

# LOBSTER FISHERY BY THE KUNA INDIANS IN THE SAN BLAS REGION OF PANAMA (KUNA YALA)

BY

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## ABSTRACT

The San Blas archipelago along the Atlantic coast of Panama is inhabited exclusively by Kuna Indians, who maintain the rights to exploit fishery resources in the area. Exportation of the spiny lobster, *Panulirus argus*, to Panama City constitutes one of the major sources of income for the Kuna economy. No published data exist on either the magnitude of the fishery or the life history and population dynamics of *P. argus* anywhere in Panama. We monitored *P. argus* export in two areas of Kuna Yala over a period spanning 16 months. We gathered data on weight, length, sex, and reproductive state of all lobsters comprising the catch of each day. Overall, the sex ratio of *P. argus* in the San Blas was not significantly different from unity. However, there was a significant excess of females among smaller size classes (<105 mm carapace length, CL), and of males among larger ones. The size of first reproduction for female *P. argus* in Kuna Yala is 67 mm CL as defined by the smallest size class including females with eggs or spermatophores, and 73 mm CL as defined by the smallest size class in which >20% of the females carried eggs. Reproductive females were present during all 9 months covered by our monitoring, with no clear peak in their proportion, indicating year-round reproduction. Average measured daily export of *P. argus* to Panama City was 11.7 kg at one locality and 20.1 kg (in one of three outlets) at the other. Total estimated annual export was 18 t from these two localities and 92.48 t from the entire San Blas region. At 1998 prices, the total income to the Kuna nation from lobster export was estimated as US\$ 620,388.00.

Median carapace length of exported lobsters (83 mm in one locality, 77 mm in the other) was only slightly larger than the size at first sexual maturity. Thus, slightly less than half of the export consists of pre-reproductive individuals. However, because Kunas only fish for lobster by free-diving during the day, there is a sanctuary for lobster in depths >20 m. Removal of small *P. argus* individuals and harvesting of shallow coral for the construction of sea walls are the greatest threats to the resource. As of 1998, the estimated yield per km<sup>2</sup> (67 kg) was relatively high compared with other areas of the Caribbean, considering that no traps, nets, or SCUBA diving are employed in the fishery.

## RESUMEN

El Archipiélago de Kuna Yala, en la costa caribeña de Panamá, está habitado exclusivamente por los Kunas, quienes mantienen el derecho exclusivo de explotar los recursos pesqueros del área. La

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exportación de la langosta espinosa *Panulirus argus* a la ciudad de Panamá constituye una de las mayores fuentes de ingresos para la economía Kuna. Existe poca información publicada sobre la magnitud de la pesca, ni de la historia de vida y dinámica de la población de *P. argus* en ningún lugar en Panamá. Monitoreamos la exportación de *P. argus* en dos áreas de Kuna Yala durante 16 meses. Recopilamos datos acerca del peso, la longitud (talla), sexo, y estado de reproducción de todas las langostas capturadas cada día. Por lo general, la proporción macho/hembra de *P. argus* en Kuna Yala no era diferente de la unidad. No obstante, hubo un exceso de hembras entre las clases pequeñas [ $<105$  mm en longitud del cefalotórax (CL)], y de machos entre las clases más grandes. La talla de la primera reproducción de la hembra de *P. argus* en Kuna Yala, definida como por la clase de tamaño más pequeña que incluye hembras con huevos o con espermatozoides, era de 67 mm CL, y 73 mm CL definida como la clase de tamaño más pequeña en la cual mayor que el 20% de las hembras llevaban huevos. Estuvieron presentes hembras reproductoras durante todos los 9 meses cubiertos por nuestro monitoreo, sin demostrar ninguna temporada más activa, lo que indica que la reproducción ocurre durante todo el año. La exportación promedio de *P. argus* a la ciudad de Panamá fue 11,7 kg en una localidad, y 20,1 kg (en uno de los tres vendedores) en la otra. La exportación anual estimada fue de 18 t de estas dos localidades, y 92,48 t de la región entera del Archipiélago de Kuna Yala. A los precios de 1998, se estimó que el ingreso total a la nación Kuna de la exportación de langostas fue de \$US 620.388,00.

La longitud media del cefalotórax (83 mm en una localidad, 77 mm en la otra) fue ligeramente más grande que el tamaño de la primera madurez sexual. De esta manera, casi la mitad de la exportación está compuesto por individuos en estado pre-reproductor. Sin embargo, los Kunas sólo pescan langostas buceando a pulmón sin equipo de buceo (SCUBA) y solo durante el día, por lo tanto, podemos afirmar que existe un santuario natural para las langostas a profundidades mayores de 20 m. La captura de individuos pequeños de *P. argus* y la colecta de los corales vivos y muertos que se encuentra en agua poca profunda, para el relleno y construcción de murallas de mar frente a las islas son las amenazas más grandes al recurso. A partir de 1998, la producción estimada por kilómetro cuadrado (67,0 kg) fue relativamente alta comparado con otras áreas del Caribe, al considerar que en la pesca de la langosta en la región Kuna, no se usa ninguna trampa, ni red, ni equipo de buceo (SCUBA).

