## CHAPTER 17

## **Spiny Lobster**

#### C. Roland Pitcher

#### I. INTRODUCTION

Lobsters are in great demand, particularly for the restaurants of such wealthy nations as the United States and Japan, which are major importers of lobsters and lobster products. Consequently, lobsters are a high-value commodity and stocks of lobsters of all types are exploited around the world. Most stocks are fully exploited – possibly even overexploited – and very few stocks are underexploited. But demand continues to grow, as does world production although it can not keep pace with demand; thus, prices have tended to increase or, at least, remain high.

The high value and marketability of lobsters, together with their simple harvest technology, live-storage potential and the durability conferred by the hard exoskeleton, make them attractive for fishery development in tropical Pacific nations (Prescott, 1988). In spite of this, the production of lobsters by Pacific Islands nations is relatively small (Table I), largely because of the small area of suitable shallow water habitat and low productivity of the tropical oceans.

Two species of spiny lobster (family Palinuridae) support significant fisheries in the tropical south-western Pacific (Prescott, 1988). The double-spined lobster, *Panulirus penicillatus* (Olivier) is the most widespread and most commonly fished lobster in the region. It supports an annual harvest of about 150 to 300 t whole weight. The ornate spiny lobster, *Panulirus ornatus* (Fabricius), is found mainly on continental shelf areas of the larger islands and continents, particularly in north-eastern Australia and south-western Papua New Guinea, where annual harvests range from 450 to 1100 t whole weight. Several other species make minor contributions to the catch of the region *e.g.* the painted coral lobster, *Panulirus versicolor* (Latreille), and the long-legged spiny lobster, *Panulirus longipes* (A. Milne Edwards).

The annual harvest of lobsters by the people of the Pacific islands nations is very important locally, both economically and socially, but the recorded production is very small in world terms (Table I). However, the recorded catch for the islands substantially underestimates the actual catch, because a significant proportion is consumed at home by fishermen and the marketing systems

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Tabl	eI.	Summary of world lobster production, contrasting P	acific production
with	the	world total (1000s of tonnes; source FAO Yearbook:	<b>Fishery Statistics</b>
vol.	64,	1987).	

	1981	1982	1983	1984	1985	1986	1987
World total fish catch	74800	76900	77600	8370	0 8600	0 92300	92700
Marine crustacean catch	3100	3300	3100	3100	3300	3700	3700
World lobster catch	158.9	161.7	173.9	181.	4 199.4	197.7	206.0
Total Pacific and rim	11.96	12.07	11.46	12.9	8 12.82	2 14.76	13.87
Lobster catch by Pacific FAO rea	gion						
Far north west (mostly Japan)	1.19	1.27	1.40	1.33	1.32	1.51	1.34
Tropical western Pacific	2.86	3.28	2.69	3.52	3.27	4.51	3.99
Central eastern Pacific	3.14	2.46	2.06	2.26	2.43	3.19	3.18
Temperate south (mostly NZ)	4.71	4.99	5.20	5.69	5.72	5.48	5.27
Far south east (mostly Peru)	0.06	0.07	0.11	0.18	0.08	0.07	0.09
World catch by Panulirus specie	s						
P. japonicus	1.19	1.27	1.40	1.33	1.32	1.51	1.34
P. argus	29.30	29.59	28.63	34.67	36.66	31.59	35.87
P. cygnus	9.96	10.48	12.46	10.69	11.26	11.00	11.03
P. spp. (all other species)	9.37	7.92	8.44	8.74	10.04	12.20	10.81
Pacific Panulirus catch by count	ry						
* American Samoa	P. penicil	latus		-	0.001	0.001	-
Australia (tropical) <sup>1</sup>	P. ornatus	5		0.330	0.537	0.872	0.605
Central Americas	P. gracilis	5		0.405	0.561	1.015	1.084
* Fiji	P. penicil	latus		0.092	0.036	0.129	0.136
* French Polynesia	P. penicil	latus		0.002	0.002	0.002	0.002
* Guam <sup>2</sup>	mostly P.p	enicillat	us	0.001	0.001	0.001	0.002
Indonesia	various			0.284	0.323	1.077	1.090
* Kiribati <sup>3</sup>	P. penicil	latus	:	≈ 0.001	≈ 0.001	0.001	0.001
Malaysia	various			0.304	0.283	0.322	0.320
Mexico	mostly P.	inflatus		1.364	1.126	1.413	1.432
* Fed. St. of Micronesia	P. penicil	latus		0.007	0.008	0.008	0.010
* New Caledonia	mostly P.p	enicillat	us	0.013	0.019	0.035	0.032
* Northern Marianas <sup>4</sup>	P. penicil	latus		0.005	0.002	0.003	0.002
* Palau	mostly P.	penicilla	utus	0.002	≈ 0.00	<b>≈</b> 0.005	≈ 0.005
Papua New Guinea	P. ornatus	5		0.115	0.187	0.243	0.138
Peru	P. gracili	5		0.135	0.046	0.024	0.049
Philippines	various			1.345	0.843	1.115	0.549
Singapore	various			0.037	0.040	0.038	0.031
* Solomon islands <sup>5</sup>	mostly P.	penicilla	atus s	≈ 0.002	≈ 0.001	< 0.001	0.001
* Tonga <sup>6</sup>	P. penicil	latus. P.	longipe	s 0.006	0.002	0.004	0.005
* Tuvalu <sup>7</sup>	P. penicill	atus	<	< 0.001	<< 0.001	<< 0.001	<< 0.001
USA (Hawaii, Cal.)	P. marein	atus. P.i	nteruptu	s 0.490	0.742	0.711	0.441
* Western Samoa <sup>8</sup>	P. penicil	latus	1	≈ 0.025	≈ 0.025	≈ 0.025	≈ 0.025
* Total Pacific islands	mostly P.	penicille	atus	0.192	0.177	0.312	0.275

(other data sources - 1: Australian Fisheries Service; 2: R. Myers and R. Hensley pers. comm.; 3: M. Kamatie pers. comm.; 4: C. Falig pers. comm.; 5: S. Diake pers. comm.; 6: Prescott, 1990; 7: T. Gentle pers. comm.; 8: King and Bell, 1991) are casual and diffuse; the true catch of the Pacific islands could be more than double that presented in Table I. Nevertheless, a projected catch of 300-600 t is small relative to the major *Panulirus* fisheries (*e.g. P. cygnus* George) in Western Australia at approximately 10,000 t, and *P. argus* (Latreille) in the western Atlantic at 30,000-35,000 t) and to the total lobster catch of the Pacific and rim (about 13,000 t). The total Pacific catch comprises only about 7 per cent of the world lobster catch and, even within the islands, lobsters comprise only a very small proportion of the total catch (usually <0.5 per cent, range 0.0-1.3 per cent; FAO, 1987).

#### **II. BIOLOGY**

#### TAXONOMY

All spiny lobsters in the south-western Pacific are Decapod Crustaceans belonging to the family Palinuridae. Two closely related families - slipper lobsters (Scyllaridae) and coral lobsters (Synaxidae) - are united with the Palinuridae under the superfamily Palinuroidae, as they all share the unique phyllosoma (leaflike) larval stage (these and other taxonomic relationships are presented in Table II). The three families are distinguished by their morphology: the palinurids have a sub-cylindrical carapace with horns over the eyes and long antennae; the scyllarids have a flattened carapace with no horns and very short, flattened antennae; the synaxids have features similar to one or other, or neither or both, of the other two families.

The spiny lobsters are further divided into subfamilies by the presence or absence of the sound-generating stridulating apparatus at the base of the antennae. Those without the apparatus, including the *Jasus* species of the southern temperate waters of the southern hemisphere, are known as Silentes. Those with the apparatus, which include the common tropical species, are known as Stridentes. There are six genera of stridulating spiny lobsters; five of them inhabit deeper water (50-1000 m), while the other is the common tropical genus *Panulirus* which has a total of 19 species distributed around the world.

The genus *Panulirus* is the most recently evolved of the six genera of stridulating lobsters, having diverged from an ancestral *Palinurus* type during the Miocene (13-25 million years before present [MYBP]; George and Main, 1967). The relationships among species within the genus *Panulirus* are not fully documented, but they have been separated into four groups (Table II) based on the morphology of the second and third maxillipeds (George and Main, 1967). The Group I species have exopods with a flagellum on both the second and third maxillipeds and are considered most representative of the ancestral type. The other groups diverge progressively from this condition: the Group II species

Table II.	Classification,	taxonomic	relationships,	and d	istribution	of spi	ny
lobsters, v	with special refe	rence to the	genus Panulir	us (syn	thesis of Ge	orge a	nd
Main, 196	67; Barnes, 1980	; Morgan, 1	980; Phillips e	t <i>al.</i> , 19	80; William	s, 198	8).

Subphylum:	Crustacea	
Class:	Malacostraca	
Subclass:	Eumalacostraca	
Superorder:	Eucarida	
Order:	Decopoda – ten-legg	ed crustaceans
Suborder	Dendrobranchiata	– prawns
	Pleocyemata	
Infraorder:	Anomura – herm	it crabs and squat lobsters
	Brachyura – c	rabs
	Caridea – shri	mps
	Stenopodidea	- cleaner shrimps
	Astacidea – cl	awed lobsters and freshwater crayfish
	Palinura – lob	sters
Superfamily:	Eryonoidae	<ul> <li>living fossil lobster</li> </ul>
	Glypheoi	dae – living fossil lobster
	Palinuroi	dae – lobsters with phyllosoma larvae
Family:	Synaxi	lae – coral lobsters
•	Scyl	laridae – slipper lobsters
	Pali	uridae – spiny lobsters
Subfamily:	Sil	entes – silent lobsters
Genus:	F	rojasus – subpolar or temperate deepwater primitive lobsters
	J	asus – southern temperate shallow-water lobsters
	Str	identes – stridulating lobsters
	L	inuparus – subtropical deepwater primitive lobsters
	F	uerulus – tropical deepwater primitive lobsters
	F	alinustus – tropical deepwater lobsters
	J	ustitia – tropical or subtropical moderate depth lobsters
	F	alinurus – temperate deepwater lobsters
	F	anulirus – tropical or subtropical shallow water modern lobsters
Species: Grou	up I P. argus – tropical wes	ern Atlantic; fisheries – Florida, Caribbean, Bahamas, Brazil
•	I P. cygnus - subtropical	southeastern Indian Ocean; fisheries - Western Australia
	I P. interruptus - subtro	bical eastern Pacific; fisheries – California
	I P. japonicus - subtropi	cal northwestern Pacific; fisheries – Japan, South China Sea
	I P. longipes - tropical L	ndo-western Pacific; fisheries – incidental in southwest Pacific
	I P. marginatus - subtro	pical northeastern Pacific; fisheries – Hawaii
	I P. pascuensis - subtrop	ical centralsouthern Pacific; fisheries – Rapanui and Pitcairn
	Group II P. echinatus -	tropical south-western Atlantic; fisheries – none
	II P. guttatus – 1	ropical western Atlantic; fisheries – none
	II P. penicillatu	- tropical Indo-Pacific; fisheries - Réunion, Philippines, Pacific Is.
	Group III P. laevicauda	- tropical western Atlantic; fisheries - Bermuda, West Indies, Brazil
	III P. polyphagus	– tropical Indo-western Pacific; fisheries – Pakistan, India, SE Asia
	III P. regius – tro	pical eastern Atlantic; fisheries – western Africa
	Group IV P. gracilis - t	opical eastern Pacific; fisheries – Mexico, Panama, Ecuador
	IV P. homarus-	ropical Indo-western Pacific; fisheries – E. Africa, Indonesia, Oman
	IV P. inflatus – s	ubtropical eastern Pacific; fisheries – western Mexico, Guatemala
	IV P. ornatus – tu	opical Indo-western Pacific; fisheries - eastern Africa, Austra, PNG
	IV P. stimpsoni-	subtropical western Pacific; fisheries - Hong Kong, South China Sea
	IV P. versicolor	- tropical Indo-western Pacific: fisheries - incidental in western
	Pacific	······································

have no flagellum on the third maxilliped; the Group III species have no exopod on the third maxilliped; the Group IV species have also lost the flagellum from the second maxilliped and are considered the most recently evolved group (George and Main, 1967).

The relationships of six species common to the western Pacific have been examined in detail using allozyme variation (Macaranas et al., 1991). The species were separated into two major groups based on Nei's genetic distance (Nei, 1978); these groups were further subdivided into the established species (Fig. 1). There are two subspecies of P. longipes: P. l. longipes is the spottedleg Indian Ocean form and P. l. femoristriga is the striped-leg Pacific Ocean form. These are genetically the most similar (Fig. 1), and Nei's distance is consistent with their subspecific status; they are also the ancestral species (Macaranas et al., 1991). The two subspecies are rarely distinguished in the literature - in this chapter they will be referred to simply as P. longipes unless the source is specific. Panulirus penicillatus (a Group II species) diverged from the P. longipes pair about 1.7 MYBP. Panulirus versicolor shows the greatest genetic divergence from the *P*. longipes pair and is considered the most recently evolved; along with the other Group IV species, P. homarus and P. ornatus (which are the most recent speciations at approximately 0.85 MYBP), P. versicolor diverged from the ancestral type 4-5 MYBP. There are three subspecies of P. homarus (Linnaeus), but only one of them is present in the Philippines where Macaranas did her study.

#### DISTRIBUTION

The 19 species of the genus *Panulirus* are distributed across the tropical and subtropical belt (*i.e.* between 35°N and 35°S) of all the world's oceans, wherever suitable habitat is available in depths under about 100 m. Thirteen of the *Panulirus* species are found in the Pacific or on its rim. Four of these are found only in the eastern Pacific, while another four are found only on the western rim and generally into the Indian Ocean as well (Table II). In the remainder of the greater Pacific, including the smaller tropical island nations, generally only four species are found (*P. penicillatus*, *P. longipes*, *P. versicolor* and *P. ornatus*), though *P. homarus* has been reported from New Caledonia and French Polynesia and an additional endemic species (*P. pascuensis* Reed) is found only in the vicinity of Pitcairn and Rapanui (Easter Island).

The most widespread species is *P. penicillatus*, which is found from southeastern Africa and the Red Sea, southern India, the south-eastern Asian archipelago, Japan, northern Australia and the southern and western Pacific islands to Hawaii, the Galapagos islands and other islands of the eastern Pacific (Williams, 1988); this species even extends as far as the west coast of Mexico (Briones and Lozano, 1982). It is the only species found on both sides of the East



Figure 1. Phylogenetic relationships among six common western Pacific species of *Panulirus* as estimated by analysis of allozyme variation (redrawn from Macaranas et al., 1991).

Pacific Barrier; a vast stretch of open ocean that divides the majority of Pacific islands from those to the east and corresponds with a major break in faunal composition (Johnson, 1974). The wide distribution of *P. penicillatus* may reflect the length of time the species has remained unchanged since it diverged from the ancestral line (Fig. 1), or its oceanic larval phase may be longer, and consequent dispersal greater, than that of other species.

