Journey into the world of age and maturity in Pacific lobster fisheries

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Introduction

The fishery research

The annual harvest of lobsters by Pacific Island nations is relatively small, estimated at about 7 per cent of the world's production, yet the lobster fishery has high economic and social importance for the Pacific communities, which stems from the ability of local fishers to catch these species without high financial costs. Given the fishery's economic and social importance, lobsters comprise only a very small proportion of the total catch of the fisheries in each country and little is known about their reproductive biology and how this is affected in a fisheries context. Estimates of the annual lobster catch are difficult to quantify, and mostly underestimated, because a significant proportion is consumed at home by fishers and their families (Pitcher 1993). Additionally, market systems for the lobster fishery are generally casual and sales are not usually recorded. Some exceptions do occur, for example, in Fiji, where commercial sales of lobster are well established, and locals earn a living from selling fresh lobsters to hotels, resorts, and restaurants.

Classification and distribution

Spiny lobsters are decapod crustaceans belonging to the family Panuliridae. There are five common species of lobsters from the genus *Panulirus* that are widely distributed in the tropical Pacific region (Prescott 1980). The abundance and distribution for each species, however, vary throughout the Pacific. The golden rock lobster, *Panulirus penicillatus* is the most abundant species and the most commonly fished species in the Pacific (Pitcher 1993; Poupin and Juncker 2010).

Morphology

Spiny lobsters exhibit considerable variation in colour and morphology. Each species has distinct characteristics such as the number of spines on the antennular plate, the colour and shape of the abdominal segments, and the colour and pattern of the shell and legs (Poupin and Juncker 2010) (Fig. 1).

Figure 1. Four species of *Panulirus*:
- (A) *P. ornatus*, ornate rock lobster;
- (B) *P. versicolor*, painted rock lobster;
- (C) *P. penicillatus*, golden rock lobster; and
- (D) *P. femoristriga*, stripe-leg spiny lobster.

(Images: A,B: ©George Shedrawi, SPC; C,D: ©Faasulu Fepuleai, Ministry of Agriculture and Fisheries, Samoa).

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Ecology

Panulirus species occupy a wide variety of benthic shallow water habitats in the tropical Pacific but are most commonly associated with coral reefs, which provide shelter and a diverse range of food (Pitcher 1993; Briones-Fourzan and Lozano-Álvarez 2013). Spiny lobsters are considered opportunistic omnivorous scavengers feeding on a range of food including molluscs (especially gastropods), crustaceans, echinoderms, seagrass and algae (Pitcher 1993). Each species responds differently to habitat gradients of depth, turbidity, temperature, salinity, coral cover and wave action (De Bruin 1969; Pitcher 1993). For example, *P. penicillatus* are restricted mainly to depths above 10 m on windward surf zones of oceanic reefs, where the water is clean and clear with minimal terrestrial influence and relatively constant water temperatures (George 1974). In contrast, *P. ornatus* (ornate rock lobster) inhabits a larger range of habitats from coral and rubble reefs to sandy seafloors with high organic content, up to a depth of 200 metres. *P. ornatus* is also relatively common in turbid conditions on continental shelves that are influenced by terrestrial run-off (George 1968; Poupin and Juncker 2010).

Reproduction

Spiny lobsters have similar life cycles and breeding behaviour regardless of species. Intermoult females with developing ovaries mate with male lobsters. Using paired penile projections at the base of the fifth walking legs (Fig. 2), a male lobster will deposit an acellular mass containing tubular spermatophores onto the fourth and fifth sternal plates of the female (Pitcher 1993) (Fig. 3). Before depositing eggs via paired gonopores at the base of the third walking legs (Fig. 4), the female scrapes the surface of the acellular mass ("tarspot") and releases the sperm using special chelae on the dactyl of the fifth walking legs (Kagwade 1988) (Fig. 5). Several hundred thousand unfertilised eggs expressed by the female are then fertilised as they pass over the spermatophoric mass inside a chamber formed by curving the abdomen over the sternum (Kagwade 1988). The female carries the eggs for about a month before they are released (Pitcher 1993). The duration of the larval stage varies with species from 4 to 22 months and passes through more than 10 morphological stages to grow into a colourless miniature adult of 50 mm total length (Phillips and Sastry 1980). At this stage, juveniles transition from oceanic to being a benthic animal (seafloor) and quickly moult into pigmented juveniles (Phillips and Sastry 1980).