## INTRODUCTION

Kuna Yala, the administrative region of San Blas, extends along the Atlantic seaboard of Panama from approximately  $79^{\circ} 16' W$  to the Colombian border. With the exception of the border town of Puerto Obaldia, it is inhabited exclusively by Kuna Indians, who maintain the sole rights to the fishery resources of the area. Most fishing in the region's lush coral reefs (Clifton et al., 1997) is for subsistence, but lobsters of the species *Panulirus argus* (Latreille, 1804) and, less often, *P. guttatus* (Latreille, 1804) and *P. laevicauda* (Latreille, 1817) are exported. Along with tourism and exportation of coconuts and mola embroidery, lobsters constitute one of the major sources of income for the Kuna economy. Published data on the lobster fishery in the San Blas, its impact on the resource, or its economic importance are virtually nonexistent. Spadafora (1998) presented information based on four field trips on fishing methods, catch per fisherman, and imports into Panama City. Ventocilla & Olaidi (1995) gave a brief description of

fishing methods and mode of export. Most of this information is anecdotal. Other than some information presented by Butler & Pease (1965), there are also no data on the life history of *P. argus* in the San Blas region or any other place in Panama.

In Kuna Yala, lobsters are caught with snares by free-divers using mask and fins, and diving out of small canoes. Neither SCUBA nor traps are used. At some locations, each day's catch is brought to a buyer, who pays for the lobsters in cash, maintains them alive in sea-water pools or pens, then re-sells them to pilots of small planes that fly out of Panama City specifically for this purpose. At other places, each fisherman sells his lobsters directly to the pilots of these airplanes. The lobsters are packed alive in burlap sacks and taken to Panama City, where they are sold to restaurants, packing plants, and the local market.

We monitored *Panulirus argus* export in two areas of the San Blas region over a period spanning 16 months. We gathered data on the weight, length, sex, and reproductive state of each lobster comprising the catch of each day. The data were used to examine life history and population parameters of the species. Also, on the basis of our data, we reached estimates on the total lobster catch in the San Blas, on the economic importance of the fishery to the Kunas, and on the impact of the fishing activities on the resource. Given the lack of data on either Kuna use of marine resources or lobster fisheries in Panama, this information is of interest both to fisheries science and to anthropology. The data can also serve as a point of departure for future comparisons that will determine the effects of continued exploitation on the lobster populations of the area.

#### MATERIALS AND METHODS

We collected data in two localities in Kuna Yala, Whichu Uala in the western extreme of the region and Niadup, half-way to the Colombian border (fig. 1). In Whichu Uala we examined all lobsters present in the holding pens of one of three buyers operating in the area. Data were taken on 66 separate occasions. In Niadup we examined the total daily export of lobsters as they were brought by individual fishermen to the airport for shipment to Panama. Data were taken on 54 days. At both localities, all lobsters present at the site on the sampling date were examined. In most cases, each sample represents the catch of a single day. However, because airplanes sometimes fail to arrive on a given day, a few of the samples may include the accumulated catch of two (or rarely three) days. All data were taken between 17 May 1997 and 17 September 1998.

We measured a total of 4271 lobsters, 2760 at Whichu Uala, and 1511 at Niadup. In each lobster, we determined the species, sex, weight (to the nearest half-pound), and carapace length (to the nearest mm). Each female was examined for the presence of eggs or attached spermatophores.