The three other species found in the waters of south-western Pacific islands nations (*P. longipes*, *P. versicolor* and *P. ornatus*) are not as widespread, being absent from many nations and often sparse or rare where they do occur. Consequently, these species' contribution to lobster fisheries is relatively minor; the exception being the continental shelf area between Australia and Papua New Guinea (PNG) where *P. ornatus* is very abundant.

## HABITAT

The species of *Panulirus* occupy a wide variety of (usually rocky) habitats in shallow waters of the tropical and temperate zones. In the south-western Pacific, spiny lobsters usually are associated with coral reefs which provide excellent shelter and support diverse food organisms. However, the species respond differently to habitat gradients such as depth, turbidity, coral cover and wave action (Figs. 2 and 3). Also, some species are fairly general in their habitat requirements (*e.g. P. ornatus*) while others are more specific (*e.g. P. penicillatus*).

Panulirus penicillatus shows the greatest habitat specificity - it is restricted mainly to windward surf zones of oceanic reefs (Figs. 2 and 3) and has been termed an "oceanic species" by George (1974). The consistent features of this habitat are that the water is clean and clear, with minimal terrestrial influence, and well oxygenated by the action of high-energy waves; thus, the oxygen content and temperature are relatively constant. This species has a very strong negative response to sunlight, and, during the day, it shelters in dark recesses in the coralline matrix of the upper reef slope, usually at depths < 10 m (George, 1974). At night, these lobsters move up through the surge channels to forage on the reef crest and reef flat. The crest typically comprises a smooth coralline pavement bound together by crustose algae and sparsely covered by stunted corals. The reef flat, partially protected by the rubble ridge at the top of the reef crest, provides a more heterogeneous habitat for small prey organisms, and P. penicillatus is commonly found there at night. The tidal period and range also are important factors that influence the extent of the habitat for this species (George, 1972, 1974). Semidiurnal tides promote more prolific coral growth because exposure during low tide is only brief, whereas diurnal tides expose corals for long periods during the day and can cause significant mortality. A small tidal range restricts the foraging area to a narrow band close to the edge of the reef, thus reducing the potential productivity of the species. P. penicillatus



Figure 2. The positions along five simplified habitat gradients occupied by four western Pacific species of *Panulirus* (redrawn from George, 1968; Pyne, 1970; and including *pers. obs.*).



Figure 3. Schematic cross-section of a tropical Pacific island with barrier reef, showing simplified habitat usage by four common western Pacific species of *Panulirus* (redrawn with additions from George, 1974).

is also found in reef passages where strong currents bring well-oxygenated water. Small juveniles have been found only in the same habitat as larger animals, and it is presumed that pueruli settle directly into the adult habitat (Prescott, 1988).

**Panulirus longipes** occurs on the windward reef slope, though slightly deeper than *P. penicillatus* (George, 1968), and its habitat extends into more sheltered areas where wave action is moderate and coral growth is more prolific (Figs. 2 and 3); George (1974) refers to *P. longipes* as a "coral species". *P. longipes* also prefers clear water and, being photonegative, is cryptic during the day, but these characteristics are not as extreme as in *P. penicillatus*. *P. longipes* does not move up onto the reef flat at night; instead, it forages on the reef slope.

**Panulirus versicolor** is found most commonly among prolific gardens of plate and massive corals and is also referred to as a "coral species" (George, 1974). Nevertheless, its other habitat requirements are quite broad – it can be found in areas ranging from exposed reef slopes where the water is clear (though deeper than *P. penicillatus*), through to sheltered lagoonal or coastal areas where the water may be relatively turbid (Figs. 2 and 3). Though nocturnal, *P. versicolor* is much more conspicuous than *P. penicillatus* or *P. longipes* and individuals are often seen aggregated together under live corals with their unique long white antennae protruding. Newly settled juveniles occupy small holes that match their body size, both in the adult habitat (George, 1968; Pyne, 1970) and in crevices in the adjacent reef top (MacDonald, 1982).

**Panulirus ornatus** exhibits the broadest habitat use: it has been found as deep as 200 m, exposed to oceanic water, outside the Great Barrier Reef; in the moderately turbid and sheltered waters of lagoons and backreefs where coral growth may be prolific; and in very turbid and silted rubble areas near river mouths and mangroves (Figs. 2 and 3). Nevertheless, *P. ornatus* is most common in relatively turbid, rocky areas on broad continental shelves with a terrestrial influence and is termed a "continental species" (George, 1974). In the Torres Strait region, *P. ornatus* is migratory; some maturing individuals may walk as far as 500-600 km from the reefs of Torres Strait through the Gulf of Papua (southern PNG) to the coastal reefs west of Port Moresby, where they breed (Moore and MacFarlane, 1984).

More recently, an alternative destination for a significant proportion of breeding adults has been discovered (Prescott and Pitcher, 1991). Breeding lobsters were observed, from a submersible, in high densities at several sites outside the far northern Great Barrier Reef at depths of 30-100 m (Prescott, Pitcher, Skewes and Dennis, *unpub. data*). Apparently, this species is not migratory in other areas of the western Pacific (Prescott, 1988). Most pueruli appear to settle into small holes on rocky seabed covered by seagrass and algae or into the interstices of epifaunal growth on a seabed of rubble and sediment (CSIRO *unpub. data*).

## **DIET AND FORAGING**

Lobsters are generally regarded as opportunistic and omnivorous scavengers, but they can be somewhat selective; the proportions of food items in the stomach may differ from their relative abundance on the foraging grounds (Phillips et al., 1980). Selection may be biased toward food items with higher nutritional and energy value. The range of food items consumed by *Panulirus* species generally includes molluscs (primarily gastropods), crustaceans, echinoderms, seagrass and algae (Phillips et al., 1980). The diets of the few tropical species that have been studied appear to be similar (Table III) and there is no evidence to support a widespread perception that tropical species must be vegetarians because they do not readily enter pots (Prescott, pers. comm.). There are often significant differences in the composition of the diet at different sites and in different seasons; these differences reflect differences in the availablity of certain food types (Joll and Phillips, 1984, 1986; Edgar, 1990; Garces and Gomez, 1990). Most striking is the difference in diet of P. cygnus at two sites in Western Australia; at Site 2, small trochid molluscs are extremely common in the habitat and in the diet whereas, at Site 1, the trochids are very rare and the lobsters consume a lot more algae (particularly coralline algae). The dietary difference is reflected in growth rates: lobsters at Site 2 grow almost twice as fast as those at Site 1 (Edgar, 1990). Lobsters at different moult stages also differ in their diets; in particular, pre- and post-moult lobsters eat very little compared with intermoult lobsters (Joll and Phillips, 1984). Different size classes of lobsters may consume different proportions of food items; e.g. as P. longipes in the Philippines grow larger they eat more crustaceans and relatively fewer chitons, foraminiferans and sponges (Garces and Gomez, 1990). In other cases, e.g. P. cvgnus, there may be no clear trend with size, or trends may change with season (Edgar, 1990). Gomez et al. (unpubl.) noted that the diets of P. ornatus and P. versicolor were similar to that of P. longipes except that echinoderms were relatively unimportant in the diet of the former. The diet of P. penicillatus has not been documented, but chitons and urchins very likely form a major component, given their use as bait in traditional trap fisheries (George, 1972), their importance in the diets of other species and the prevalence of these prev in reef crest and flat habitats. Prescott (pers. comm.) has observed polychaetes, gastropods, urchins and small crustaceans in the the gut of specimens of P. penicillatus.

Relatively little detailed information exists on the foraging patterns of spiny lobsters. It is generally known that *P. penicillatus* forages during dark nights on the reef crest and flat when the tide is high, but the size of individual foraging areas is not known. *P. longipes* forages below the crest on the reef slope, *P. versicolor* probably covers most of the coral garden habitat in lagoons, and *P. ornatus* generally forages over relatively flat rocky seabed rather than on

Species	P. cygnus		P. ornatus		P. longipes	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Molluscs	7.2	24.4	62.2	38.6	19.6	16.0
Crustaceans	2.2	2.4	4.6	44.3	19.1	22.1
Echinoderms	nc	nc	5.3	5.7	18.9	22.2
Panulirus	2.5	11.6	nc	nc	nc	nc
"Worms"	1.4	0.7	nc	nc	0.2	2.2
Algae	51.6	22.1	3.0	0.7	2.8	0.5
Seagrass	12.8	6.3	0.5	0.0	nc	nc
Other	22.3	32.5	24.4	10.7	39.4	37.0
Source:	Joli and P	hillips, 1984;	Joll and	Phillips, 1986;	Garces a	nd Gomez, 1990

Table III. Percentage by volume of different categories of food items in the foreguts of three species of *Panulirus* (nc = no category in study, combined with "other").

high-relief coral structures. More detailed information is available for P. argus and P. cygnus - this information may indicate the activity pattern for southwestern Pacific species. P. argus individuals leave their dens at dusk and move up to 300 m off the reef onto seagrass beds; here lobsters meander solitarily while foraging until a few hours before dawn, when they return directly to the den (Herrnkind, 1980). The foraging activities of P. cygnus have been studied in detail using electromagnetic tracking equipment (Jernakoff, 1987a). Most activity begins just prior to dusk when lobsters leave their dens and move out onto seagrass beds; activity is rather constant throughout the night, with rates of movement averaging one metre per minute (range 0-18). Lobsters return to their dens when light levels increase around dawn. The foraging paths taken by lobsters may be long and circuitous, long and directed, or short and circular (Jernakoff, 1987b); the distance travelled by 95 per cent of the tracked lobsters ranged from 75 m to 585 m (Jernakoff et al., 1987). This information indicates that lobsters have access to large areas from which to obtain food and are not limited by what is available close to their dens.

## **REPRODUCTION**

The different species of *Panulirus* have relatively consistent life cycles and breeding behaviour. Male lobsters, possibly attracted by a sex pheromone, mate with intermoult females that have developing ovaries. The males deposit an acellular mass containing tubular spermatophores, via paired penile projections at the base of the fifth walking legs, onto the fourth and fifth sternal plates of the females.

Courtship has rarely been observed, but it is similar in two species (P. homarus – Berry, 1970; P. ornatus – Prescott, 1988). Initially the male follows the female, for as few as 15 minutes or for many hours – touching her continuously with his antennules and first three pairs of walking legs, which may be greatly elongated in large mature males. Eventually the intensity of the activity increases and the male rushes at the female head-on, attempting to grab and lift her into the mating position; these attempts may fail several times but, when successful, the male lifts the female into contact with his sternum for 5-8 seconds and the spermatophoric mass is deposited. The physical effort required for mating prompted Berry (1970) to suggest that males would have to be larger than females to succeed, but this is apparently not essential (Chittleborough, 1974).

Within a few days, the females extrude several hundred thousand eggs from the paired gonopores at the base of the third walking legs into a chamber formed by curving the abdomen over the sternum; the eggs are fertilised as the female releases the sperm by scraping the spermatophore with special chelae on the dactyl of the fifth walking legs. In some species the entire spermatophore is used in one spawning, *e.g. P. homarus* (Berry, 1970); in other species it is possible that the spermatophore is shared between two spawnings, *e.g. P. penicillatus* (Prescott, 1988) and *P. ornatus* (MacFarlane and Moore, 1986). The fertilised eggs adhere to the ovigerous setae of the endopodite of the biramous pleopods (*cf.* males which have only single, or uniramous, pleopods). The female may take up a vertical position, or even lie on her back, while oviposition occurs (Berry, 1970).

The eggs are carried under the tail of the female for about a month before the tiny phyllosoma larvae are released. The female may stimulate larval release by rapidly flexing the raised abdomen and the time of release may be cued to the onset of dawn (e.g. Jasus edwardsii – MacDiarmid, 1985) and to the full moon (e.g. P. ornatus – Dennis et al., 1992). In addition, the female may move to areas where currents are stronger and directed to carry the larvae into the oceanic environment; in some species, this may involve a major movement or migration into deeper water or to areas bordering oceanic water masses (e.g. P. cygnus – George, 1958; P. argus – Herrnkind and Kanciruk, 1978; P. ornatus – Moore and MacFarlane, 1984).

The transparent phyllosoma larvae may remain in the ocean for 4-12 months or more, passing through 10 or more morphological stages and growing to as long as 50 mm total length, before they moult into the puerulus stage which resembles a colorless miniature adult and may last from a few days to a few months (Phillips and Sastry, 1980). The pueruli undertake the transition from the oceanic to the benthic environment, where they settle in or near the adult habitat and quickly moult into pigmented juveniles (Phillips and Sastry, 1980).

The size at which lobsters become mature is a basic biological parameter that is also an important consideration for management. Size at maturity has two aspects that must be considered: physiological maturity, when the gonads are capable of producing viable gametes; and functional maturity, when all secondary attributes have developed sufficiently to enable successful mating and production of viable offspring in the natural habitat (Aiken and Waddy, 1980). These considerations are especially important in males because testicular development can occur in males that are much smaller than the smallest females with developed ovaries; thus these small males may be unable to mate with mature females (George and Morgan, 1979). Consequently, the presence of spermatozoa may not equate with male maturity.

Although there are no conclusive external indicators of male maturity, there are some secondary characteristics that can be measured. In male *P. penicillatus*, the carapace shape changes from sub-cylindrical to barrel-like as they mature, but this has not been studied in detail. In some other species, the change in allometric growth of the first three pairs of walking legs has been examined for its utility as a maturity indicator. For *P. versicolor*, linear regression methods have shown that a change in relative leg length occurs at a carapace length (CL) of approximately 72 mm (Fig. 4.; George and Morgan, 1979) and, though gonad indices were not measured, it was thought that secondary features would not develop until after gonad maturity.

However, the value of this index must be treated with caution if males have to be larger than females to mate successfully, because the smallest berried female *P. versicolor* found at Palau was 82 mm CL (MacDonald, 1982)–*i.e.* > 72 mm CL at which the change in male leg length occurs. Male *P. penicillatus* from the Philippines show a similar change in relative leg length at approximately 70 mm CL (in comparison the size of the smallest berried female was only 41 mm CL), and this change was taken to indicate the size of onset of functional male sexual maturity (Juinio, 1987). In male *P. ornatus* that participate in the breeding migration through the Gulf of Papua, the change in leg length (at 110-115 mm CL) is very abrupt, rather than manifesting as a constant differential growth ratio (Fig. 4). The abrupt jump in leg length is reminiscent of a maturity moult, but the size at which it occurs roughly corresponds with the modal size of migrating males. Thus, to conclude that the size at maturity was 110-115 mm CL would imply that about half of the males migrating to the breeding grounds were immature.

Clearly, size at maturity of male lobsters is difficult to determine. If there are concerns that males must be larger than females to mate successfully - and, as a consequence, if it is also considered that a minimum size should be set to protect males up to the size required to mate with females of average size at first maturity - then the relative mating success of males of different sizes must be established by experimentation.