Growth and size-at-maturity

Like other crustaceans, spiny lobsters grow between increments of moulting (Lyle and MacDonald 1983). Growth rates are affected by biotic and abiotic factors including water temperature, food availability, salinity and injury (Robertson and Butler 2003), which in turn can affect the size at which lobsters mature (Briones-Fourzan and Lozano-Álvarez 2013). This means a single species can exhibit a different size at first maturity depending on their environment, which has implications for local and regional management of these species (Briones-Fourzan and Lozano-Álvarez 2013). In general, growth rates slow as females become larger and more fecund because they divert energy into producing eggs and reproduction rather than growth (Hunt and Lyons 1986; Pitcher 1993).

The size-at-maturity (L_{50}) is defined as the size at which 50% of individuals are functionally or physiologically able to reproduce. Environmental factors and high fishing pressure can reduce size-at-maturity by removing large individuals that reach maturity at larger sizes (i.e. above legal size limits) (Atherley et al. 2021). This reduces their input into the genetic structure of the population; therefore, individuals in the population below the legal-size limits that reach maturity at earlier ages or smaller gradually become dominant (Atherley et al. 2021). Therefore, estimating L_{50} for a species has important implications for management because it can be used to determine a minimum legal catch length (MLL). In the case of the length-based spawning potential method used by Prince (2015), MLL is usually set around 1.2–1.4 times functional size-at-maturity. Size-at-maturity as they transition into the adult reproductive phase is also different for males and females (George and Morgan 1979). The stage of maturity of an individual can be estimated by visual assessment of the gonads, especially around spawning periods. However, outside reproductive periods histological examination of the gonads may be required.

There are two important methodologies used to assess maturity in lobsters. First, functional maturity is when all secondary attributes have developed sufficiently to enable successful mating and production of viable offspring in their natural habitat (Aiken and Waddy 1980). Second, gonadal or physiological maturity is when the gonads can produce mature gametes (Aiken and Waddy 1980). Functional size-at-maturity for female lobsters can be visually assessed by the presence of eggs under the abdomen (ovigerous or berried females) and the presence of "soft windows" or "tarspots" on various segment of the sterna (Comeau and Savoie 2002). The morphological features, however, are different between species; for example, some external features used to assess functional maturity such as "soft windows" on the sternum plate are absent for *P. longipes* (George 2005). It is difficult to determine the maturation stage of male lobsters by just considering the external morphological features alone, such as the penile process, because these can be difficult to stage (George and Morgan 1979). There are clear external changes observed, however, in some spiny lobsters; for example, in *P. versicolor* growth in the length of first leg is observed and penile processes on the sterna are pointed, serrated and have fine hairs (George and Morgan 1979; George 2005). For *P. penicillatus*, the shape of the carapace changes from sub-cylindrical to barrel-like as they mature (Pitcher 1993). The penile process used to determine functional maturity in males is just as critical as female maturity because testicular development may occur in males that are much smaller than the smallest mature females; therefore, these small males may be unable to mate with mature females due to their small size and may thus be unable to reproduce before being caught if minimum legal sizes are set by female maturity stages (George and Morgan 1979). It thus becomes important to consider smaller males in the population, when setting minimum legal length.

Previous studies on size-at-maturity in the region

There have been very few studies on the size-at-maturity of spiny lobsters in the region and those that were undertaken occurred decades ago and are location or country specific. For example, *P. penicillatus* has been studied in countries including Marshall Islands (Ebert and Ford 1986), Solomon Islands (Prescott 1988), Tonga (Zann 1984; Udagawa et al. 1995), Samoa (King and Bell 1989; Coutures 2003) and Palau (MacDonald 1988); *P. versicolor* in Palau (MacDonald 1988) and *P. ornatus* in Papua New Guinea (MacFarlane and Moore 1986) (Table 1).