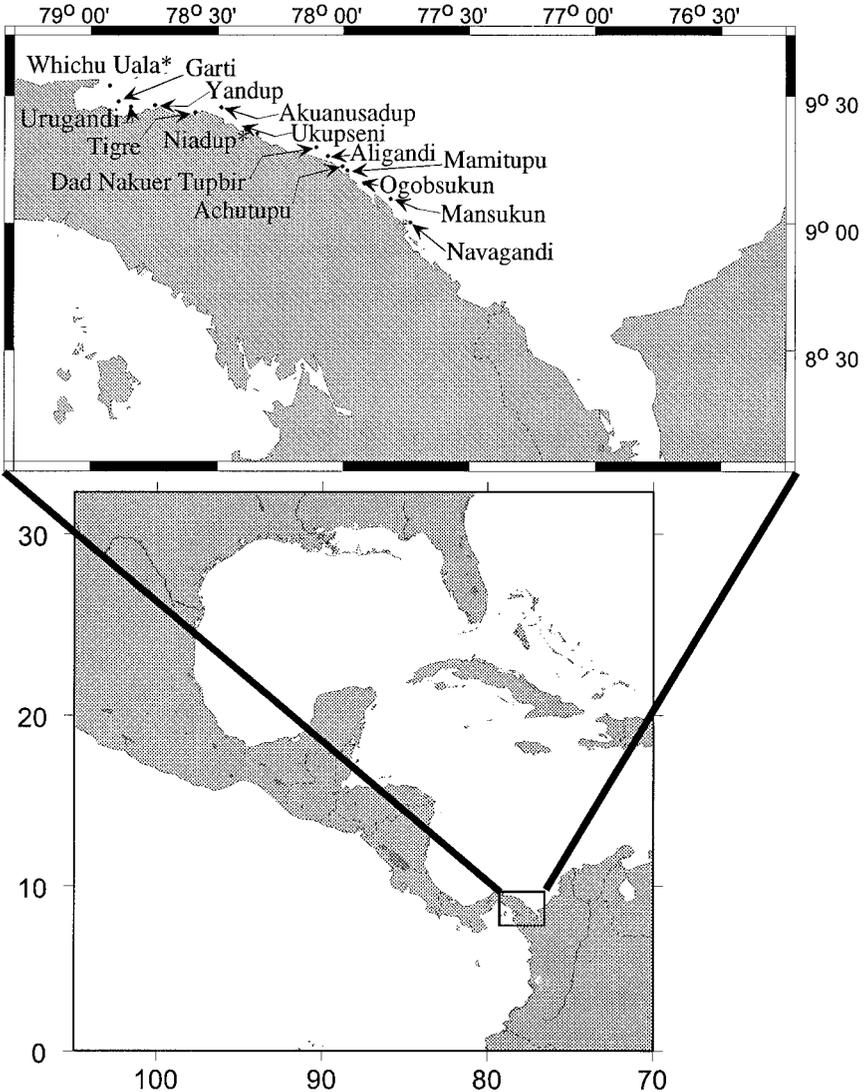


Fig. 1. The San Blas area of Panama. The two localities at which data were taken are indicated by asterisks. Other localities from which lobsters are exported are also indicated.

### RESULTS

#### Magnitude of export

Daily export of *Panulirus argus* fluctuated between 4.9 and 62.6 kg at Niadup and between 1.8 and 61.8 kg at Whichu Uala (fig. 2). This corresponded to a range of 6 to 37 lobsters exported daily from Niadup and 3 to 56 lobsters exported from Whichu Uala (fig. 3). The total export from Niadup over the 54 days we monitored

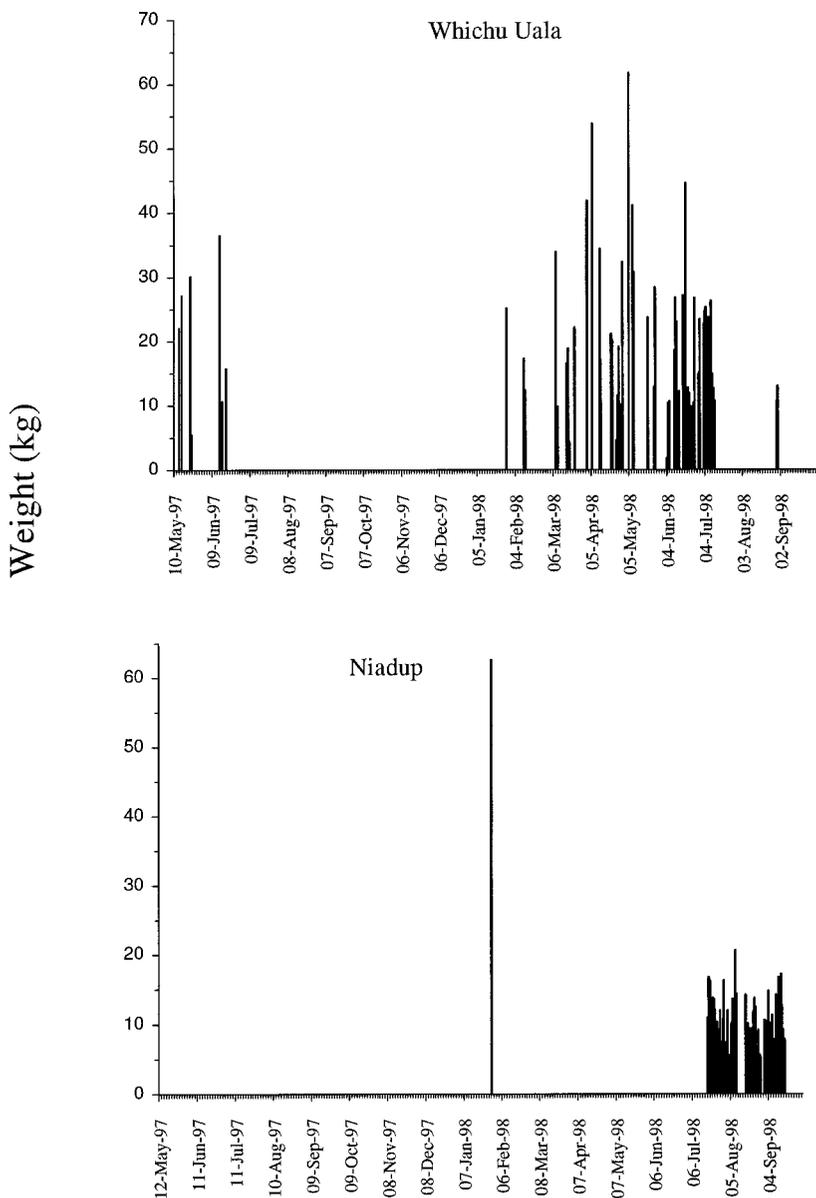


Fig. 2. Combined weight of all *Panulirus argus* (Latreille, 1804) exported by one re-seller (at Whichu Uala) and by all fishermen (at Niadup) at each day in which data were taken.

was 631.3 kg, or an average of 11.7 kg per day. Over 66 days, the buyer in Whichu Uala exported 1325.0 kg, or 20.1 kg per day. Assuming that the airplanes arrive 250 days out of the year (they do not fly on Sundays, or in exceptionally bad weather), and using the average daily export as a guide, yearly production from Niadup is

estimated at 2,925 kg. If the other two buyers in Whichu Uala process the same average volume of lobster as the one we monitored, yearly production from this area would be three times our estimated handling by the one reseller, or 15,075 kg.