Disparity between gonad maturity and functional maturity can also occur in female lobsters. In *P. argus*, ovarian development begins in smaller lobsters



Figure 4. Changes in relative length of anterior walking legs in two tropical species of *Panulirus*. In *P. versicolor*, the entire length of the third leg was measured (redrawn from George and Morgan, 1979); in *P. ornatus*, the length of the carpus+propodus segments only were measured (CSIRO, *unpub. data*).

than those that spawn, and these immature females can be mated (Lyons *et al.*, 1981). Consequently, it is not wise to base maturity indices on the presence of a spermatophore. Maturing female lobsters may also exhibit changes in allometric growth of the tail and walking legs, and in the length (or absence or presence) of ovigerous setae on the pleopods. Breeding female lobsters have relatively wider tails than males, but in very small animals there is no difference. In female North Atlantic clawed lobsters, this dimorphism in relative tail width develops with the onset of maturity and is used as a maturity index (Aiken and Waddy, 1980). However, in spiny lobsters there is no evidence of a distinct change - the tail width simply increases in proportion to carapace length faster in females than in males (*P. homarus* – Berry, 1971; *P. ornatus* – Skewes *et al.*, 1992).

There is also a change in the relative leg length of the females of some species, but, unlike males, the legs tend to become relatively shorter (*P. versicolor* George and Morgan, 1979; *P. marginatus*-Prescott, 1984). The change is only very slight and, consequently, the estimated point of change (at 63-69 mm CL in *P. versicolor*; about 59 mm CL in *P. marginatus*-cf. Table IV) has wide error margins. The caution expressed about males also applies to females: in Palau, female *P. versicolor* may be mated at about 68 mm CL, which corresponds to the change in leg length, but the smallest ovigerous females were about 82 mm CL.

Ovigerous setae have been used as a maturity index for Jasus edwardsii in southern Australia; setae usually appear at, and only occasionally before, the maturitymoult (Fielder, 1964). In several species (e.g. Jasus lalandii-Paterson, 1969 and Silberbauer, 1971; Panulirus japonicus – Nakamura, 1940; P. argus – Sutcliffe, 1953; P. cygnus – George, 1962) the ovigerous setae are present only during the breeding season; in others (e.g. P. homarus – Berry, 1971; P. ornatus – pers. obs.) the setae are present throughout the year. In P. ornatus, setae are present on the pleopods of very small females (approximately 50 mm CL, pers. obs.), though the setae may undergo differential growth at maturity.

The most conclusive index of maturity in females is the presence of eggs, although this index also has problems. For example, the maturity status of an individual female cannot be assessed unless eggs are present; relatively large samples have to be taken; and, depending on how the index is defined, the increase in spawning frequency with size (Berry, 1971; Prescott, 1988) may have to be taken into account. Ideally, the size at maturity might be defined as the average size at which females produce their first brood. However, prior breeding history is usually unknown and a commonly used proxy is the size at which the frequency of berried females is half the maximum frequency. The proxy index will often overestimate size at maturity compared with the *ideal* definition because larger females usually produce broods more frequently than small females; thus the probability of sampling larger females with eggs is greater. This bias can be corrected only if the spawning frequency of different

Species and Location	Smallest ovigerous	50% of max. % ovigerous	50% ovig. corrected	Fecundity at 100 mm CL	Source
P. penicillatus					
Philippines	41	45-50		389,000	Juinio, 1987
Enewetak	62				Ebert and Ford, 1986
Solomon Is.	50	80-84	75-79	373,000	Prescott, 1988
W. Samoa	52	75.3			King and Bell, 1991
Tonga	55	75-79		388,000	Zann, 1984
P. marginatus					
Hawaii	53	75-80		408,000	McGinnis, 1972
P. versicolor					
Palau	82	80-90			MacDonald, 1982
P. ornatus					
Papua	67			480,000	MacFarlane and Moore, 1986

# Table IV. Size at maturity and fecundity of female spiny lobsters of the genus Panulirus in the southern and western Pacific

sized females is known (e.g. Prescott, 1988 — Table IV). Such data rarely are available as they require considerable time and effort to collect.

The most appropriate type of maturity index will depend on the intended use of the information. If, for example, comparisons are to be made between lobster populations in different places, then any consistent, yet simple, index will suffice (Table IV). However, if the egg-producing potential of the population is to be protected, a minimum size cannot simply be set at some postulated index of maturity. Additional information on how fecundity, spawning frequency and relative abundance vary with size is required (see discussion on egg-per-recruit later in this chapter).

The fecundity of *P. penicillatus* varies with size in a similar way in different areas (Table IV, Fig. 5). Although the fecundity versus size relationship would be expected to be exponential, the available data are usually very scattered and often published in linear form. Female *P. penicillatus* from Tonga, the Philippines and Solomon Islands, and *P. marginatus* from Hawaii all carry similar numbers of eggs, whereas *P. penicillatus* from Hawaii appear to carry fewer eggs for their size. *P. ornatus* of all sizes appear to be more fecund than the other species (although there is insufficient information to test this statistically). However, the relationship for *P. ornatus* was derived from berried females that were collected early in the distinct breeding season even though fecundity declines significantly with subsequent broods through the



Figure 5. Relationship between the fecundity and size of Pacific spiny lobsters genus *Panulirus: P. ornatus* from the Gulf of Papua (MacFarlane and Moore, 1986); *P. marginatus* from Hawaii (McGinnis, 1972); *P. penicillatus* from Tonga (Zann, 1984), Solomon Islands (Prescott, 1988), the Philippines (Juinio, 1987), and Hawaii (McGinnis, 1972).

season (MacFarlane and Moore, 1986); thus, it would be more equitable to compare the average fecundity of *P. ornatus* with that of the other species.

The seasonality of breeding activity varies substantially with species and location (Fig. 6). Where breeding seasonality has been studied in *P. penicillatus*, activity varies from continuous and aseasonal (*e.g.* Solomon Islands), through continuous but reduced in cooler months (*e.g.* Hawaii), to discontinuous with a seasonal peak in the warmer months (*e.g.* Philippines). It is possible that latitudinal changes in seasonal patterns of water temperature influence the cycle of breeding activity, but there are insufficient data to test this proposition. Similar variability in seasonal breeding activity is likely to occur in other species studied, but information is available only from single locations: *P. marginatus* from Hawaii (Fig. 6); *P. versicolor* from Palau breed continuously and aseasonally (Fig. 6.– fluctuations arise from small sample sizes); *P. ornatus* in the Gulf of Papua are active for only a few months during the summer (Fig. 6).

Berried females are often found to have redeveloping gonads, and it is generally considered that females produce several broods each year. Of the species studied, P. ornatus has the shortest breeding season, although almost all females produce at least two broods and many produce three or perhaps more broods in a season (MacFarlane and Moore, 1986). In those locations and species where breeding is continuous, it is estimated that females produce at least four broods per year and even as many as 11 broods per year in the most active size class (95-105 mm CL) of P. penicillatus in Solomon Islands (Prescott, 1988).

The relative egg-producing potential of different size classes of lobsters is an important consideration if the reproductive capacity of the population is to be protected. Relative egg-producing potential depends on the abundance of different size classes, the proportion of breeding females in each size class and their fecundity.

Sufficient information was available to permit such an analysis for *P. penicillatus* females from Tonga, Solomon Islands and the Philippines. The relative abundance of size classes was estimated using growth and total mortality (Z) parameters because catch data do not reveal the true relative abundance of smaller lobsters – natural mortality (M) was set to 0.46 from Prescottt (1980a) and reanalysis of data from Ebert and Ford (1986). The relative number of ovigerous females by size was then calculated using published data on the annual average frequency of ovigerous females by size (Fig. 7a). Finally, the relative number of eggs produced by each size class was estimated using published fecundity-size relationships (Fig. 5). The patterns for the three areas differed considerably (Fig. 7b) as a result of differences in the underlying relationships, with fishing mortality (F) probably having the greatest impact. F is relatively high in the Philippines and there are relatively fewer larger lobsters; thus, most



Figure 6. Seasonal changes in the percentage of berried females in populations of Pacific spiny lobsters genus *Panulirus*: *P. penicillatus* from Hawaii (McGinnis, 1972), the Philippines (Juinio, 1987) and Solomon Islands (Prescott, 1988); *P. marginatus* from Hawaii (McGinnis, 1972); *P. versicolor* from Palau (MacDonald, 1982); and *P. ornatus* from the Gulf of Papua (MacFarlane and Moore, 1986).

of the contribution to egg production comes from smaller lobsters. In contrast, F is relatively low in Solomon Islands and there are relatively more large lobsters with greater fecundity; thus, most of the egg production comes from larger lobsters. The situation in Tonga is intermediate. In addition to the differences in the relative production patterns, there are also absolute differences in the egg production of the lobster populations from the three locations. From current estimates of the underlying relationships, the estimated total egg production of each cohort entering Solomon Islands fishery is about 1,770 eggs for each recruit of about 50 mm CL. In the Tongan fishery, egg production is about 910 eggs for each recruit of 20 mm CL (EPR); and in the Philippines fishery, EPR is only about 370.

The EPR is sensitive to the population-dynamics parameters of the stock. In particular, it varies in response to two parameters that fishery managers can control, i.e. size at first capture and the amount of fishing effort. The effect of these two parameters on EPR is assessed and the implications are discussed in the fishery research and management sections of this chapter.

## LARVAL ECOLOGY

Spiny lobsters have a peculiar leaf-like transparent planktonic larval form (known as a phyllosoma) that is shared only by the coral and slipper lobsters, thus is unique to the Palinuroid crustaceans. Very little is known about the ecology of the phyllosoma larvae of the south-western Pacific species, but it is likely to be similar to that of other species that have been studied (*e.g. P. cygnus* – Phillips and McWilliam, 1986; *P. argus* – Lewis, 1951).

The duration of the larval stage in the ocean is long, with periods from 4-22 months having been recorded, though 6-12 months may be more usual (reviewed in Phillips and Sastry, 1980). In the best studied species, *P. cygnus*, planktonic life may be 9-11 months (Chittleborough and Thomas, 1969); in *P. ornatus*, the delay between highly seasonal breeding in PNG and subsequent settlement in Torres Strait suggests a planktonic life of 4-10 months (CSIRO, *unpub. data*).

During the long pelagic phase, the larvae go through several distinct stages. In many species, the first stage after hatching from the egg may be a naupliosoma (Fig. 8a), which is <2 mm long and swims by beating its antennae; however, there is some controversy about whether this is a natural stage (Phillips and Sastry, 1980). After a short life (<12 hours), the naupliosoma moults to the first phyllosoma stage (Fig. 8b) which has the typical flattened, leaf-like form. Having only short, simple antennae, first-stage phyllosoma use the feathery exopodites of the "walking" legs for swimming. As the larvae grow, they may progress through 10 or more different phyllosoma stages, moulting several times within each stage. All the stages have basically the same form; though the gills and the fifth walking legs do not develop until the later stages,



Figure 7. Frequency (percent) of ovigerous females (a) and relative egg production by size (b) of *Panulirus penicillatus* from Tonga, Solomon Islands and the Philippines estimated using data on total mortality, proportion of ovigerous females and fecundity-size relationships from Zann (1984), Prescott (1988, 1990) and Juinio (1987). Natural mortality was set at M = 0.46 in each case. Samoan data from King and Bell (1991).

the tail becomes progressively more developed, and the main (second) antennae, which are shorter than the antennules in early stages, become relatively much longer (Fig. 8).

Phyllosoma larvae caught from the ocean rarely have observable food particles in the gut. Consequently, little is known of the feeding ecology of lobster larvae (Phillips and Sastry, 1980). In the laboratory, the larvae of some species have been fed succesfully on brine shrimp (Artemia) nauplii (e.g. P. longipes - Saisho and Nakahara, 1960; P. inflatus - Johnson and Knight, 1966; P. japonicus - Inoue, 1978), but the larvae of some other species showed no response to this diet (e.g. J. edwardsii - Batham, 1967; J. lalandii -Silberbauer, 1971). The early stage phyllosoma larvae of P. interruptus have been observed to eat larger soft-bodied prey items, such as chaetognaths and medusae, from a mixture of wild caught plankton (Mitchell, 1971) while the larvae of J. lalandii have been reared on hydromedusae (Williamson in Thomas, 1963). Indeed, the phyllosoma larvae of several slipper lobsters have even been observed riding on the top of particular types of medusae (e.g. Thomas, 1963) and this appears to be a significant association rather than just a coincidence (Herrnkind et al., 1976). It is possible that these larvae actually consume portions of their host as nematocysts have been found in the gut and faeces of some unidentified slipper lobster larvae (Sims and Brown, 1968).

During the long pelagic phase lobster larvae can be dispersed widely by the ocean's currents. Indeed, phyllosoma larvae are characteristic of open ocean plankton and most of the larval development occurs 100s-1,000s km out to sea from where the eggs were hatched (Phillips and McWilliam, 1986). The phyllosoma larvae of *P. penicillatus* have been found throughout the tropical eastern Pacific, some 3,500-4,000 km west of the nearest likely source (the Galapagos Islands – Johnson, 1974); this crossing of the East Pacific Barrier, together with a very wide distribution throughout the Indo-Pacific, indicates that *P. penicillatus* phyllosoma larvae may be unique in their dispersal ability or larval life.

Nevertheless, the phyllosoma larvae do not drift uncontrollably with the currents even though they are weak swimmers. They can maintain their vertical position in the water column thus exposing themselves to opposing current systems (Johnson, 1974; Rimmer and Phillips, 1979). In the case of *P. cygnus* in the eastern Indian Ocean, phyllosoma of all stages undergo diurnal vertical migration – to the surface or near-surface during the night and into the deeper layers during the day. However, the pattern of vertical migration changes as the larvae develop: the early stages maintain a somewhat shallower position in the water column (generally <60 m) than do the later stages; this causes early-stage larvae to be transported 300-1,000+ km offshore in the summer offshore wind drift. Conversely, the late-stage larvae become increasingly photonegative and tend to avoid the surface layers (generally >50 m during the day), which causes





Figure 8. Examples of the pelagic larval stages of spiny lobsters genus *Panulirus*: (a) naupliosoma and (b) first phyllosoma stage of *P. ornatus*, and (c) stage VI and (d) stage X phyllosoma of *P. penicillatus*. An = antenna; Al = antennule; Cs = cephalic shield; M = mandibles; G = gills; 5Pr = fifth pair of walking legs; and Ab = abdomen. (a) and (b) drawn by D. Dennis, (c) redrawn from Prasad and Tampi (1959) and (d) redrawn from Johnson (1971) by D. Dennis.



them to be transported nearer the coast in the easterly sub-surface flow (Rimmer and Phillips, 1979). For most species the data on larval behaviour and current systems are very limited, so possible dispersal and recruitment pathways are largely speculative (Rimmer and Phillips, 1979).

Larvae in the final phyllosoma stages usually grow to about 35 mm in total length (though some giant specimens up to 65-88 mm long have been found) before moulting into the nektonic puerulus (Phillips and Sastry, 1980), which looks like a transparent miniature lobster about 20-30 mm long. Pueruli make the transition from the pelagic larvae to the benthic juveniles. In spite of its important role, little is known of the puerulus stage.

Unlike the phyllosoma, the pueruli are capable of sustained forward and backward swimming by beating their pleopods, as well as using the familiar, tailflicking escape-response of adult lobsters. It is believed that the pueruli swim some distance from the open ocean to the shallow settlement habitats (Phillips and McWilliam, 1986).