Age

Age is also a vital component to know when trying to understand the life history of aquatic animals. Age is an important parameter for population modelling or fisheries stock assessment and it cannot always be inferred from size (Zhu et al. 2018). Knowing the age structure of populations improves our understanding of longevity, and size or reproductive maturity at a specific age (Becker et al. 2018). For fish, there are a range of structures that can be used for ageing including otoliths, statoliths, fins, teeth, scutes and skeletons (Sheridan et al. 2016). Direct ageing in crustaceans has proven elusive, however, because long-term calcified structures are lost as growth occurs, such as through consecutive moulting of the calcified exoskeleton (Gnanalingam et al. 2018). Nevertheless, for some species of crustacean, the age of an individual can be determined through analyses of sequentially deposited growth marks in some calcified structures including gastric mill ossicles and possibly eye-stalks (Leland et al. 2015).

Table 1. A comparison of the estimated size-at-maturity (SAM) of the spiny lobster among various studies in the region using different methods.

Species	Country	SAM – carapace length (mm)	Source	Method
Panulirus penicillatus	Enewetak Island, Marshall Islands	62	Ebert and Ford 1986	Ovigerous females ≥ 62 mm CL
Panulirus penicillatus	Solomon Island	50	Prescott 1988	Smallest ovigerous female
Panulirus penicillatus	Tonga	53	Udagawa et al. 1995	Smallest ovigerous female
Panulirus penicillatus	Tonga	65–69	Zann 1984	50% of the females ovigerous
Panulirus penicillatus	Western Samoa	75.3	King and Bell 1989	First maturity
Panulirus penicillatus	Palau	100	MacDonald 1979	Based on the average size of berried females
Panulirus penicillatus	Western Caroline Islands, Palau	69	MacDonald 1988	Smallest ovigerous female
Panulirus penicillatus	American Samoa	70	Coutures 2003	50% of the females ovigerous
Panulirus versicolor	Western Caroline Islands, Palau	82	MacDonald 1988	50% of the females ovigerous
Panulirus ornatus	Papua New Guinea	78.6	MacFarlane and Moore 1986	Smallest ovigerous female

Current and future work

Because life-history characteristics of single lobster species can differ across gradients of influence, regional differences in reproductive and population characteristics must be considered on a country-by-country basis where possible. Hence, the Pacific Community (SPC) has begun working with interested member countries and territories to collect relevant information on their lobster populations. With the support of SPC and using SPC's data collection tools (Web Applications and IKASAVEA App)[3] Samoa, New Caledonia and Fiji have already started fishery-dependent data collection on their lobster populations.

It is anticipated that SPC's ongoing and future training with data collection tools and sampling methodologies will provide a smooth path for more of the SPC member countries and territories to incorporate assessments of their lobster populations as part of sustainable fisheries management.

To ensure data collection is consistent across countries and territories, SPC is developing standardised protocols for documenting and recording size-based indicators on *Panulirus* species in the region. The areas of focus are:

A. external morphology, which will provide guidelines for identifying general differences between male and female spiny lobsters and enable macro-staging of functional maturity;
B. internal morphology, which will provide guidelines for identifying differences between male and female gonads and determine their physiological maturity; and
C. exploring the potential of using gastric mill ossicles and eye-stalks to determine age.

Protocols

A. Gross external morphology in spiny lobsters (functional maturity)

There are several features that can be used to identify the male and female spiny lobsters.

I. Penile process

Panulirus species exhibit well-developed prominent penile projections at the bases of the last pair of legs (George 2005) (Fig. 2). The penile processes are used to deposit a spermatophore at the ventroposterior end of the female lobster's thorax which is called the "tarspot" (George 2005). The tarspot develops when the spermatophore hardens in seawater (George 2005). The size and shape of the penile process varies over the life cycle of males and between species (George 2005).