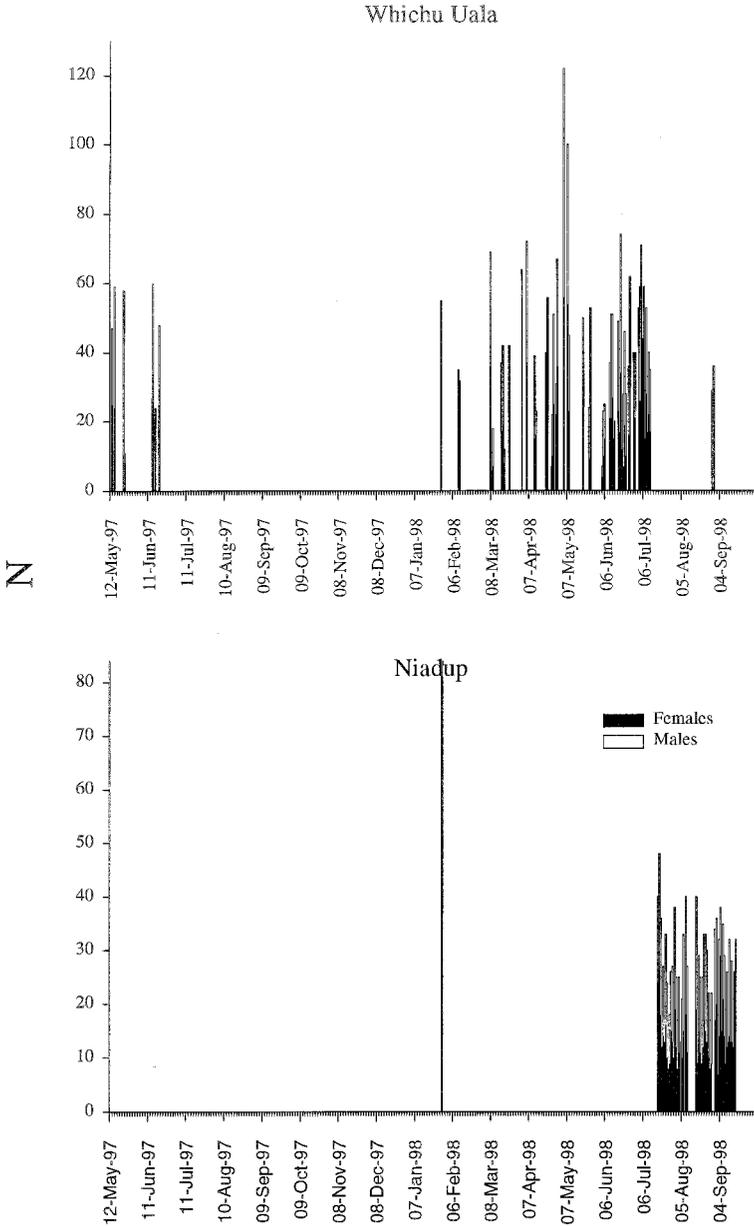


Fig. 3. Numbers of *Panulirus argus* (Latreille, 1804) (differentiated by sex) exported by one re-seller (at Whichu Uala) and by all fishers (at Niadup) at each day in which data were taken.

Size distribution n

Sizes of lobsters shipped to Panama varied between 33 and 172 mm carapace length (CL) (fig. 4). Twenty-five percent of the lobsters were less than Panama's minimum legal limit of 64 mm CL. Thirty-nine percent were below the minimum

