culture in Panama has opened the door for research on scallop mortality, predation, competition, reproduction, and other factors that may be affecting population recovery. These techniques should be investigated further, because they could lead to the repopulation of A. ventricosus natural banks that in turn may enhance the stocks in the archipelago.

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