Figure 2. The penile process of three *Panulirus* species.
A *P. versicolor*,
B *P. penicillatus*, and
C *P. ornatus*

(Images A–B: ©Prakriti P. Rachna, SPC; C: ©Prakriti P. Rachna)

[3] See: Shedrawi G., Bosserelle P., Vigga B., Magron F., Gislard S., Tiitii S., Tanielu E., Fepuleai F., Rachna P., Halford A.R. 2021. Using COVID-19 travel bans to precipitate a digital transition in coastal fisheries science. SPC Fisheries Newsletter 165:24–27. https://purl.org/spc/digilib/doc/qzcjs

II. Soft windows, tarspot and gonopores

The adult and mature females also have segments of soft tissue or sets of round or oval decalcified "windows" formed at the sternum on the thorax (Lindberg 1955; Berry 1970). These windows are named "soft windows" (George 2005) (Fig. 3A). This is where the spermatophore mass is deposited by the male lobster, which becomes the tarspot (Fig. 3B). Females have a pair of gonopores present at the base of the third walking legs, which release mature eggs during reproduction (Pitcher 1993) (Fig. 4).

III. Nipper claws

Female spiny lobsters have nipper claws and males do not (Fig. 5). The purpose of the nipper claw is to release the sperm by breaking the spermatophore deposited by the males (Pitcher 1993).

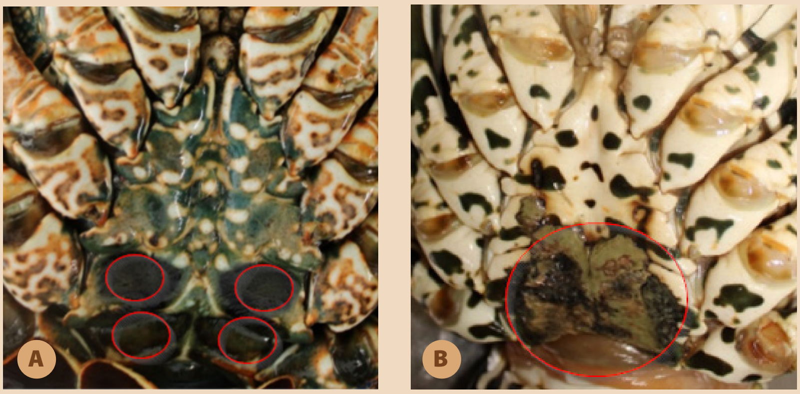

Figure 3. Sternum plates of female lobsters:
A soft windows on *P. penicillatus*, and
B tarspot on *P. versicolor*

(Images: ©Prakriti P. Rachna)

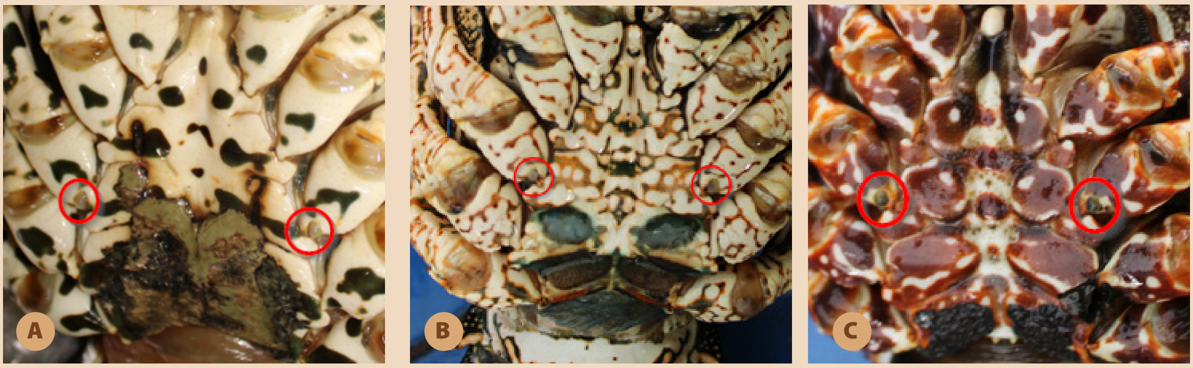

Figure 4. A pair of gonopores at the sternum of the thorax of *Panulirus* female lobsters. A *P. versicolor*; B *P. penicillatus* and C *P. fermoristriga*. (Images: ©Prakriti P. Rachna)