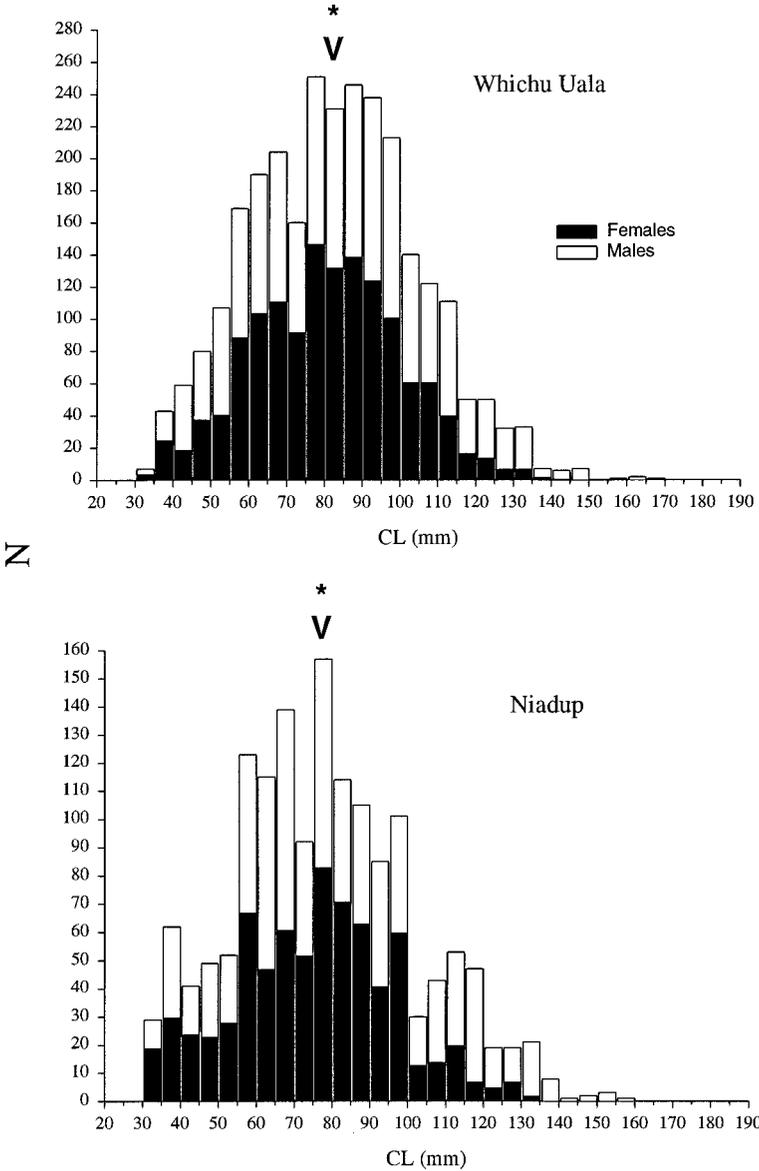


Fig. 4. Size distribution of all *Panulirus argus* (Latreille, 1804) (differentiated by sex) exported by one re-seller (at Whichu Uala) and by all fishers (at Niadup). V, median; \*, mean.

Florida legal limit of 76 mm CL. Though the largest lobster was measured in Niadup, the median size at Whichu Uala (83 mm CL) was larger than the median size at Niadup (77 mm CL) (Mann-Whitney Rank Sum Test,  $P < 0.0001$ ).

#### Sex ratio

On certain days, males predominated in the catch (fig. 3), but overall the male/female ratio (1384/1376 in Whichu Uala, 774/737 in Niadup) was not significantly different from unity ( $\chi^2$  test,  $P > 0.05$  in both cases). There was, however, a difference in the size distribution of the sexes (fig. 4). All individuals larger than 145 mm CL were male. The male/female ratio in individuals larger than 105 mm CL (464/311 in Whichu Uala, 179/68 in Niadup) was significantly larger than 1 ( $\chi^2$  test,  $P < 0.001$  in both cases). Conversely there was a significant deficit of males among size classes smaller than 105 mm CL ( $\chi^2$  test,  $0.025 < P < 0.05$  in Niadup,  $0.001 < P < 0.005$  in Whichu Uala).

#### Size of first reproduction

As fishermen do not avoid collecting females with eggs or spermatophores, and as the minimum collected size is very small, the catch probably provides an unbiased estimate of the smallest size at which *Panulirus argus* females become reproductive in the San Blas. For the purposes of this analysis, the Whichu Uala and Niadup samples were combined. The smallest female with eggs measured 67 mm CL, the smallest female with spermatophores attached to her ventrum also measured 67 mm CL. However, only 2.3% of females of this size had eggs. In fact, out of 209 females with CL < 73 mm, only 4.8% were berried. At 73 mm CL, however, this proportion jumps to 20.7%, indicating that this is the minimum size at which it is relatively common for female *P. argus* in the San Blas region to be carrying eggs. Only a few of the size classes included >50% ovigerous females, so this criterion of first sexual maturity applied by some investigators (e.g., Sutcliffe, 1952) could not be used.

#### Reproductive seasonality

We plotted the percentage of females with CL > 67 mm that were carrying eggs or spermatophores over time. As it is unlikely that time of reproduction would vary between localities so close together, the data from the two localities were pooled. The data (fig. 5) indicated that reproductive females were present at all times between the end of January and the beginning of October. We have no data for the remaining three months of the year, but it is unlikely that reproduction ceases during this time. No clear-cut reproductive season is evident. Days in which the percentage of females with eggs appears high are followed by days in which this percentage drops.