Swimming speeds of around 9 cm.s<sup>-1</sup> have been recorded for the pueruli of *P. interruptus* (Serfling and Ford, 1975) and *P. argus* (Calinski and Lyons, 1983), whereas observed speeds for *P. cygnus* pueruli averaged about 15 cm.s<sup>-1</sup> and reached a maximum of 46 cm.s<sup>-1</sup> (Phillips and Olsen, 1975). The pueruli of *P. cygnus* probably swim 40-60 km from off the edge of the continental shelf of Western Australia to the coastal settlement habitat, taking perhaps 2-3 weeks to do so (Phillips *et al.*, 1978). The pueruli may be able to navigate towards the coast, perhaps by using special setae on the antennae to sense the vibrations caused by waves breaking on the shore (Phillips and MacMillan, 1986). The ability of the puerulus to return to the benthic habitat is crucial to settlement success and subsequent recruitment to fisheries.

## RECRUITMENT

The settlement of pueruli into the benthic habitat is the earliest stage at which recruitment into a lobster population can be estimated. Special collectors have been designed to sample the settling pueruli of several species that support major fisheries around the world. Such species include *P. argus* (Witham *et al.*, 1968), *P. cygnus* (Phillips, 1972) and *J. edwardsii* (Booth, 1979). The number of pueruli sampled by such collectors can provide an index of settlement and a forecast of future recruitment into the fishable stock; this information is of great value to both managers and fishermen.

The longest time-series (>20 years) of settlement indices is available for P. cygnus in Western Australia (Phillips, 1986). The numbers of pueruli that settled differed by more than a factor of 10 between the years of lowest and highest settlement. These fluctuations in abundance as established at settlement were apparent in the catch of the fishery four years later (Fig. 9). Indeed, the

variability in puerulus settlement accounts for about 75 per cent of the variability in subsequent catches and can be used to predict future catches (Phillips, 1986). It has recently been found that major environmental perturbations in the ocean (such as El Niño or Southern Oscillation events) can account for about 28 per cent of the variability in puerulus settlement, thus can also influence subsequent catches of the fishery (Pearce and Phillips, 1988).

The newly settled post-pueruli are very cryptic and juvenile lobsters are not usually observed in any abundance until 6-12 months after settlement, when they begin to aggregate. The post-pueruli of P. penicillatus have been observed only rarely, but, when seen, they were in the same high-energy reef-front habitat as the adults (J. Prescott pers. comm.). The post-pueruli of P. argus preferentially inhabit clumps of red algae (Laurencia) although they have been observed in a wide range of other micro-habitats (Herrnkind and Butler, 1986). The postpueruli of P. cygnus were believed to inhabit the coastal seagrass beds of Western Australia (Phillips et al. 1977). However, recently, intensive searching by divers (Jernakoff, 1990) showed that they sheltered in small holes in limestone patch-reefs that were covered with algae. The post-pueruli of P. ornatus have recently been discovered hiding in small holes on rocky seabed, 5-30 m deep, between coral reefs in Torres Strait; the post-pueruli did not appear to show any preference for holes with additional algal or seagrass cover or for the habitat to be elevated from the seabed (CSIRO, unpub. data). There was a close relationship between the size of P. ornatus post-pueruli and the size of the hole they occupied; such a relationship has also been found for P. japonicus post-pueruli (Yoshimura and Yamakawa, 1988).

Settlement of P. penicillatus pueruli probably occurs throughout the year in much of the tropical Pacific, especially within 10°N and 10°S, as a consequence of the continuous spawning in this region; this leads to the absence of obvious modes in size-frequency distributions (e.g. Solomon Islands - Prescott, 1988). Towards the edge of the tropic zone where spawning is more seasonal, settlement may also be more seasonal, potentially leading to the appearance of modes in size-frequency distributions (possible examples include: Enewetak -Ebert and Ford, 1986; Philippines - Juino, 1987; Tonga - Munro, 1988). The spawning of P. ornatus in southern Papua New Guinea is highly seasonal, occuring from November to February (Fig. 6), and settlement in Torres Strait occurs between the following May and October. This discrete settlement is carried through into distinct modes in the size-frequency distribution of the catch (CSIRO, unpub. data). Although recruitment to some tropical Pacific fisheries may be continuous, it is unlikely to be constant and up to ten-fold differences between maximum and minimum years would be expected (as in the case of P. cygnus). In spite of this, a constant level of recruitment is assumed in some methods of estimating mortality (see below).

The source of P. penicillatus recruitment to most tropical Pacific reefs is



Figure 9. The catch of *Panulirus cygnus* for 1961-1984 and the index of puerulus settlement (mean annual catch per collector) for 1969-1984, showing the relationship between settlement and the catch four years later (redrawn from Phillips, 1986).

unlikely to be local because of the long duration and extensive disperal of the larval stages. Further, relatively few of the total number of reefs likely to be inhabited by *P. penicillatus* are actually fished, so conceivably there is a large unexploited breeding stock. Because of this, local overfishing would probably have little impact on the breeding potential of the regional stock; thus, there is little risk of recruitment overfishing of lobster fisheries in most Pacific islands states (Prescott, 1988).

## GROWTH

Lobsters can increase in size only at the time of moulting and so, although growth of internal tissues is continuous, growth in size is not. It proceeds in steps as a combination of the increments at each moult and the time interval between moulting. As lobsters grow, the moult increment, expressed as a proportion of the size of the lobster, decreases and the interval between moults increases; thus, the rate of growth slows with increasing size (Fig. 10). Generally, a linear relationship exists between the logarithm of the moult increment and the carapace length, and between the logarithm of the moult interval and the carapace length (Mauchline, 1977). Together these relationships provide a complete description of the growth of lobsters, although, in practice, growth is rarely described in this way because of the difficulty of obtaining the moult increment and interval information for lobsters in the natural habitat (Morgan, 1980). The moult frequency of a range of sizes can be estimated from tagrecapture studies by plotting the proportion of recaptures that have moulted against the time interval between release and recapture, then determining the average time at which 100 per cent of recaptures have moulted. If either moult increment or interval vary through the year (perhaps because of seasonal temperature variations), this method may produce biased results (Morgan, 1980). In the tropical Pacific, temperature fluctuations are minimal and the growth of P. penicillatus in Solomon Islands has been described using this method (Fig. 10; Prescott, 1988).

In the absence of detailed moult increment and interval information, a variety of other methods are available for describing growth. Most methods estimate various parameters of the von Bertalanffy (1938) growth function, which has the formula:

$$L_t = L_{\infty} [1 - e^{-K(t-t_0)}]$$

where  $L_t = \text{length}$  at age t,  $L_{\infty} = \text{asymptotic carapace length}$ , K = growth coefficient, and  $t_0 = \text{a parameter that positions the function on the age-axis so that length and age (from hatching) of recruited size classes correspond ($ *i.e.* $the age when the function intersects the age-axis – see Fig. 10). The parameters <math>L_{\infty}$  and





Figure 10. The relationships between moult increment and moult interval for (a) male and (b) female *Panulirus penicillatus* from Solomon Islands (Prescott, *unpub. data*), combined to show the stepwise growth curves (c and d) of a hypothetical post-puerulus settling at about 270 days old and at about 9 mm CL. Von Bertalanffy equations fitted to these growth relationships (for CL > 40 mm) depart from the step-curves at CL < 30 mm and cross the age-axis at  $t_0$ .

K may be estimated from tag-recapture data by methods such as Fabens (1965) equation (e.g. Ebert and Ford, 1986) or by the Gulland and Holt (1959) plot (e.g. Prescott, 1988). Size-frequency data may also be used to estimate L\_and K by means of several methods that include Wetherall (1986) plots and the ELEFAN (Pauly et al., 1980) computer program (e.g. Munro, 1988), or modal progression (e.g. Uchida and Tagami, 1984). These methods are described in detail in a variety of stock assessment manuals (e.g. Ricker, 1975; Gulland, 1983; Pauly, 1983a; Pauly and Morgan, 1987; Sparre et al., 1989). The von Bertalanffy growth function usually describes the growth of the exploited size classes adequately (Morgan, 1980) and has the advantage that its parameters underly the majority of stock assessment techniques. However, the function may depart from the actual size-age relationship in the smallest or largest size classes (Fig. 10) and the parameter  $L_{m}$  is estimated by extrapolating well beyond the range of the data. Consequently, the value of L\_usually has large confidence limits and is very sensitive to any biases in data. Further, the value of K is strongly negatively correlated with, therefore very sensitive to, L... That is, inappropriately high L\_estimates lead to inappropriately low K estimates and vice-versa. If not corrected, these errors can escalate when the growth parameters are used to estimate other population parameters such as mortality (see Majowski et al., 1987, for a critical review).

The growth of lobsters in the Pacific is most often reported in the von Bertalanffy form, so it is possible to compare growth curves between the sexes and among different areas and species (Fig. 11, Table V). Because of the likelihood that different methods of estimating  $L_{\infty}$  provide different results, and of the large confidence limits of  $L_{\infty}$ , comparisons should be restricted to the size range of the exploited size classes (*i.e.* usually 50-110 mm CL). In addition,  $t_0$  is not always reported, and is sometimes reported inconsistently (as a negative value) because age = 0 is incorrectly set at puerulus settlement, with  $CL \approx 9$  mm, instead of at hatching. Usually,  $t_0$  would be a positive value, probably within a few months of the age at settlement (see Fig. 10). For these reasons,  $t_0$  was omitted from the growth functions (Fig. 11) and CL is plotted against relative age (from theoretical  $t_0$ ).

The most noticeable difference in patterns of growth is between male and female *P. penicillatus* throughout the Pacific (Fig. 11a, *cf.* b). Female *P. penicillatus* initially (*i.e.* <80 mm CL) may grow slightly faster than males but then slow substantially, probably as a result of the diversion of energy into egg production with the onset of sexual maturity, whereas the males continue to grow relatively quickly. Male *P. penicillatus* appear to grow fastest in Tonga and slowest in Enewetak; those in the Philippines, Western Somoa and Solomon Islands are intermediate. Female *P. penicillatus* in Tonga, Western Somoa and Solomon Islands all appear to grow at a similar rate; those in Enewetak probably

Table V. Estimates of the growth parameters of male and female *Panulirus* penicillatus for five locations in the Pacific, compared with four other species of *Panulirus*. L\_=asymptotic carapace length, K=growth coefficient. Italicised value of K for females in the Philippines is in doubt and was recalculated as K = 0.26 (see "Growth").

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Species and Location	Sex	L_	K	Method	Source
		64			
P. penicillatus					
Enewetak	m	147	0.21	Tag-recapture	Ebert and Ford (1986)
	f	97	0.58	and Fabens equation	
Solomon Is.	m	144	0.29	Tag-recapture	Prescott (1988)
	f	113	0.49	and Gulland-Holt	
Tonga	m	179	0.27	Wetherall Plot	Munro (1988)
	f	128	0.32	and ELEFAN	
W. Samoa	m	153	0.32	Wetherall Plot	King and Bell (1991)
	f	121	0.39	and ELEFAN	
Philippines	m	161	0.22	Wetherall Plot	Arellano (1988)
	f	149	0.16	and ELEFAN	
Pacific average	m	157	0.27		
	f	122	0.41		
P ownatus					
Torres Strait	m	164	0.45	Tag-recapture and	CSIRO (unpub. data)
	f	149	0.54	Fabens+Gulland-Holt	
P. longipes					
Tonga	m	133	0.31	Wetherall Plot	Munro (1988)
U	f	118	0.42	and ELEFAN	
P. marginatus					
Oahu	m	128	0.27	Modal progression	Uchida and Tagami
	f	107	0.39		(1984)
P. cygnus					
Western Australia	m+f	114	0.49	Manzer and Taylor (1947)	Chittleborough (1976)



Relative age (years)



Relative age (years)

Figure 11. Von Bertalanffy growth curves of (a) male and (b) female *Panulirus penicillatus* from (T) Tonga (Munro, 1988), (P) the Philippines (Arellano, 1989), (W) Western Samoa (King and Bell, 1991), (S) Solomon Islands (Prescott, 1988), and (E) Enewetak (Ebert and Ford, 1986); and (c) males and (d) females of five Pacific *Panulirus* species: (o) *P. ornatus* (Torres Strait – CSIRO *unpub. data*), (p) *P. penicillatus* (average of a and b respectively), (l) *P. longipes* (Tonga – Munro, 1988), (m) *P. marginatus* (Oahu – Uchida and Tagami, 1984), and (c) *P. cygnus* (Chittleborough, 1976). Note that  $t_0$  was set to zero in all cases and relative age is years from  $t_0$ .

do not grow as large as elsewhere (Fig. 11, Table V). The growth curve of female *P. penicillatus* in the Philippines (Arellano, 1989) contrasts strongly with the curves for other areas (Fig. 11), but is probably misleading: recalculation of K, with the same method as used by Arellano (comparative growth performance indices  $(\emptyset')$ -Pauly and Munro, 1984), but with comparative data only from *P. penicillatus* in the Pacific instead of from a variety of species, yields K = 0.26 and indicates faster initial growth as is typical of other areas.

The growth rates of different species of *Panulirus* also differ substantially (Fig. 11c, d). Male *P. ornatus* grow faster than males of the other species and *P. penicillatus* males grow faster than *P. longipes* and *P. marginatus*; male (and female) *P. cygnus* initially grow relatively quickly but then slow substantially, following a similar pattern as female *P. penicillatus* (Fig. 11c). Female *P. ornatus* also grow faster than females of the other species and *P. marginatus* females grow the slowest; female *P. penicillatus*, *P. longipes* and *P. cygnus* all grow at a very similar, intermediate, rate (Fig. 11d).

Growth rates are likely to be influenced by factors such as food, temperature and density (Morgan, 1980). Although no information is available on the effects of these factors on the growth of lobsters in the Pacific, research on *P. cygnus* has shown that food supply (Chittleborough, 1975) and food quality (molluscs better than algae – Joll and Phillips, 1984) are important; temperatures above or below 26°C, excessive loss of limbs (>4) and low oxygen saturation reduced growth (Chittleborough, 1975); and density appeared to have no effect (Ford *et al.*, 1988), although juveniles held in isolation moult less frequently thus grow more slowly (Chittleborough, 1975). The growth of *P. penicillatus* does not vary consistently with latitude, and *P. cygnus*, a temperate species, does not grow more slowly than the tropical species (Fig. 11c, d).