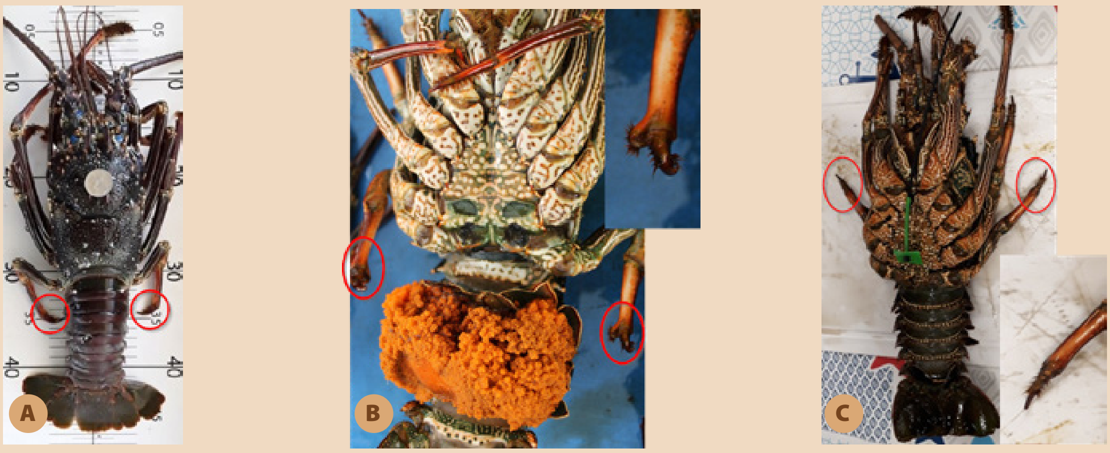

Figure 5. Image of A the claw on the fifth walking leg of a male *Panulirus penicillatus*; B the nipper claw of a berried female *P. penicillatus*; and C the claw on the fifth walking legs of a male *P. penicillatus*.

(Images A: ©Faasulu Fepuleai, Ministry of Agriculture and Fisheries, Samoa; B: ©Prakriti P. Rachna; C: ©Prakriti P. Rachna, SPC)

IV. Pleopods

The size and the number of pleopods or swimmerets differ between males and females. Males have one pair of smaller pleopods on each segment of the tail (Fig. 6), whereas female spiny lobsters have one pair of large pleopods (exopodite) and a second pair of pleopods with feathery appendages (setae) underneath the tail called endopodites (Kizhakudan and Patel 2010). The extra pair of pleopods on the first segment of the tail are about the same size as the exopodite. These extra appendages under the tail of a female allow attachment of eggs after fertilisation and development of larvae until they are released (Pitcher 1993) (Fig. 6).

B. Internal morphology in spiny lobsters

A pair of scissors was used to cut at the base of the carapace to remove it, which exposed the inner moult-layer, which holds the viscera in the cephalothorax (Fig. 7A). This was gently cut to expose the viscera where the gonads and gastric ossicles are located (Figs 7C and 7D). The gonads were gently removed, weighed, staged and placed in 10% formalin with an ID tag for later examination.