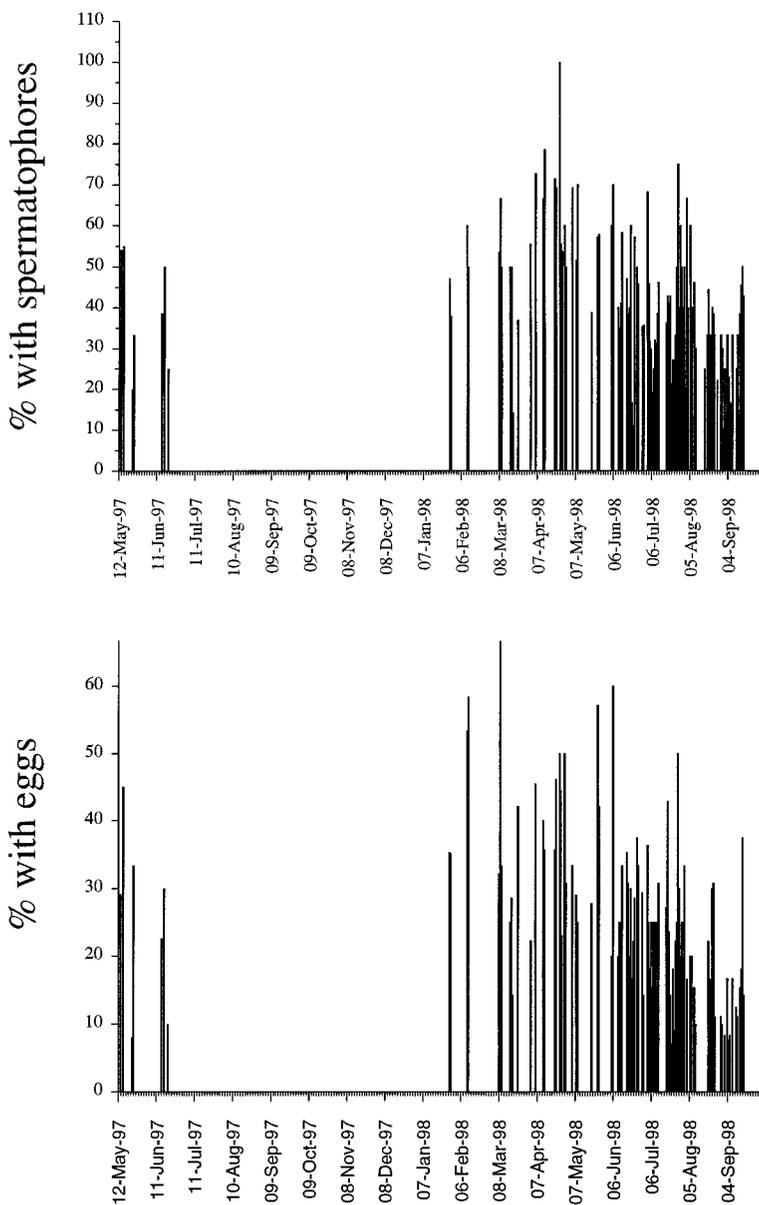


Fig. 5. Percent of females of *Panulirus argus* (Latreille, 1804) with carapace length > 67 mm that carried eggs or had attached spermatophores, over time. Data from Whichu Uala and Niadup have been combined.

#### DISCUSSION

The data are far from complete, but they can be used to reach certain conclusions, both regarding basic life-history parameters of *Panulirus argus* in the San

Blas and on the economic importance of lobster fishery to the Kunas. On the basis of this information, along with our personal experience on Kuna fishing practices, some deductions can also be made regarding the impact of the fishery on the resource and the long-term prospects for continued exploitation.

#### Life history and population parameters of *Panulirus argus* in the San Blas

Our data indicate that *Panulirus argus* in the San Blas (at least as represented by the catches of Kuna divers) have a 50 : 50 overall sex ratio. However, this ratio is not constant across size classes. There are significantly more females among smaller lobsters, and significantly more males among larger ones. Overall sex ratios close to unity have been reported from the Atlantic side of Panama (Butler & Pease, 1965) and other areas of the Caribbean (Feliciano, 1958; Buesa, 1965; Padilla-Ramos & Briones-Fourzán, 1997), but Simpson (1976) has found an excess of males in Bahamian catches. Munro's (1983) data from Jamaica are occasionally cited as showing equal numbers of males and females (e.g., Lyons et al., 1981), but when analysed statistically, they show a significant excess of males in two separate localities (Port Royal,  $0.01 > P > 0.005$ ; Pedro Bank,  $P < 0.001$ , both by  $\chi^2$ ). Lyons et al. (1981) have found that in deeper water, females outstrip males, a pattern they attribute to the tendency of females to move deeper to release their eggs (Sutcliffe, 1952; Lozano-Alvarez et al., 1991). Larger mean sizes in males than in females and a concomitant bias in sex ratio amongst the largest lobsters have been also reported from Florida (Lyons et al., 1981), Jamaica (Munro, 1983; Aiken, 1983), U. S. Virgin Islands (Barr et al., 1971) and the Bahamas (Simpson, 1976). It is clear that observed sex ratios in the catch from a given area will be dependent on the depth at which fishing is taking place, the season of the year relative to spawning activities, and (because of differential growth or survival among the sexes) the size of the gathered lobsters.

The size of first reproduction for female *P. argus* in the San Blas region is 67 mm CL, as defined by the smallest size class including a female that had eggs or carried spermatophores, and 73 mm CL as defined by the smallest size class in which >20% of the females carried eggs. Butler & Pease (1965) report that the smallest female with eggs in their trap catches from the San Blas and Bocas del Toro was 69 mm. Reported female size of first maturity in *P. argus* is different in various areas of the Caribbean, but it is not entirely clear whether this is the result of real biological differences, varying sampling effort among the smaller size classes, or varying criteria between researchers as to how to define this important life history parameter (Evans et al., 1995). Munro (1983) reported that the smallest female bearing eggs in Jamaica measured 83 mm CL, whereas Aiken (1983) shows data from the same area indicating 37% of the females 70-79 mm CL as having eggs.

At the other extreme, Smith (1951) reported egg-carrying females with a CL of 1.5 in (38 mm) in the Bahamas. Other studies from around the Caribbean reported intermediate values (reviews by Lyons et al., 1981; Evans et al., 1995). Lyons et al. (1981) carefully reviewed the previous literature on the subject and concluded that a few females with CL as small as 63 mm may be carrying spermatophores and a few females with CL of 65 mm may be bearing eggs, but the most likely size of first reproduction is approximately 70 mm CL. Our data from Panama are in agreement with this conclusion. They also agree with the data of Padilla-Ramos & Briones-Fourzán (1997) from the Yucatan Peninsula, which show that the smallest ovigerous female in this area measures approximately 68 mm CL. Various attempts have been made to explain the geographical differences in size of first reproduction as the result of dissimilarities in temperature regimes (Davis, 1975; Morgan, 1980) or in degree of exploitation of the populations (Warner et al., 1977; Lyons et al., 1981). However, the similarity of size at first reproduction between the relatively unexploited populations from thermally stable Panama [commercial fishing in Kuna Yala intensified only in the 1980s (Ventocilla & Olaidi, 1995)] and the highly exploited populations of thermally fluctuating Florida suggests that such hypotheses are not likely to have wide explanatory power.