## MORTALITY

The total mortality rate (Z) of an exploited population of lobsters is a combination of deaths due to natural causes (natural mortality = M), such as predation and disease, and deaths due to fishing activities (fishing mortality = F) so that Z = M + F. Mortality rates (Z, M and F) are usually expressed in "instantaneous" form *i.e.* the constant of the exponent of the exponential decline in the abundance of a cohort from year to year (see Gulland, 1983). Proportional survival (S) from one year to the next can be calculated from the instantaneous mortality rate (*i.e.*  $S = e^{-2}$ ). Because it is not possible to determine the age of lobsters, the methods normally used to estimate their total mortality rates are based on estimates of the von Bertalanffy growth parameters and samples of the size-frequency distribution of the population; both of which are estimated with error and may bias the estimates of mortality. The methods commonly used to estimate the mortality rates of lobsters in the Pacific include

"length-converted catch curves" (Pauly, 1983b) and the Beverton and Holt (1956) model. These methods (and others) are described in detail in a variety of stock assessment manuals (as cited in the growth section). Length-converted catch curve (LCCC) analysis involves plotting the decline in cohort abundance after the abundance-at-length data is converted to abundance-at-age data where the growth equation is used to estimate age from length. The Beverton and Holt model is based on the influence that growth and mortality rates have on the shape of the size distribution of the population – so if the growth parameters are known and size-frequency data are available, mortality can be estimated according to the equation:

$$Z=K(L_{-}i)/(\bar{l}-l)$$

where l = a length, or greater, at which lobsters are fully recruited to the fishery and  $\overline{l}$  average length of lobsters greater than l. Both methods are susceptible to bias because of errors in the estimation of growth parameters and because of variation in the size of individuals at any given age. Further, both assume that recruitment does not differ from year to year and that mortality and catchability do not change with age (size). LCCC analysis also has difficulty dealing with animals close to, or greater than,  $L_{a}$ .

The effects of fishing on a lobster population can only be understood fully if the proportion of the total mortality that is due to fishing (F) can be separated from that due to natural causes (M). F and M can be separated by plotting estimates of Z against a wide range of fishing efforts (f) and determining the Zintercept where f = 0, thus F = 0 and M = Z (see Gulland, 1983, pp. 107-109), that is assuming no density-dependent changes in M at different values of F. However, this method requires extensive catch records (Morgan, 1980), and it has not been attempted in any Pacific fishery. Tagging studies may also enable separation of F from M, although there are a multitude of biases that are likely to confound estimates obtained in this way (Ricker, 1975). In the Pacific, the natural mortality of P. penicillatus has been estimated only where fishing effort is absent (e.g. Enewetak - Ebert and Ford, 1986; Solomon Islands - Prescott, 1988) by estimating Z using length-based methods and setting F=0. The natural mortality estimates reported by Ebert and Ford (1986) have been used to estimate fishing mortality from total mortality (F = Z - M) as part of stock-assessments in areas where there are fishing activities (e.g. Tonga – Munro, 1988; Western Samoa – King and Bell, 1991); this assumes that M at Enewetak is representative of other areas and that there are no density-dependent changes in M at different levels of F. However, Ebert and Ford incorrectly applied the Beverton and Holt model: instead of choosing I = length at which lobsters are fully recruited to the fishery, which would have been 65-75 mm CL for males and 80 to 90 mm CL

for females, they set  $l = l_r = length$  at which lobsters *first* recruit to the fishery (*i.e.* at about 45 mm CL). Consequently, their estimates of annual M are too low (males, M = 0.284; females, M = 0.244) and the subsequent stock assessments are also miscalculated. Reanalysis of the Enewetak data with use of more appropriate values of l, yielded higher estimates of M (males,  $M \approx 0.36$ ; females,  $M \approx 0.48$ ). It would be worthwhile to check the sensitivity of Z to l by calculating the model with several values of l in the range thought to be appropriate.

Total mortality rates have been published (or have been estimated from published data) for a number of areas and species in the Pacific (Table VI). Assuming that the estimates of M for P. penicillatus at Enewetak and Solomon Islands are representative of other areas and that there are no densitydependent changes in M with different amounts of fishing (*i.e.* different F), then some estimate of the relative fishing pressures impacting lobster stocks in different areas is possible (Table VI). The greatest fishing mortality on P. penicillatus probably occurs in the Philippines, and the size-frequency distributions of the catch reflect this; most lobsters in the catch are small relative to other Pacific fisheries. The modal size of female P. penicillatus in the Philippines is only about 50 mm CL and only 10 per cent of the catch is larger than 80 mm CL (Arellano, 1989); in almost all other fisheries, the mean size is greater than 80 mm CL (sources in Table V). The modal size of male P. penicillatus in the Philippines is only approximately 60 mm CL and only 10 per cent are >90 mm CL (Arellano, 1989); in most other fisheries, the mean size is >90 mm CL (sources in Table V). Fishing mortality is intermediate in Tongatapu and Western Samoa and is a little lower in the more remote Tongan islands of Ha'apai (Table VI). In Solomon Islands, lobsters are exploited at a relatively low level (F  $\approx$  0.3), although there was no fishing where Prescott (1988) conducted his tag-recapture study.

In some *P. penicillatus* fisheries, the fishing mortality on females appears greater than on males (*e.g.* Samoa and the Philippines), whereas in other fisheries (*e.g.* Tonga), the converse is true (Table VI). The combination of the behaviour of lobsters and the fishing method used may cause this discrepancy. It has been observed that female *P. penicillatus* tend to forage on the reef flats more than do males (Ebert and Ford, 1986); consequently, fishing methods that are restricted to shallow water (*e.g.* reef walking, traps) may be more likely to exploit female lobsters. Indeed, a substantial proportion of the catch in the Philippines is biased towards females (1.22: 1-Arellano, 1988), although it is approximately 1: 1 in Samoa (King and Bell, 1991). Conversely, fishing methods that give access to deeper habitats on the reef slope (*e.g.* diving) may be more likely to exploit male lobsters: in Tonga, diving is the preferred method of fishing (Prescott, *pers. comm.*) and the sex ratio of the catch is biased strongly towards males (0.63: 1-Munro, 1988). However, this pattern does not occur

Table VI. Estimates of the instantaneous mortality coefficients of male and female *Panulirus penicillatus* for five locations in the Pacific, compared with four other species of *Panulirus*. M = natural mortality, F = fishing mortality, Z = total mortality and LCCC = length-converted catch curve. Italicised values of F were estimated from Z minus average M from Enewetak and Solomon Islands.

Species & Location	Sex	М	F	Z	Method	Source
P. penicillatus						
Enewetak	m f	0.36 0.48	0 0		Beverton and Holt	reanalysis of Ebert and Ford (1986)
Solomon Is.	m f	0.39 0.43	0 0		LCCC	Prescott (unpub.)
Tongatapu	m f		1.29 0.88	1.66 1.33	LCCC	Munro (1988)
	m f		0.66 0.49	1.03 0.94	Beverton and Holt	analysis of Prescott (1990)
Ha'apai	m f		0.38 0.43	0.75 0.88	LCCC	Munro (1988)
	m		0.32	0.69	Beverton and Holt	from Prescott (1990)
West. Samoa	m f		0.40 0.65	0.77 1.10	LCCC	King and Bell (1991)
Philippines	m f		0.80 0.95	1.17 1.40	Beverton and Holt	reanalysis of Arellano (1988)
P. ornatus	_					
Torres Strait	m+f		0.09- 0.16	0.43- 0.91	catch and surveys	CSIRO (unpub. data)
P. longipes Tongatapu	m f			1.19 1.41	LCCC	Munro (1988)
Ha'apai	m f			0.61 ≈ 0.89?	LCCC	Munro (1988)
P. marginatus						
Oahu	m f			0.91 1.69	Beverton and Holt	analysis of Uchida and Tagami
(1984) P. cygnus						
West. Australia	m+f	0.23	0.64- 0.78	0. <b>87-</b> 1.01	Beverton and Holt	Morgan (1977)

in all fisheries, probably because the behaviour of the lobsters varies (Prescott, *pers. comm.*) depending on geology (continental, volcanic, carbonate atoll, limestone etc.) and the influence of the tidal cycle on reef structure (width of reef crest and flat, reef height relative to mean sea level etc. – George, 1972).

The total mortality of other lobster species in the Pacific is similar to the range of Z for P. penicillatus (Table VI) and, where F has been estimated, it ranges from relatively low (0.09-0.16) in the lightly exploited P. ornatus stock in Torres Strait to high (0.64-0.78) in the fully exploited P. cygnus stock in Western Australia. The total mortality of P. longipes and P. marginatus is relatively high and, if the natural mortality of these species is similar to that for P. penicillatus, it can be inferred that the level of exploitation of these species is also high.

#### ABUNDANCE

The absolute abundance of lobster populations has rarely been measured, although relative abundances have been estimated from catch data in most of the larger lobster fisheries (Morgan, 1980). In the Pacific, the absolute abundance of *P. penicillatus* has been estimated in only a few limited areas of reef slope. In two small areas of reef in Solomon Islands, the abundance of *P. penicillatus* was estimated by tag-recapture methods. There were about 550 lobsters at Site 1 and about 160 lobsters at Site 2, which was roughly equivalent to 111 and 128 lobsters per kilometre of reef slope or 46 and 57 per hectare (Prescott, 1988). In three small areas of reef in Enewetak, the abundance of *P. penicillatus* was estimated by depletion-fishing methods. There were 328, 173 and 141 lobsters at Sites 1, 2 and 3, which was roughly equivalent to 164, 87 and 35 lobsters km<sup>-1</sup> of reef slope or 71, 38 and 15 ha<sup>-1</sup>. These estimates were extrapolated to estimate the total population for the exposed side of Enewetak Atoll, which is about 50 km long (or about 1.2 km<sup>2</sup>), as being 7,800 lobsters (Ebert and Ford, 1986).

The absolute abundance of *P. ornatus* in a 25,000 km<sup>2</sup> area of Torres Strait was estimated, in 1989, at 14 million  $\pm 20$  per cent by making visual counts of lobsters in almost 600 strip-transects (Pitcher *et al.*, 1992); the density of this population was about 6.5 ha<sup>-1</sup> overall and almost 60 ha<sup>-1</sup> in the best habitat (approximately 1000 km<sup>2</sup>). Similar methods were used to estimate the absolute abundance of *P. argus* in the 62,000 km<sup>2</sup> area of the Little and Great Bahama Banks at 31 million  $\pm 110$  per cent (Smith and van Nierop, 1986). This is equivalent to about 5 ha<sup>-1</sup> overall and almost 10 ha<sup>-1</sup> in the best habitat (approximately 9,000 km<sup>2</sup>). The range of densities estimated for *P. penicillatus* are generally higher than for other species; however, other commercially important species are distributed widely across shallow habitat whereas the area of habitat available for *P. penicillatus* is limited to a 20-25 m wide strip of windward reef slope. For this reason, stocks of *P. penicillatus* are relatively small and can only be expected to sustain small fisheries.

#### MOVEMENT

As spiny lobsters grow and mature they typically move from nursery grounds in shallow water to breeding grounds in deeper water, although the extent of the movement may vary from a few km to substantial migrations of >500 km, depending on the species and location (reviewed by Herrnkind, 1980). The typical case is perhaps exemplified by P. cygnus, which spends about four years in coastal nursery reefs and seagrass beds before moving 30-50 km offshore into deeper water (30-150 m); most move during spring though some may move at other times (Phillips, 1983). In the Pacific, both extremes of movement patterns have been reported: tagging studies have shown that P. penicillatus moves only short distances, the maximum being about 2 km when tagged lobsters were unintentionally released outside their normal habitat (Prescott, 1988); at the other extreme, P. ornatus undergoes one of the longest migrations known for spiny lobsters, leaving Torres Strait in August-September and arriving on coastal reefs at the eastern Gulf of Papua, >500 km away, in December-January (Moore and MacFarlane, 1984; Bell et al., 1987). The lobsters mature and hatch at least one brood on the migration, and most females may hatch two more broods at the destination (MacFarlane and Moore, 1986). The physiological condition of the lobsters deteriorates as the migration and breeding season progresses (Trendall & Prescott, 1989), and almost all the lobsters that arrive on the eastern Gulf of Papua coastal reefs die during the 3-4 month breeding season (Dennis et al., 1992).

However, possibly less than half of the lobsters emigrating from Torres Strait move across the Gulf of Papua and <10 per cent of these arrive on the Papuan coastal reefs. A possible destination of a significant proportion of the lobsters has recently been discovered by surveying the deep waters of the Gulf of Papua and the far northern Great Barrier Reef with a manned submersible (Prescott and Pitcher, 1991).

Although very few lobsters were seen in the Gulf of Papua, high densities were seen at several sites 30-100 m deep on the edge of the continental shelf outside the Great Barrier Reef (Prescott, Pitcher, Skewes and Dennis, *unpub.*), and this area may support a significant breeding population for the Torres Strait fishery. The full extent of these breeding grounds and the mortality rate of the lobsters after breeding have yet to be determined.

## **III. PACIFIC FISHERIES**

#### **FISHING METHODS**

Traditionally, traps of various kinds were used widely in the Pacific to catch lobsters; nowadays, however, they are used in only a few fisheries (George,

1972). These traps caught P. penicillatus and P. longipes, but P. versicolor and P. ornatus almost never entered traps (Prescott, 1988). The traditional traps were made of natural materials in a variety of shapes and sizes (George, 1972): Western Samoan fishermen used 50 cm banana-shaped wicker baskets wedged into cracks in the volcanic lava and retrieved the next day; American Samoan fishermen used round wicker baskets with a single inverted neck opening at the top; Tongan fishermen used similar beehive-shaped pots (funaki) made from vines, baited with sea-urchins and wedged in the shallow end of surge channels; Ni-Vanuatu fishermen also used cane or wicker beehive pots (0.6-0.9 m diameter) baited with chitons or sea-urchins and set in pools or crevices in the reef edge. Traps are still used in the Philippines between March and May each year, prior to intense spear-fishing during the calm season (Juinio and Gomez, 1986). Philippino fishermen set 6-8 cylindrical bamboo traps that have openings at each end lined with bamboo slats; the traps are set in surge channels and undercuts in the surf zone, secured with wooden stakes during low tide, baited with crushed sea-urchins, and checked the following day.

The reported catch rates for traditional traps vary greatly: in the Philippines, catches may be up to 2 lobsters per trap but average only about 1 lobster per 5 traps (Juinio and Gomez, 1986); in Tonga, *funaki* caught up to 6 lobsters per trap night (George, 1972); in Vanuatu, four men operating about 20 traps during neap tide periods caught up to several hundred lobsters per month (George, 1972).

Other traditional methods of fishing for *P. penicillatus* included fishermen walking over the reef flats at night with coconut flare-torches, catching lobsters either by hand or by using spears, though pressure lanterns or battery torches have replaced the coconut flares in many locations. Two unusual traditional methods were used in parts of Solomon Islands. In the first, vine hoops (approximately 0.9 m diameter) baited with chitons were set over the reef edge. Lobsters attracted to the bait would cling tightly while feeding and could be gently lifted into a canoe 2-3 days later (George, 1972). In the second method, a chiton bait was tied to a line on a bamboo pole and lowered into surge channels at night, when a lobster grabbed the bait, the fisherman hoisted it up onto the exposed reef (Prescott, *pers. comm.*).

Current methods of fishing for *P. penicillatus* include reef walking at night (as described previously) and, most commonly, spearing or catching them by hand while free-diving on the reef-slope and crest. Light is provided by an underwater torch, or a lantern on a boat or held by a companion on the reef. Divers may occasionally take *P. longipes* or *P. versicolor* and, in a few areas, some diving is carried out during the day. The lunar and tidal cycles have important influence on fishing activities, as well as on the habitat available to *P. penicillatus* (see habitat section). Reef walking is restricted to stages of the tide when the water is shallow enough for the fishermen but deep enough for the lobsters to move up onto the reef flat (Prescott, 1988), usually during neap tides

(King and Bell, 1991). Rough sea conditions are unsuitable because visibility through the water surface is reduced. In addition to the overriding influence of the weather conditions, catches are affected by the behaviour of the lobsters, which are less active and more wary on moonlit nights; nevertheless, the best catch rates occur not during the new moon phase but in the week or so after the full moon, during the dark period between sunset and moonrise (Prescott, 1988).