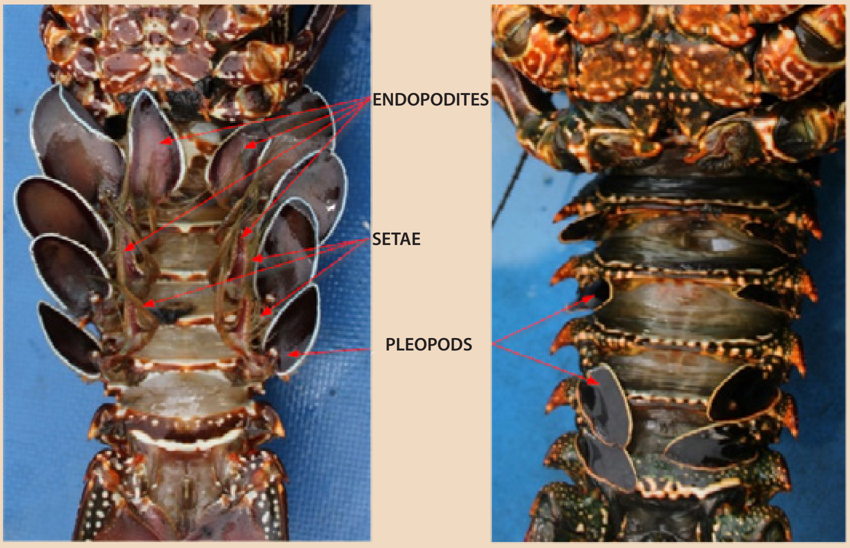

Figure 6. The tail of female *P. femoristriga* (left) and male *P. penicillatus* (right) lobsters showing the endopodites, setae and pleopods.
(Images: ©Prakriti P. Rachna)

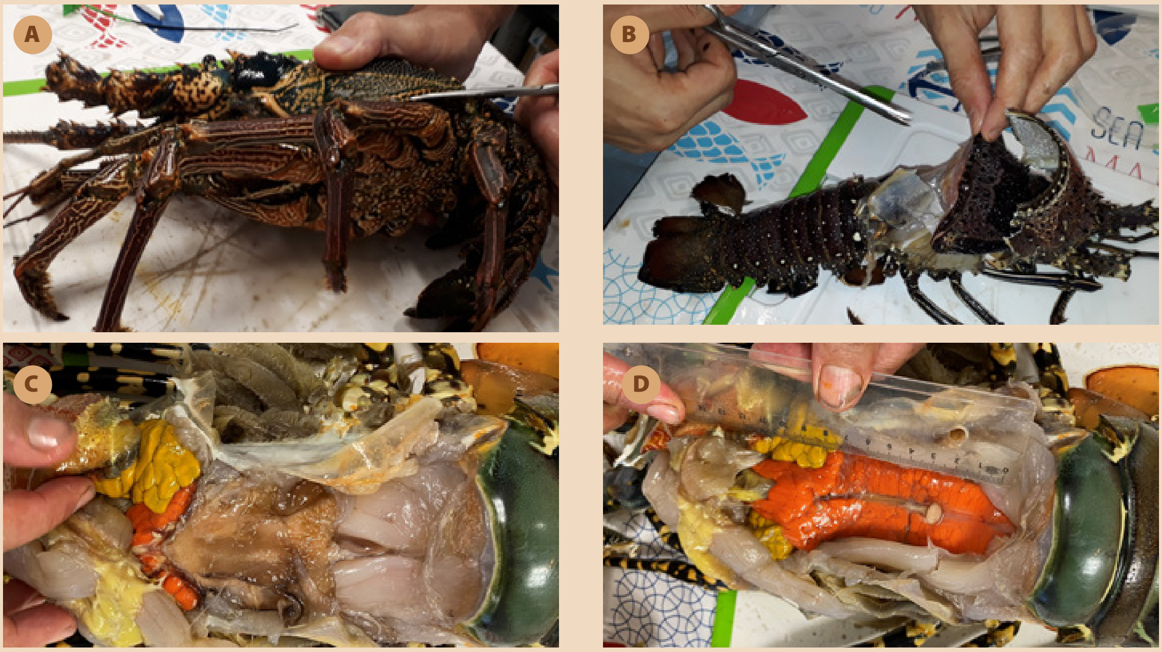

Figure 7. Opening the carapace to see the inside the cephalothorax. (A) cutting the carapace of a *Panulirus penicillatus*; (B) removing the intermoult layers of a *P. longipes*; (C) the dorsal view of a *P. ornatus cephalothorax* after removing the carapace and inner moult layers exposing gastric ossicles; and (D) the location of the gonad (ovary) in the viscera of a *P. ornatus* cephalothorax after removing the gastric ossicles. (Images A–B: ©Prakriti P Rachna, SPC; C–D: ©George Shedrawi, SPC)