Reproduction around the year appears to be the rule in *Panulirus argus*, though some seasonality in reproduction is evident in subtropical environments. Munro (1983) stated that there are no apparent peaks in Jamaica. Aiken (1977), on the other hand, while agreeing that there is year-round reproduction, indicated that in Jamaica there is enhanced reproductive activity between March and June. Subsequently (Aiken 1983), on the basis of more data, he amplified this to include the period between January and July. Year-round reproduction with some unclear peaks appears to be occurring in the Bahamas (Smith, 1951), Mexico (Padilla-Ramos & Briones-Fourzán, 1997; Briones & Lozano, 1994), and Venezuela (Cobo de Barany et al., 1972). The Florida populations have more eggs between May and June, with a decline in reproduction after July (Lyons, 1981; Lyons et al., 1981). In Cuba, peaks occur in February and March (Cruz & De Leon, 1991), while in Brazil between January and May (Soares et al., 1998). Our data from Panama indicate that reproduction in *P. argus* occurs throughout the year. If there are some differences in reproductive activities between seasons in Kuna Yala, our sampling was not extensive enough to detect them. The statement of Ventocilla & Olaidi (1995) that most mating and egg production of lobster in the San Blas take place between March and July is not supported by our data.

Thus, the biological data gleaned from the lobster catch we monitored in the San Blas are in agreement with what has been found for *Panulirus argus* in other areas of the Caribbean. Considering that lobster larvae remain in the water column for 6 to 14 months (Lewis, 1951; Farmer et al., 1989), and that (contrary to

a preliminary report of population subdivision; Menzies & Kerrigan, 1979) the entire Caribbean appears to contain a single genetic population (Silberman et al., 1994a, b), this agreement is not surprising. The value of these data lies primarily in confirming that a relatively unexploited population in the southwestern Caribbean is biologically very similar to those in other areas.

### Production of *Panulirus argus* in the San Blas

Ehrhardt (1994) has stated that no catch statistics exist for Panama, but estimates of total spiny lobster landings for the whole country amount to “less than 20 t per year”. Presumably, this represents catches of *P. argus* in the San Blas and the Bocas del Toro area (estimated by Butler & Pease (1965) to be more productive than the San Blas), as well as landings of *P. gracilis* Streets, 1871 from the Pacific. Spadafora (1998), on the other hand, estimated annual landings of *P. argus* during 1995 in the San Blas alone to have totaled between 90.7 and 136 t. Her estimates are based on monitoring the landings of 86 fishermen, then multiplying the average catch by the number of fishermen she assumed to be operating in the San Blas and the number of days during which they operate. Of the two widely different estimates, our data support Spadafora’s (1998).

The two localities we monitored produced average daily exports that suggest a combined annual production of 18 t. In addition to these two, lobsters are exported from the airstrips at the islands of Garti, Urgandi (Rio Sidra), Yanndup (Nargana), Akuanusadup (Corazon de Jesus), Tigre, Ukupseni (Playon Chico), Dad Nakuer Dupbir (Tupile), Ailigandi, Achutupu, Mamitupu, Ogobsukun (Usdup), Mansukun, and Navagandi (see fig. 1). Quantities exported from each island vary, but our own experience is that three of these areas, Achutupu, Nargana, and Garti, ship quantities of lobster much larger than the rest, because they concentrate the catches of many more fishermen. If, in the absence of any data, we assume that production in these three areas is equal to that of Whichu Uala, while in the rest it is equal to Niadup, then the total estimate of lobster exports out of Kuna Yala in 1998 was 92.48 t. This figure agrees rather well with that reached by Spadafora (1998) from a different combination of measurements and assumptions.

San Blas has a coastline of approximately 230 km, and the coral reefs extend an average of 6 km from the shore, so the total area potentially exploited by the lobster fishery is 1380 km<sup>2</sup>. If our estimates of annual production are correct, the yield per km<sup>2</sup> was 67 kg. By way of comparison, Cobo de Barany et al. (1972) found that mean annual lobster production at Los Roques Archipelago of Venezuela between 1961 and 1970 was 111.78 t from 1032 km<sup>2</sup> (108.3 kg/km<sup>2</sup>); Fonteles-Filho (1994) reported *P. argus* annual production in Brazil between 1965 and 1990 to be 5,389 t from 84,534 km (63.7 kg/km<sup>2</sup>); and Aiken (1983) estimated the total Jamaican

production in 1973 to be 446 t from 1,600 km<sup>2</sup> (279 kg/km<sup>2</sup>). Considering that in Jamaica, Venezuela, and Brazil the fishery uses traps, while the Kunas fish exclusively by free-diving, the comparison suggests that lobster yield of Kuna Yala is quite high.