The reported catch rates for reef walking and diving vary greatly. The average nightly catch of live lobsters for fishermen reef walking in Solomon Islands was 5 lobsters (Prescott, 1988); in Tahiti, two-man teams caught about 20 lobsters per night (George, 1972); in Enewetak, a 4-person research team caught from 1 to 57 (mean = 23) lobsters per night (Ebert and Ford, 1986). The average nightly catch for spear-fishermen diving in the Philippines was generally 4-6 lobsters (Juinio and Gomez, 1986); in Tonga, the catch was usually 5-12 lobsters, but was occasionally more than 60 (Prescott, 1990); in Samoa, teams of 2-4 men speared 5-10 (max  $\approx$  30) lobsters per team in about a 2-hour period per night (George, 1972).

The fishermen in the vicinity of Yule Island in the eastern Gulf of Papua use a variety of methods to catch P. ornatus. During the day, the fishermen dive on the shallow fringing reef and hand-catch the lobsters from under coral bommies or surround bommies with short tangle nets and disturb the lobsters from their dens into the nets. At night, fishermen may set tangle nets on the reef or, working from a canoe with light from a pressure lantern, they may catch foraging lobsters with a hoop net on the end of a long pole. Spears are not used to catch lobsters due to a traditional taboo. Daily catch rates average about 5 lobsters per fishing team, but may exceed 50 (Dennis *et al.*, 1992). In contrast, the divers fishing for P. ornatus in Torres Strait use short spears and many also have hookah breathing equipment. The average daily catch for a team of a diver and a dinghy driver is about 16 kg of tails (approximately 40 lobsters), though catches >70 kg of tails (>150 lobsters) are not uncommon.

#### **DESCRIPTION OF FISHERIES**

The nature of the lobster fisheries in the Pacific varies greatly in terms of species composition and abundance, fishing methods, level of capitalisation, commercial and market (domestic and export) development, and regulation by management. A summary of the available information on many of the southern and western Pacific lobster fisheries follows.

American Samoa comprises two small volcanic high islands that have very narrow fringing reefs of coralline algae with few live corals. The reefs are dissected by surge channels (George, 1972). The only species of *Panulirus* reported is *P. penicillatus*, which, in 1970, was fished by teams of about four

people diving and spearing at night on the shallow reef flat. Catches were usually approximately 10 lobsters per night, but sometimes reached 30 (George, 1972). Wicker traps were traditionally used and, in 1965, experimental traps made of  $76 \times 102$  mm welded wire mesh were trialled off the reef edge. Catches of about 15 lobsters per trap were obtained. In the early 1970s, the total catch was apparently consumed by locals; the hotels and restaurants imported lobster tails because the supply and quality of the local product could not be guaranteed (George, 1972). Annual production is currently  $\leq 1$  t (Table I).

**Cook Islands** comprises six small volcanic high islands to the south and 11 atolls to the north. The high islands have fringing reefs and one is surrounded by an atoll lagoon. The tidal range is small (<0.5 m; George, 1972). *P. penicillatus* is the most common species of *Panulirus* and *P. longipes* has been reported. On the remote atolls, fishermen catch lobsters by hand while reef walking at night. Around Rarotonga, the main island, fishing activity is greater and fishermen also use spears while diving during the day or night; catch rates may be up to approximately 15 lobsters per person per night (George, 1972).

Fiji comprises two main high islands and several groups of smaller islands; most of the islands are volcanic, though there are many coral atolls and low islands, particularly in the Lau Group (George, 1972). The main islands receive high rainfall, thus providing a terrestrial (coastal) influence, and are surrounded by lagoons and barrier reefs. The low islands are relatively dry and have extensive coral-reef platforms. Four species of Panulirus have been reported in Fiji (George, 1972; M. Lagibalavu, pers. comm.): P. penicillatus is the most abundant overall, particularly on the reefs of the eastern groups of islands; P. versicolor is quite common and is present in the lagoons and sheltered waters of most islands; P. ornatus is occasionally caught from the reefs of the main and western islands (Prescott, pers. comm.); P. longipes femoristriga is very rare and only a few specimens have been reported. Traditionally lobsters were caught by fishermen reef walking at night. In the early sixties, New Zealand lobster pots were trialled without success. Later and into the 1970s, the Fiji government assisted the fishermen of the eastern islands by providing the Fisheries Division's vessel for fishing trips to the more remote eastern reefs. Currently, fishermen spear or hand-catch lobsters at night, and there are no large-scale operators; participation in fisheries is intended for Fijian nationals and traditional sea-rights are recognised (M. Lagibalavu, pers. comm.). Sport divers catch some lobsters around the main tourist centres. A minimum size has been set at 70 mm CL. Recorded production is now 100 t (Table I), but this only includes the catch sold through markets monitored by the Fisheries Division; a substantial proportion of the catch is consumed at home or bartered in the villages (M. Lagibalavu, pers. comm.).

French Polynesia includes the main volcanic islands of the Tahiti group, the smaller volcanic islands of the Marquesas and Gambier groups, the chain of

atolls of the Tuamotu group, and the raised limestone islands of the Tubuai group. Some of the larger high islands have narrow lagoons that are influenced by run-off and are separated from the ocean by narrow barrier reefs; the low atoll islands are drier. The tidal range is small (<0.5 m) and the coralline algal habitat of the reef front is very narrow (George, 1972). P. penicillatus is the most common Panulirus species, though P. longipes and P. homarus are also found. Lobsters are hand-caught while fishermen reef walk at night and are kept alive to be transported to markets at population centres. Highest catch rates are about 20 kg per night (George, 1972). Despite the limiting habitat for P. penicillatus the resource is underexploited because there are many unexploited remote reefs (George, 1972). Annual reported catches are about 2 t (Table I). Guam is a volcanic high island, the southernmost in the Mariana chain and has a fringing reef and relatively high rainfall. P. penicillatus is the most common species of Panulirus and is caught by islanders spearfishing at night; P. longipes and P. ornatus are also caught occasionally (R. F. Meyers, pers. comm.), the latter in more sheltered areas where the influence of run-off is greater. Most fishermen are non-commercial and spear lobsters incidentally; the total annual catch is only 1-2 t (Table I). Lobsters are valued for home consumption and fishing activity increases prior to important festivities (R. Hensley, pers. comm.). Regulations protect small lobsters (<0.45 kg) and berried females during May, June and July; the government is proposing to prohibit spearing of lobsters (R. F. Meyers, pers. comm.).

Kiribati comprises a group of more than a dozen coral atolls with low islands; rainfall is low and the reef flats are well developed and broad. Three species of Panulirus have been reported: P. penicillatus is the most abundant, P. versicolor is relatively common and P. ornatus has been caught in tangle nets in Tarawa lagoon (Prescott, 1977; M. Kamatie, pers. comm.). P. penicillatus is caught by hand at night while fishermen walk on the reef flat or dive on the reef edge; P. versicolor is caught while fishermen dive in the lagoons (M. Kamatie, pers. comm.). Organised commercial fishing has been attempted at least twice: in 1981, a processing plant was set up in Tarawa and lobsters were transported from remote atolls by seaplane; in 1985, a company began operating a multipurpose fishing vessel that travelled among the atolls buying and fishing for lobsters and other seafood products. However, both shut down after about a year due to unreliable supplies of lobsters from fishermen. Currently, fishermen in Tarawa sell lobsters to local restaurants, hotels and fish retailers, and, when supply is short, lobsters may be airfreighted live from the remote atolls; the Fisheries Division arranges internal marketing. The main hotel currently buys about 2 t of lobsters per year, but most of the catch is probably consumed at home by the local population. Regulations protect small lobsters (<85 mm CL) and berried females throughout the year (M. Kamatie, pers. comm.). Micronesia comprises the Federated States of Micronesia: Pohnpei, Chuuk,

Yap and Kosrae. They include many volcanic and raised limestone islands and atoll low islands; often all three island types are present inside a well-developed atoll reef. The larger volcanic islands have high rainfall and run-off; the low islands are generally dry (George, 1972). Four species of *Panulirus* have been reported: *P. penicillatus* is the most common; *P. versicolor* is less common; *P. l. femoristriga* is uncommon; a larger species found in deeper waters of the lagoons or reef slopes may be *P. ornatus* (George, 1972). Traditionally, island people walked on the reefs at night to spear or hand-catch *P. penicillatus* for cultural festivities; nowadays, fishermen also dive, catching and spearing lobsters for sale (George, 1972). Lobsters are marketed at the major centres and a few t of live and frozen product may be exported annually to Guam (R. Hensley, *pers. comm.*); annual production now may exceed 10 t (Table I).

New Caledonia's main island is large  $(400 \times 40 \text{ km})$  and mountainous, with relatively high rainfall and significant run-off into the coastal zone. The main island and many smaller islands are enclosed by an offshore barrier reef that is relatively narrow on the exposed southern and eastern sides and more developed on the sheltered northern and western sides. Five species of *Panulirus* have been reported: *P. penicillatus* is the most common, particularly on the exposed reefs; progressively less common are *P. l. femoristriga*, *P. ornatus*, *P. versicolor* and, living in the most sheltered conditions, *P. homarus* (George, 1972), which has now been given endemic species status as *P. branarus* (P. du Couëdic de Kergoaler, *pers. comm.*). Lobsters are fished by divers using spears and much of the catch is consumed at home, although tourist hotels provide a steady market. The recorded commercial catch, which does not include the important recreational or subsistence component, has ranged between 25-50 t in recent years. Regulations prohibit the capture, transport and sale of lobsters <90 mm CL (P. du Couëdic de Kergoaler, *pers. comm.*).

Northern Marianas includes a chain of more than a dozen volcanic high islands with surrounding reefs, which extend northwards above Guam. Three species of *Panulirus* have been reported: *P. penicillatus* is the most common; *P. versicolor* and *P. longipes* are also found in significant numbers (C. M. Falig, *pers. comm.*). Local fishermen spear lobsters incidental to other seafood and most of the catch is consumed at home. It is only if the catch greatly exceeds subsistence requirements that lobsters are sold through markets or to hotels. Trials were made with US lobster traps in 1977, but the results were not encouraging. The current commercial catch is 2-5 t (Table I) and the total catch would be more than double that. Present regulations prohibit the capture of lobsters <76 mm CL and of egg-bearing females (C. M. Falig, *pers. comm.*).

**Palau** includes several volcanic and raised limestone islands in a lagoon with a barrier reef; there are also several small coral atolls in the about 70 km long archipelago. The main volcanic high island has high rainfall and run-off (George, 1972). Three species of *Panulirus* have been reported: *P. penicillatus* 

is the most common; *P. versicolor* is about half as abundant; *P. l. femoristriga* is uncommon. Commercial fishing for *P. penicillatus* and *P. versicolor* began in 1966 and fishermen spear lobsters incidentally while diving for finfish during the day and night (MacDonald, 1982). Lobsters are marketed through the Palau Fishermen's Cooperative at the major centre (Koror) and some product is exported to Guam (MacDonald, 1982); annual recorded production is about 5 t (Table I).

Solomon Islands comprises a chain of large continental high islands and numerous smaller islands of volcanic origin, and some raised limestone and coral atoll islands. The high islands generally have high rainfall and run-off and coral reefs fringe most of the coastlines. Reefs exposed to the south-east trade winds are narrow, dominated by coralline algae and deeply dissected by surge channels; in progressively more sheltered areas, the reefs become broader and live corals become more prolific; the tidal regime also has an important influence on reef structure (George, 1972). Four species of Panulirus have been reported: *P. penicillatus* is the most common, particularly in exposed habitats, P. versicolor is caught occasionally in moderately exposed habitats, and P. l. femoristriga and P. ornatus are rare. Traditionally P. penicillatus were caught on vine hoops baited with chitons; through the 1970s they were handcaught by fishermen reef walking at night and were stored alive in cages (George, 1972); nowadays, some fishermen also dive in shallow areas and may use spears (S. Diake, pers. comm.). In the early 1970s a fishing company operated a freezer vessel around the islands to process lobsters stored alive by fishermen; the company initially exported several t per year. Currently, there is no organised commercial fishing, although some fishermen near larger population centres may sell their catch direct to hotels and restaurants. The annual recorded catch is about 1 t, but probably most of the catch is consumed at home (S. Diake, pers. comm.). Berried females used to be protected by legislation, but this was revoked in 1978; however, there remains a minimum size of 250 mm total length (tip of supraorbital spines to tip of telson – S. Diake, pers. comm.). Tonga comprises an archipelago of many small islands, some of which are volcanic, but most are coralline or raised limestone. There are many small reefs protected by a ribbon of barrier reefs to the east. The south-east trade winds prevail from March to October and the exposed eastern reefs are narrow with little coral growth. Only a few sheltered areas of the larger islands (Tongatapu and Vava'u) are subject to terrestrial influence. Three species of Panulirus have been reported: P. penicillatus accounts for about 67 per cent of the catch, P. longipes approximately 28 per cent and P. versicolor <5 per cent (Prescott, 1990). Traditionally, fishermen caught P. penicillatus with traps, or by spearing or hand-catching while reef walking at night. Around 1970 a company operated a freezer vessel around the islands to process the catch of the islanders, who caught lobsters while reef walking by day and night and while diving during the day (George, 1972). Since then numerous small companies have tried to organise commercial marketing structures, and one company operated a fishing vessel. But by 1990 only two small companies were buying lobsters, one in Ha'apai and one in Vava'u; in Tongatapu fishermen sold their catch direct to the public, restaurants, hotels and small retailers (Prescott, 1990). Nowadays, lobsters are caught incidentally by fishermen diving and spearing for finfish; daily catches are usually between 5-13 kg per team; the total annual recorded catch ranges between 3-7 t, but does not include the subsistence component, which may be substantial (Prescott, 1990).

**Tuvalu** comprises about nine coral-reef atolls with low islands; rainfall is low. Apparently *P. penicillatus* is the only species of *Panulirus* present on the exposed reef and *P. versicolor* may be found in the lagoon (T. Gentle, *pers. comm.*). Lobsters are caught by divers at night. Most lobsters are eaten during community festivities, and very few are sold at local markets. One attempt to export live lobsters to Fiji has been made, but it was unsuccessful because of problems with airfreight (T. Gentle, *pers. comm.*). Total annual catches may be only a few hundred animals.

Western Samoa comprises two main volcanic high islands with high rainfall and two small volcanic islands. Coral reefs have formed off older lava flows, beyond the influence of freshwater that seeps through the porous lava into the intertidal zone (George, 1972). Two species of *Panulirus* are found: *P. penicillatus* is most common and *P. versicolor* is found occasionally (King and Bell, 1991). Traditionally, *P. penicillatus* were caught in traps; around 1970, fishermen speared or hand-caught lobsters while diving on the reef edge at night, and some live lobsters were transported to the major markets (George, 1972). Nowadays, islanders catch lobsters primarily with spears while reef-walking at night and some of the catch is sold through markets or to hotels (King and Bell, 1991). The recorded total annual commercial catch is about 26 t; the catch consumed at home or sold through village markets may amount to an additional 40 t (King and Bell, 1991).