I. Macro staging of gonads to determine maturity in spiny lobsters (physiological maturity)

Physiological maturity can be assessed by observing the stage and condition of the ovary and the presence of mature oocytes for females (Pérez-González et al. 2009; Yusnaini et al. 2019), and presence of mature spermatozoa in testes for males (Atherley et al. 2021). The gonads can be categorised at different gonad maturity levels (GML), using gonadal shape and size that occur before and after release of spermatophore or eggs (Salim et al. 2019). Additionally, the gonadosomatic index can be calculated and used to assess the stage of maturity (Salim et al. 2019). Gonadosomatic index (GSI) examines the development of the gonads resulting from the ratio of gonad weight (WG) to body weight (WB) expressed in percentage (Salim et al. 2019). The equation is as follows:

$$GSI = WG/WB \times 100\%.$$

The GSI is used to acquire information on spawning seasons and reproductive cycles in a range of crustaceans (Minagawa and Sano 1997). For management of fisheries resources related to stock status, it is important to find out the size at which the gonad of an individual first matures, and the condition of the gonad pre and post spawning (Salim et al. 2019). The size of sexual maturity in crustaceans may change over time, and therefore periodic assessments are recommended so that appropriate adjustments to the minimum legal size can be made, especially in heavily fished populations (Öndes et al. 2017).

Female gonads

Figure 8. The different stages of gonad (ovary) development in three *Panulirus* species with the stages of maturity. A *P. ornatus* (ripe); B *P. versicolor* (mature); and C *P. longipes* (early maturation). Stages of gonad maturation described by Kizhakudan (2014). (Images A: ©George Shedrawi, SPC; B-C: ©Prakriti P Rachna, SPC.)

Male gonads

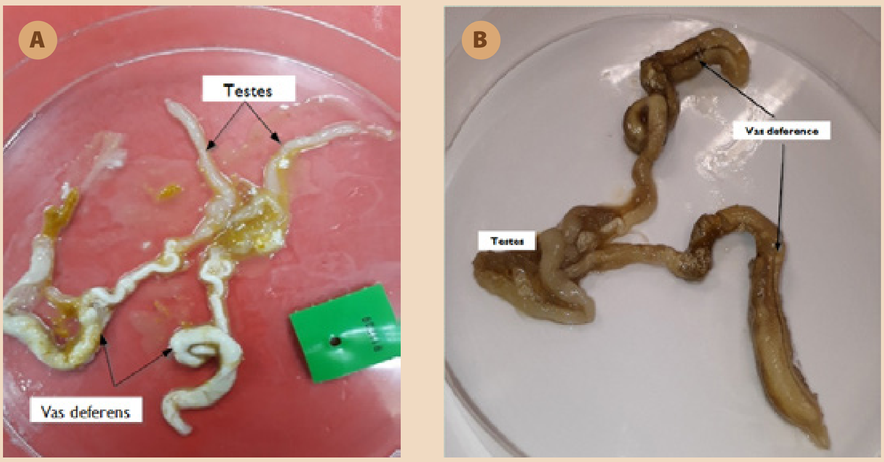

Figure 9. The reproductive tract of a male lobster, vas deferens and testes of A *P. longipes* and B *P. pencillatus*. (Image A–B: ©Prakriti P Rachna, SPC.)