### Economic importance

In our data, 822 out of the total 4272 lobsters (19.2%) had carapaces less than 60 mm in length. They represent a cumulative weight of 95.3 kg or 210 pounds (lbs) (4.9% of the catch in terms of weight). The larger lobsters weighed a total of 1861.2 kg or 4103.3 pounds. During 1998 the price paid to the fishermen was US\$ 1.00 per pound for lobsters smaller than 60 mm CL and US\$ 3.15 per pound for lobsters larger than 60 mm CL. Our sample, therefore, represented US\$ 13,135.00 gained by Kuna fishermen. If our estimates for total lobster export of 2,925 kg (6,450 lbs) out of Niadup and 15,075 kg (33,240 lbs) out of Whichu Uala are correct, and assuming that 95% of the weight was worth US\$ 3.15/lb, the monetary value of the *P. argus* catch during 1998 was US\$ 19,621.00 at Niadup and US\$ 101,083.00 at Whichu Uala. The estimated 92.48 t of total annual export from the entire region (always assuming that 5% of the weight is in small lobsters) represents an income of US\$ 620,388.00 for the Kuna Nation. According to the Departamento de Estadística de Salud de Región de Kuna Yala, in 1998 there were approximately 40,000 Kunas in the San Blas region, including the non-coastal communities. The estimated annual per capita income from lobster export is, therefore, approximately US\$ 15.50, a substantial sum in an area where a daily wage for non-skilled labor is US\$ 3.00 to 7.00.

### Conservation of the resource

Kunas are worried about lobster overexploitation, but the lack of biological data has been a hindrance in establishing a rational policy of management (Ventocilla & Olaidi, 1995). However, certain practices established by necessity or custom are ensuring that there will not be a complete destruction of the resource. The practice most beneficial to continued availability of *Panulirus argus* in the San Blas region is the customary method of fishing. Some efforts to evaluate and introduce trap fishing in the San Blas had been made in the 1960's (Butler & Pease, 1965), but Kunas continue to fish lobsters exclusively by diving. SCUBA diving in the San Blas is prohibited by decree of the Kuna General Congress, the supreme authority among the Kunas. This means that lobsters have a refuge below a depth of 20 m, where they cannot be reached by free-divers. As *P. argus* grow older, they move into deeper water (Sutcliffe, 1952; Lozano-Alvarez et al., 1991); gravid females also seek deeper water in order to release their eggs (Sutcliffe,

1952). Thus, individuals with the highest reproductive value are more likely to find sanctuary beyond the reach of the fishermen. What is more, Kuna divers never go diving at night, which is the period of active foraging by *P. argus* (cf. Lipcius & Cobb, 1994; Cox et al., 1997). It could be argued that as long as the Kunas are successful in limiting exploitation of the marine resources to their own artisanal efforts, and as long as they continue fishing by the same methods, *Panulirus argus* will continue to be present in the San Blas.

This, however, does not mean that catch per unit effort is not decreasing with time. Fishermen complain that lobsters are becoming harder to find (Ventocilla & Olaidi, 1995). Given that the net movement of *P. argus* during its ontogenetic cycle is from shallow to deep water where they are likely to remain out of reach of Kuna divers, large reproductive individuals in deep water are beneficial for the Caribbean-wide lobster stock, but not necessarily to Kuna fishers. Shallow water populations, except for the occasional random wanderings of individuals out of deep water, will only be replenished by larval recruitment, which is not likely to originate from local deep water populations. *P. argus* recruit preferentially to shallow water (Herrnkind et al., 1994), but, in addition to a stock of larvae, recruitment depends on the availability of suitable habitat. Clearly the Kuna practices of not sparing berried females and of removing pre-reproductive individuals (both evident in our data) are inimical to the Caribbean-wide stock of larvae. That small lobsters are not given a chance to grow to a size that fetches a higher price is also counterproductive to the fishers' own interests. In addition to these problems, habitat destruction contributes to reduced recruitment. In populated islands of the San Blas, mangroves are removed to create living space and to discourage insects. Mangroves act as nurseries of lobster (Acosta & Butler, 1997), but mangrove forests are still abundant along the San Blas coastline. The more seriously destructive effects of mangrove removal are indirect: because the low sand islands tend to wash away after mangrove removal, it is common Kuna practice to harvest shallow corals in order to build sea walls (Porter & Porter, 1973). The result is that tops of reefs near inhabited islands are left with low three-dimensional structure. *P. argus* pueruli settle preferentially in clumps of algae in shallow areas (Herrnkind et al., 1994), but as they grow they increasingly occupy rock crevices (Marx & Herrnkind, 1985; Herrnkind & Butler, 1986; Herrnkind et al., 1994). Shelter from predation is important for the maintenance of lobster populations (Childress & Herrnkind, 1994; Mintz et al., 1994; Acosta & Butler, 1997). Thus, the destruction and harvest of coral is likely to have a negative effect on recruitment and on availability of medium-sized lobsters in shallow water. Increased sediment loads on San Blas near-shore reefs, the result of wide forest destruction outside the Comarca, is also likely to reduce recruitment, because juvenile *P. argus* avoid silted habitats (Herrnkind et al., 1988). The mass mortality of the sea urchin *Diadema antillarum*

Philippi, 1845 (cf. Lessios et al., 1984; Lessios, 1988), from which the species has not recovered (Lessios, 1995), is also likely to adversely affect lobster recruitment, because juvenile lobsters sometimes use the long spines of this sea urchin for cover (Davis, 1971).

In 1999 the Kuna General Congress established a season closed to export from 1 March to 31 May. From the biological standpoint, the actual timing of the closed season is not important, because, according to our data, the intensity of reproduction in the San Blas does not vary predictably through the year. However, a closed season will undoubtedly be beneficial to the fishery in increasing catch per unit effort, as it does in Florida (Lyons et al., 1981) and Mexico (Lozano-Alvarez et al., 1991).

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