**Philippines** comprises an archipelago of large, mountainous, continental islands with generally high monsoonal rainfall. A broad range of marine habitats are represented; habitats range from coral reefs exposed to the ocean through to sheltered areas with strong terrestrial influence. Six species and subspecies of *Panulirus* have been reported: *P. penicillatus* is the most common, particularly along the exposed eastern coasts of the islands, and makes up >90 percent of the total Philippines catch; the two subspecies of *P. longipes* are second most common, followed by *P. versicolor*, *P. ornatus* and *P. homarus* (Juinio and Gomez, 1986; Arellano, 1988). Fishermen use various methods to fish for lobsters: traps; spearing and hand-catching while reef-walking or diving (sometimes with a hookah), generally at night; incidental catches are made in fish traps and fish corrals, on hooks and lines, and in gill nets (Juinio and Gomez, 1986;

Arellano, 1988). Some finfish are usually retained for subsistence, whereas the more valuable lobsters are sold through a series of fish brokers until they are eventually purchased by hotels, restaurants or exporters; total annual recorded catches may exceed 1000 t (mostly tails, probably), of which about 10 per cent may be exported (Juinio and Gomez, 1986; Arellano, 1988).

Torres Strait is a shallow area (generally <30 m deep), between Papua New Guinea and Australia's Cape York, that includes many coral reefs, several small continental islands and some coral low islands. The eastern side of Torres Strait is influenced by the clear waters of the Coral Sea, whereas the central and western areas are influenced by river outflow and strong currents that mobilise the sediments. Six species of *Panulirus* are present: the predominant species is P. ornatus, which makes up virtually 100 per cent of the catch, although P. versicolor is not uncommon; P. longipes, P. penicillatus P. homarus and P. polyphagus are rare. P. ornatus does not enter traps and is caught exclusively by fishermen using spears while diving during the day from small outboardpowered dinghies. Most of the P. ornatus population lives under small rocks and in small holes and crevices on the open seabed between the reefs, 5-25 m deep, where they are easily visible and divers using hookah compressors are able to access them. Lobsters living on the reefs are usually relatively conspicuous at the entrance to their dens and are fished by free-divers. The average daily catch for a team of a diver and dinghy driver is about 16 kg of tails (40 lobsters), though catches >70 kg tails (>150 lobsters) are not uncommon (CSIRO, unpub. data). Only one year-class of P. ornatus is fished; each year-class enters the fishery when 18-24 months old and emigrates from Torres Strait between 32-34 months old in order to breed in deeper water. The P. ornatus resource is shared between Australia and PNG and, in total, several hundred Torres Strait Islander and Papuan fishermen are active in the fishery, returning their catch to island-based processors or semi-permanently moored processor vessels: there are also 15-20 smaller freezer vessels that work the more remote grounds and each supports 2-6 dinghies.

The processing companies and many of the operators of smaller freezer vessels export most of their product, primarily to the USA with the remainder being marketed in mainland Australia. The total annual catch from Torres Strait is 150-350 t of tails landed in Australia and about 30-75 t of tails landed in PNG. In Australia, the minimum size is 100 mm tail length, which is approximately 75 mm CL. The annual breeding emigration of *P. ornatus* from Torres Strait across the Gulf of Papua used to be targeted by trawlers, which caught up to 200 t in a season, but this activity was banned in 1984. Currently, the only exploitation of the breeding population occurs around Yule Island, in the eastern Gulf of Papua, where there is a small artisanal fishery which lasts only 2-4 months each summer (see "Fishing Methods" section above). The total catch during the short fishing season at Yule Island is highly variable: often it is <5

t of tails but has exceeded 30 t (PNG-DFMR, *unpub. data*). Elsewhere in PNG, there are low levels of subsistence fishing for *P. penicillatus* (Prescott, 1988).

#### **IV. FISHERY RESEARCH**

#### PAST RESEARCH

There have been relatively few studies of the aspects of population dynamics important for management of spiny lobster stocks in the tropical southern and western Pacific; those few studies include four on *P. penicillatus* in the Pacific islands (*i.e.* Solomon Islands – Prescott, 1980a; Tonga – Zann, 1984 analysed by Munro, 1988 and Prescott, 1990; Enewetak – Ebert and Ford, 1986; Western Samoa – King and Bell, 1990) and one in the Philippines (Arellano, 1988), and one on *P. versicolor* at Palau (MacDonald, 1982). In addition, ongoing studies on *P. ornatus* in Torres Strait have been undertaken by PNG-DFMR and CSIRO. Much of the content of these studies has been reviewed in the preceding sections on biology. The biological aspects of particular importance to fishery research include the parameters of growth and mortality. Once these parameters are known, a variety of stock-assessment techniques can be applied; in particular, yield-per-recruit analysis, which has been the technique most commonly applied to lobster fisheries in the Pacific.

Yield-per-recruit (YPR) analysis has been carried out in the past because it provides advice that helps managers prevent growth overfishing (a condition that occurs when many small lobsters are caught before they have grown to optimum size) by indicating the optimum size at which the fishery can begin to catch lobsters at any given value of fishing mortality (F) – two parameters over which managers can have some control by implementing minimum legal size ( $l_s$ ) restrictions or controls on fishing effort (Gulland, 1983). Nevertheless, maximising YPR is not the only important management objective and, in some circumstances, it may not even be an optimal strategy (see "Management Considerations").

The analysis of YPR requires information on the length-weight relationship and works by examining the way the biomass of a year-class changes with growth and mortality. The biomass initially increases with the rapid growth of young lobsters, even though year-class abundance is decreasing due to mortality; then it reaches a maximum and, as the growth rate slows and mortality continues, decreases eventually to zero. Taking these underlying biomass changes into account, the YPR analysis estimates the yield from each year-class (per recruit) for a range of F and I, then the combinations of F and I that maximise yield can be identified. If required, the economic YPR can be examined when the value of lobsters of different sizes is included in the analysis; this can be important because intermediate-sized lobster tails (120-300 g) are generally more valuable than very small or very large tails (e.g. see Prescott, 1988). Although any assessment of a fishery is uncertain, YPR is relatively robust compared with other assessments, provided that estimates of input parameters are accurate, and a relatively high level of confidence can be placed in the management advice that YPR analysis provides (Gulland, 1983).

Analysis of YPR has only been attempted for P. penicillatus in four areas of the Pacific: Enewetak (Ebert and Ford, 1986); Tonga (Munro, 1988); Solomon Islands (Prescott, 1988); Western Samoa (King and Bell, 1991). Prescott (1988) mentioned the effect of different minimum sizes but did not demonstrate the effect graphically, and the other analyses are inaccurate because they used what has since been shown to be an incorrect value of natural mortality (see "Mortality"). Consequently, YPR has been reanalysed for Tonga, Solomon Islands and Western Samoa. The YPR of *P. penicillatus* in the Philippines had not previously been estimated but is analysed here using information from Arellano (1988 – see Tables V and VI). Note that, in the analyses presented here, selection curves were included such that a minimum legal size (1) was considered to correspond to the size at which probability of capture was 10 per cent (*i.e.*  $I_{10\%}$ ) and lobsters did not become fully recruited to the YPR model until several size classes  $> l_s$  to simulate the situation in a real Pacific fishery. These modifications were implemented because experience in Torres Strait has shown that some lobsters smaller than l, would always be speared and neither l, (size at first recruitment) nor l (average size at first capture) were appropriate. In addition, although YPR responds to F as well as to I, the discussion in this section considers only the setting of l for the current level of F in each fishery because fishing effort generally has not been controlled in the Pacific and would be difficult to control.

The YPR-analyses provide three-dimensional surfaces of the response of YPR to F and  $l_s$ , and these surfaces can be contoured. The YPR surfaces for *P. penicillatus* are generally ridge-shaped, though relatively flat on top (Fig. 12). The lowest YPR occurs at very low values of F and there is little change in YPR at different values of  $l_s$ ; thus, at low F, there is no advantage in legislating for  $l_s$ . However, as F increases, so does YPR, although it becomes highly dependent on  $l_s$  so that the highest values of YPR are around the center of the right half of the graphs (Fig. 12). Thus, at very high F, values of  $l_s$  ranging approximately between 60-110 mm CL, depending on sex and location, are clearly maximal.

In Solomon Islands, the *P. penicillatus* fishery is under-exploited and only slightly suboptimal with respect to YPR because current sizes at about 10 per cent probability-of-capture  $(l_{10\%} \approx \text{effective minimum size}, l_s), i.e.$  about 75 mm CL at  $F \approx 0.2$  for males and approximately 70 mm CL at  $F \leq 0.3$  for females (from Prescott, 1980a), are only slightly greater than those for maximum YPR at the same F (*i.e.*  $l_s \approx 60 \text{ mm CL}$ ). However, current legislation prohibits the taking



of lobsters <250 mm total length ( $\approx$  114.5 mm CL for males and 96.5 mm CL for females); this is too large for the maximum YPR at current F and, if enforced, would reduce the yield of the fishery.

Each of the three other P. penicillatus fisheries (Tonga, Samoa and the Philippines), in contrast to Solomon Islands, could benefit in the long term from the introduction of legislation on and enforcement of minimum sizes (Fig. 12) because current values of l<sub>10%</sub> at current F are less than l<sub>s</sub> for maximum YPR at the same F. In Tonga,  $l_{10\%} \approx 60$  mm CL at F  $\approx 0.5$  for males and  $l_{10\%} \approx 55$  mm CL at  $F \approx 0.45$  for females (Tongatapu and Ha'apai together; from Prescott, 1990), whereas, at the same F, maximum YPR is obtained with an effective l in the range 80-100 mm CL for males and 55-70 mm CL for females. In Western Samoa,  $l_{10\%} \approx 57$  mm CL at F  $\approx 0.4$  for males and  $l_{10\%} \approx 53$  mm CL at F  $\approx 0.65$ for females (from King and Bell, 1991) whereas, at the same F, maximum YPR is obtained with an effective l in the range 70-90 mm CL for males and 60-70 mm CL for females. In the Philippines, the current yield from the fishery is well below the potential maximum based on YPR because the larger lobsters have been overfished and there is considerable fishing pressure on very small lobsters; currently,  $l_{10\%} \approx 45$  mm CL at F  $\approx 0.8$  for males and  $l_{10\%} \approx 45$  mm CL at F  $\approx 0.95$ for females (from Arellano, 1988), whereas, at the same F, maximum YPR occurs with an effective l in the range 75-85 mm CL for males and 70-80 mm CL for females. The YPR surfaces show that there is little to be gained from setting l toward the upper end of the ranges given above (in fact, there may be significant losses - see "Management Considerations" below). It is also impractical to set different l for males and females or for different areas of the fishery, and so an intermediate I should be chosen. Additional considerations for setting 1, such as marketability of different sizes, are also discussed in "Management Considerations".

The YPR of *P. longipes* in Tonga has been analysed (Munro, 1988), but some of the input parameters either were not determined robustly or were unavailable and proxy values were substituted from other species in different areas. The advice from such an assessment is questionable (Prescott, 1990) and management action should await assessments that have locally determined parameters as inputs.

Figure 12. (left) Yield-per-recruit surfaces for male and female *Panulirus* penicillatus in Solomon Islands, Tonga, Western Samoa and the Philippines as functions of fishing mortality (F) and minimum legal size ( $l_{,}$ ). Underlying data from Prescott (1988), Munro (1988), King and Bell (1991) and Arellano (1988). The small filled circles show the estimated current status of the fisheries in terms of F and size at about 10 per cent probability of capture; contours are intervals of 10 per cent of maximum YPR, starting with 0 per cent at the left axis.



Figure 13. Egg-per-recruit expressed as percentages of the maximum EPR when there is no fishing, at a range of minimum sizes (CL mm) and levels of fishing mortality (F), for *Panulirus penicillatus* from Tonga, Solomon Islands and the Philippines. The approximate current condition of each fishery is represented by the filled circles at the estimated effective minimum size and estimated level of F (underlying data and sources as in Fig. 7.); contours are intervals of 10 per cent of maximum EPR, starting with 100 per cent at the left axis.

The YPR of *P. ornatus* in Torres Strait also has been analysed (CSIRO, *unpub.*) and shows, as in Fig. 12, that at low F (*i.e.* at  $F \approx 0.1$ ), minimum sizes do not improve YPR. Nevertheless, there is a minimum size of 100 mm tail length (equivalent to 75 mm CL) which corresponds to the maximum YPR for F > 1.0, although such high levels of F are probably unsustainable.

The analysis of the number of eggs produced per recruit (EPR) follows a procedure similar to YPR (see Caddy, 1979; e.g. Annala and Breen, 1989) and, although EPR has not been assessed for any Pacific *P. penicillatus* fishery, it is an important consideration if there are concerns that the reproductive potential of the population has been seriously diminished. In theory, an exploited population is most productive when its breeding biomass has been reduced to half of unfished levels, but in practice this may lead to over-exploitation and more conservative strategies for exploitation are recommended (Gulland, 1983). Consequently, if a fishery is thought to be largely self-recruiting, which may be unlikely for populations of *P. penicillatus* in the Pacific (see "Recruitment"), then consideration must be given to management strategies that maintain the reproductive potential of the population–probably at levels > 50 per cent of unexploited EPR – by manipulating  $l_{e}$  or F.

Like YPR, the EPR is also sensitive to the population-dynamics parameters of the stock. In particular, both analyses focus on the two parameters, size at recruitment and fishing mortality (F), which can be influenced by management actions such as effort controls or more usually minimum sizes  $(l_s)$ . Thus, there is a link between YPR and EPR because strategies that influence one also influence the other. For the purpose of comparison and to illustrate the analysis, EPR was calculated for the three Pacific fisheries for which there were sufficient data (*i.e.* Tonga, Solomon Islands and the Philippines): the egg production analysis, presented in the "Reproduction" section (Fig. 7), was expanded for a range of F and  $l_s$  (10 per cent probability-of-capture,  $l_{10\%}$ ).

The resulting contours of the EPR surfaces for *P. penicillatus* are gullyshaped (Fig. 13) with maximum EPR (100 per cent) occuring at F = 0 (along the Y-axis) and the lowest EPR (<10 per cent of maximum) occuring in the lower right-hand corner of the graphs (Fig. 13). At small minimum sizes, increased fishing pressure reduces EPR substantially (Fig. 13), whereas at larger minimum sizes, increased fishing pressure reduces EPR less dramatically.

The current status of EPR in a fishery is given by the current combination of  $l_{10\%}$  and F for females. In Solomon Islands,  $l_{10\%} \approx 70$  mm CL at  $F \approx 0.3$  (from Prescott, 1980a) and EPR is about 60 per cent of the maximum at F=0. In Tonga,  $l_{10\%} \approx 55$  mm CL at  $F \approx 0.45$  (Tongatapu and Ha'apai together; from Prescott, 1990) and EPR is only about 40 per cent of the maximum. In the Philippines,  $l_{10\%} \approx 45$  mm CL at F 0.95 (from Arellano, 1988) and EPR has been reduced to <20 percent of the maximum. The EPR analysis demonstrates clearly that differences in size at recruitment and fishing mortality have a substantial effect

on egg production of the population and are responsible for most of the difference in absolute EPR (see "Reproduction") among these three Pacific fisheries.