C. Gastric mill ossicle and eye-stalks as a potential for age determination in spiny lobster

After opening the cephalothorax, the gastric mill ossicles were firstly removed, cleaned, and stored for age examination (Fig. 10). The gonads were carefully removed, weighed, and photographed. The eye socket was also removed to examine the eye-stalk for determining if the ageing method can be applied.

Direct anatomical ageing methods for crustaceans are not available. Previous and indirect methods of ageing in crustaceans was done by captive rearing of known-age individuals, and tag and recapture in the wild (Leland and Bucher 2017). There were several challenges using the latter method, especially because of the seasonality of reproductive cycles or recruitment events, and it was only applicable if growth increments and intermoult periods did not vary too much among individuals (Becker et al. 2018).

Using eye-stalks to age crustaceans is used mainly in krill and shrimps; however, for the larger decapod crustaceans, the endoskeleton structures in the foregut – called gastric mill ossicles – have been explored (Becker et al. 2018). Leland (2011) developed a new anatomical approach to ageing crustaceans, which has been increasingly applied over the last decade. In this method, the strongly calcified cuticular structures and bands were observed in the cross-sections of the endocuticle as annual growth increments. For some species, the number of endocuticular bands increases with body size (Becker et al. 2018; Leland et al. 2011), and a larger and older individual will thus have more endocuticular bands (Fig. 10).

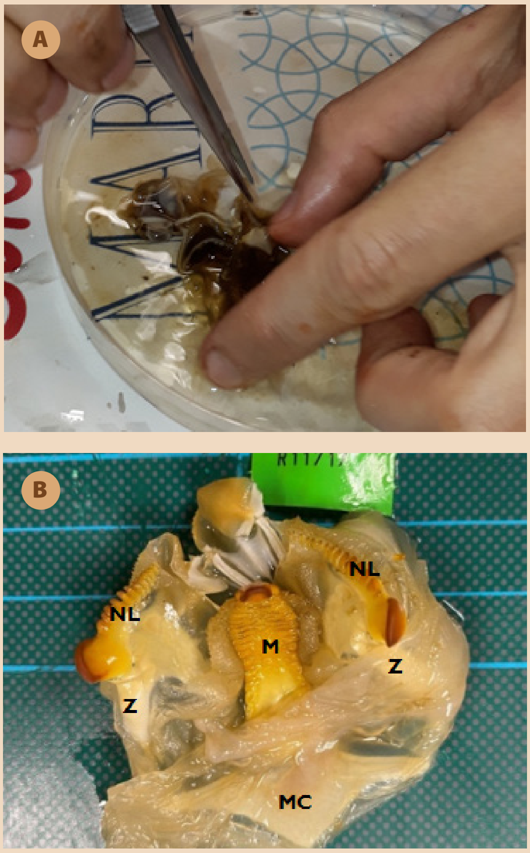

Figure 10. (A) Cleaning of the foregut, and (B) ventral view of the gastric mill from a 159-mm carapace length (CL) *P. ornatus*, with the medial tooth (M); new lateral teeth formed during the premoult period (NL); zygocardiac ossicles (Z); the mesocardiac ossicle (MC). The parts of gastric mill described by Sheridan et al. (2016). (Images A: ©Prakriti P Rachna, SPC; B: ©George Shedrawi, SPC.)

Next steps

1. Produce a set of well-designed sampling protocols and training programmes to enable Pacific Island countries and territories to collect these data effectively and efficiently.
2. Develop a biological sampling database where data can be centralised and managed for member countries and territories.
3. Develop a set of spawning potential ratio (SPR) indicators for use in fisheries management.

Conclusion

Invertebrates are an understudied resource across the Pacific, yet they are a crucial food source in most communities. Lobsters are a significant component of the invertebrate fauna and command a high price in markets, making them a highly targeted group. Limited resources in fisheries management are usually focused on finfish, which form the bulk of coastal fisheries catches. Nevertheless, SPC continues to design and implement effective and efficient methods to assist PICTs with their invertebrate resource assessments. Biological information and data accumulated through standardised protocols such as those illustrated here will enable members to develop effective management plans for sustainable coastal fisheries.

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