In some fisheries, the most appropriate  $l_s$  for YPR considerations (*i.e.* generally  $l_s \ge 75 \text{ mm CL} - \text{see "Management Considerations") may fortuitously maintain EPR > 50 per cent; this would be the case for Solomon Islands and Tonga. However, where F for female$ *P. penicillatus* $is greater than 0.6-0.7, the <math>l_s$  required to achieve EPR > 50 per cent would need to be larger; *e.g.* in Western Samoa,  $l_s$  would have to be  $\ge 80 \text{ mm CL}$  to achieve EPR > 50 per cent, and, in the Philippines,  $l_s$  would have to be  $\ge 85 \text{ mm CL}$ .

## **FUTURE RESEARCH**

There are many possibilities for research on lobster resources in the tropical southern and western Pacific, but the cost of research relative to the small size of most Pacific fisheries must be taken into account — even though the problems and questions arising of small fisheries are no less important or difficult than those of large fisheries. Consequently, future research will be tactical, generally limited to finding direct and immediate answers to management requirements. Good research provides significant benefits to fisheries and management; but it is an investment, and funds should be allocated to maximise the expected benefits (Lindner, 1989).

Yield-per-recruit is probably the most cost-effective assessment that can be done for the management of Pacific lobster fisheries. However, additional, rigorous estimates of natural mortality (M), which are representative of the different areas of the Pacific, are urgently needed so that YPR advice will be sound. Estimates of M can be most easily obtained by analysing size-frequency data from research lobster fishing on unexploited reefs near local fisheries around the Pacific (e.g. as suggested by Prescott, 1990). A caveat on any such size-frequency approach is that reliable growth data are essential for reliable estimates of mortality. In particular, estimates of the growth coefficient (K) should be determined independently of size-frequency data. Tagging studies can provide reliable estimates now that new techniques (e.g. ventral abdomenal tagging with small Floy T-bar tags - R. Brown pers. comm.) are available to solve some of the problems that have previously plagued tagging studies (e.g. tag loss due to grooming - Prescott, 1988). Tagging studies should be carried out in the same area as the experimental fishing activities: this would avoid duplication and minimise the cost; further, the growth and mortality parameters would be matched for the same population and biases would be minimised because the researchers would have complete control over the project.

The computer program ELEFAN has been used to estimate the growth

parameters of lobsters in the Pacific. However, ELEFAN should be used with caution because year-class modes in Pacific lobster stocks can be blurred where recruitment is continuous, growth rates are variable and the species are long-lived. If the size-frequency data include lobsters larger than the statistical average  $L_{\infty}$ , the program will not give reliable results. Further, ELEFAN requires very large samples of size-frequency data, and this is often difficult or sometimes impossible in Pacific lobster fisheries (Prescott, *pers. comm.*).

Research fishing studies, if planned according to the sampling strategy for depletion fishing experiments, are also likely to provide rough estimates of the density of P. penicillatus (e.g. Ebert and Ford, 1986). Further, if a set of sample reefs is selected to be representative of the full spectrum of reef types in the fishery, then it may be possible to estimate total stock abundance. Once abundance estimates have been made, preliminary estimates of potential yield that will assist those planning fisheries development (King and McIlgorm, 1989) may be possible using a variety of simple yield models; e.g. Yield =  $aMB_{a}$ , where M is natural mortality,  $B_n$  is the unexploited biomass and a is a constant with a value of about 0.3 (see Garcia et al., 1989 for a critical review). However, a precise estimate of total stock would likely require more depletion sampling than is economically feasible. An alternative might be to calibrate rapid-visualtransect census methods with a few depletion fishing experiments and use the faster visual censuses to sample greater numbers of reefs, which should be stratified according to exposure and fishing effort, to obtain more precise estimates of abundance in a more cost-effective manner. The strong influence of the lunar cycle on lobster activity patterns must be taken into account (Prescott, 1990) in the sampling design, otherwise the results are likely to be biased.

Several consultants have recommended resurrection of traditional trapping techniques (eg. George, 1972) to provide high quality live-caught product. Research could determine the most appropriate traditional trap designs that have been used both within and outside (*e.g.* De Bruin, 1960) the Pacific region as well as any modifications, modern materials or techniques that may improve designs.

The assumption that *P. penicillatus* phyllosoma larvae disperse widely and thus, that unexploited reefs provide a protected source of recruitment for exploited, or even over exploited, reefs should be assessed before the fisheries in the majority of Pacific nations become fully developed. This seemingly reasonable prior assumption underlies current perceptions of the robustness of the Pacific *P. penicillatus* stocks; if it is incorrect, then stock-recruitment relationships must be considered – a far more time-consuming and difficult task than, for example, YPR. The validity of the assumption may also vary around the region (Prescott, 1988), depending on the proximity and number of adjacent reefs, and the intensity and areal extent of fishing. One approach to assess this assumption may be to research the genetic variation of P. penicillatus within the Pacific and compare it with distant locations in the Indian Ocean – limited genetic variation would indicate potentially greater larval dispersal, whereas greater genetic variability would indicate increased likelihood of self-recruitment.

Finally, but most important, collection of basic fishery data is essential. The types of data that should be collected regularly include: total catch, individual catches per unit effort (man-night), catch location, species, size-frequency, sex and reproductive status (George, 1972; Prescott, 1990). These data would assist fisheries development, by providing inputs for stock-assessment research and a trace of the effects of fishing on the stock when management questions arise. Although many Pacific lobsters stocks are under exploited at present and there may appear to be little need to keep records, fishing of these stocks will undoubtedly develop with time and exploitation will increase; if good records have been kept, they will prove invaluable for future assessments. The importance of good catch records cannot be overstated.

## V. DEVELOPMENT AND MANAGEMENT

## **DEVELOPMENT CONSIDERATIONS**

A primary consideration for both managers and investors in the Pacific is the size of the lobster resource: although the densities of *P. penicillatus* may be relatively high on the reef slope, crest and flat, which can lead to over-optimistic expectations from surveys of virgin stocks, the habitat is very narrow and the abundance of lobsters is generally too low to support highly capitalised fisheries (Prescott, 1988) – long-term catch rates may be less than half that obtained in initial surveys (King and McIlgorm, 1989). Larger operations involving freezer vessels and teams of divers may only be economic if other marine products (*e.g.* finfish, bêche-de-mer, trochus and other shellfish) are also exploited (Prescott, 1988) – *i.e.* a multi-species basis is desirable. In addition, larger commercial operations should keep mobile, exploiting reefs in rotation and moving when the catch rate on any one reef declines; between visits, the stock would increase due to growth and recruitment.

Other logistic impediments to exploitation of lobsters, especially *P. penicillatus*, include: the exposure of the surf zone habitat to high energy waves, particularly during the tradewind season, makes fishing difficult or even dangerous and restricts access to periods of good weather (Prescott, 1988); the lunar cycle affects lobster activity patterns so that catch rates for most of the lunar cycle may be only one third of those during the first quarter (*e.g.* King and Bell, 1991); reef walking is further restricted to periods when the tide is neither too

high nor too low. Also, logistical problems arise in transporting the product from remote reefs where lobsters are more abundant to markets where the human population is larger but the lobster population is smaller (George, 1972).

Availability of markets determines the viability of fisheries (Owen, 1989); often, however, local markets (such as tourist developments) that could sustain local commercial fishing are lacking, and, without local markets, new or small companies find it difficult to extend themselves and develop export markets. The importance of local markets for sustaining local commercial fishing is demonstrated in Fiji, which has extensive tourism, and where local fishermen supply > 100 t of lobsters annually. Conversely, Solomon Islands has limited tourism and, although the lobster resources may be as extensive as those in Fiji (Prescott, pers. comm.), the annual catch is < 5 t (Table I) – a significant local market in Solomon Islands may stimulate growth of an export fishery. The implications are that potential investors should consider the presence or absence of local markets and national governments may need to encourage the development of potential local markets. Market research is essential for successful export market penetration; the ability to recognise changes and trends in consumer demands may allow exporters to establish a niche in competitive overseas markets (Williams, 1989).

High quality product is essential for development and retention of commercial local and export markets, and it also minimises any health risk (Prescott, 1990). However, many consultants reporting on aspects of *P. penicillatus* fisheries in the Pacific have mentioned product quality, identifying spearfishing as the main cause of poor quality product. They have suggested that live catching of lobsters should be encouraged to improve quality (*e.g.* George, 1972; Prescott, 1980b, 1980c, 1990; King and Bell, 1991). This recommendation seems sensible, particularly when given the widespread lack of ice-making facilities and freezers, and that lobsters are usually sold whole rather than tailed. Live catching would also allow undersized lobsters and, if necessary, berried females to be returned to the sea alive. Live lobsters can also be readily stored and transported; with only simple facilities required (Prescott, 1980b, 1980c). *P. penicillatus* can readily be hand-caught alive by divers or reefwalkers; in addition, the reintroduction of traditional traps (or modifications thereof) is probably worthwhile (George, 1972).

The development of any fishery, which involves significant capital investment, should be preceded by a structured appraisal of the potential of the resource: initially, background information from the literature and from the knowledge of traditional fishermen (Johannes, 1989), should be collated then a preliminary assessment of the resource and economic viability should be done (this should consider marketing potential and transport and processing costs given limited infrastructures). If the results are encouraging, details of marketing and economic feasibility should be studied, followed by full-scale stock survey and assessment research (King and McIlgorm, 1989). Generally, catching and processing costs must be low for success (King and McIlgorm, 1989), and it is important not to overcapitalise – this usually leads to excessive debt and overfishing, which, in turn, causes economic and social impoverishment among fishermen and the depleted resource may barely support subsistence fishing activities (Johannes, 1978). Consequently, development should only proceed in a cultural, social and economic framework that is appropriate to the Pacific islands; otherwise, indigenous peoples and small national economies may be worse off than without so-called development (Brown and Waugh, 1989). In this context, significant domestic benefits should be secured from joint ventures and other fishery development projects (Doulman, 1989).

## MANAGEMENT CONSIDERATIONS

Given the probable wide dispersal of *P. penicillatus* phyllosoma larvae and the many unexploited reefs that can potentially provide recruitment to exploited reefs (George, 1972; Prescott, 1988), reasonable assumption suggests that *P. penicillatus* stocks in the Pacific will be resilient to recruitment overfishing. The management significance of this is that, with a few exceptions (*i.e.* possibly the Philippines), there is little current need to be overly concerned about the reproductive capacity of lobster stocks. Therefore, there is little need to protect berried females or introduce closed seasons, particularly as females tend to breed throughout the year; either of these measures would reduce the capacity of the fisheries (George, 1972). The main biological concern of management, then, is to maximize yield from the available stock by carrying out YPR research and setting appropriate minimum sizes. This requires reliable data on growth rates, fishing mortality rates and natural mortality rates, which should be determined for local populations rather than substituted from other fisheries or species (see "Future Research").

The choice of the most appropriate minimum sizes will be a compromise among the optimums for different sexes and species (given that enforcement of different  $l_s$  for each would be very difficult), concern (if any) over reproductive capacity and the initial negative impact of the  $l_s$  excluding small lobsters from catches. The YPR contour surfaces for the two sexes in the different fisheries (Fig. 12) show that a compromise value of  $l_s$  would be in the range of 75—80 mm CL; although this range tends to be a little large for females and a little small for males, it would produce the highest YPR overall and is not grossly suboptimal for either sex. Further, an  $l_s$  of 75-80 mm CL corresponds with the lower end of the preferred size range in the international market and, thus, commands the best prices (see Prescott, 1988).

The introduction of a minimum size in Solomon Islands would have little initial negative impact as only a small proportion of lobsters under about 75 mm

CL are currently caught. However, in Tonga, Western Samoa and the Philippines, the impact would be greater as larger proportions of the catch are under approximately 75 mm CL and these would become unavailable to the fishermen. The Philippines represents the worst case as only 10-20 per cent of the catch is greater than about 80 mm CL (see Arellano, 1989). Prescott (1990) calculated that the introduction of a minimum size of 75 mm CL to the Tongan fishery would reduce catches by nearly 25 per cent in the first year - this may be too severe, given that YPR is currently only about 10 per cent below the maximum. Because of the unpalatability of reducing recruitment to the fishery by more than 10-20 per cent per annum while a minimum size limit is being introduced, consideration should be given to incrementing the l gradually. The rationale is that lobsters grow through the debated size range at a rate of 20-30 mm per year; an annual increment in l of 20 per cent of this rate (i.e. at about 5 mm), beginning at current  $l_{10\%}$ , would maintain recruitment at sufficiently high levels to minimise the impact on the fishery. When the desired l has been attained, the benefit of YPR maximisation will begin to be realised - in the case of the Philippines, this could take 7-8 years to achieve.

Management should endeavour to keep fishing methods simple (*i.e.* "appropriate technology") to discourage overcapitalisation and its consequences (see the preceding section; Johannes, 1978, 1989). At the same time, diving for lobsters should be encouraged in areas where it is currently not practised, because diving gives access to additional productive habitat (the reef slope) and may also improve egg production by shifting effort from female lobsters, which frequent the reef flat, to males. Concern for quality product should be paramount; high quality can be achieved by discouragement of spear-fishing and encouragement for live catching and improve handling (see Prescott, 1980b). Consideration should be given to legislation that prohibits spear-fishing and requires that lobsters be first sold alive. Quality is the key to successful marketing, especially in export markets – without markets there can be no economic future for Pacific lobster fisheries.

The strategy for managing Pacific lobster fisheries should take account of traditional reef-tenure systems for village-based fishermen (Johannes, 1989). Under these systems, clans are custodians of their own fishing grounds, and there are strong incentives not to overfish these grounds (Ruddle, 1989). Traditional reef tenure thus discourages overfishing, is more likely to be understood and accepted by traditional fishermen, and becomes self-policing – which is important when enforcement capability is limited (Johannes, 1978). Management that involves reef-tenure should also adapt to new fisheries and circumstances (Johannes, 1978); larger-scale mobile operations may have to be excluded from, or require permission to enter, clan "home reefs" to prevent undermining of the custodial ethos.

Overall, managers of Pacific lobster fisheries should not regulate too heavily

because these fisheries need encouragement for future development (George, 1972). However, managers also need to be a little conservative as it is very difficult to reduce effort or size at first capture once overfishing has occurred (King and McIlgorm, 1989). The establishment and maintenance of systems for recording fundamental fisheries data (*e.g.* catch, effort, basic biological data) are primary responsibilities for managers: these data are essential for assessments when the fisheries develop and exploitation increases (George, 1972; Prescott, 1990). Finally, although the economic efficiency of developing fisheries in the Pacific must be considered, managers must ensure that clear benefits accrue to their Pacific states (Doulman, 1989), that their states' economies are improved by development, and that traditional culture and social fabric are integrated with the economic and management systems of their fisheries (Brown and Waugh, 1989).

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