

Review

Evolution of life cycles, including migration, in spiny lobsters (Palinuridae)

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Abstract A comparison of the documented ecology and behaviour of the separate phases in the life cycles is presented. Data gathered during the review show that during the evolution of the family from deeper-water habitats to the more rapidly fluctuating shallower waters, there have been many biological adjustments at each phase in their life cycles. In the more ancient Stridentes genera, like *Puerulus*, the larvae are found well below the surface waters and the pueruli often settle at greater depths than those of the adults. Long incubation times, few larval instars, and year-round spawning are probably their life cycle characteristics. As an “intermediate-evolved” genus of Stridentes, *Palinurus* lives along the outer shelf, grows slowly, matures late, and breeds seasonally once a year. Incubation time is long, the larvae live at depth, the number of larval instars is limited, and the puerulus is a weak swimmer. Settlement is often downstream of the breeding stock. Incubation times are short for the more recently evolved Stridentes *Panulirus*, the larvae pass through many instars in the surface waters to c. 200 m. Some pueruli settle in special coastal habitats, others settle in the same habitat as the adult. Breeding in the cooler water First Major Lineage species is seasonal, one or two broods being produced. Most of the species in the tropical Second Major Lineage are faster growing, breed repetitively over a long breeding season, and have a shorter larval life. For the Silentes, the trend in biological

changes from deep to shallower water is comparable with that of Stridentes. Incubation is probably long in the more ancient *Projasus*, the larvae are rare in surface waters and the pueruli settle at depths similar to those of the adults. *Sagmariasus* and *Jasus* breed once during a defined season, incubation time is moderate, and the larvae pass through many instars. The pueruli of *Sagmariasus* settle downstream and exhibit contranant migration whereas the pueruli of *Jasus* swim strongly to their shallow habitats. In each life cycle phase, migration methods range from vertical paddling in phyllosomata, horizontal swimming in pueruli, and horizontal walking when juveniles move to adult habitats. Adult movements are associated with foraging, searching for shelter, avoiding adverse seasonal conditions, or walking to preferred offshore locations for moulting and reproduction.

Keywords evolution; spiny lobsters; Palinuridae; life cycles; migration strategies

INTRODUCTION

Past tectonic movements, energetic intensification of oceanic and coastal systems, as well as general climate changes have combined to create a multitude of new shallow-water habitats by altering surface water temperatures and enhancing current systems (George 1997). These environmental constraints continually force new biological modifications that are necessary for the successful invasion of these more variable shallow-water environments by the more recently evolved spiny lobsters and ... “life history strategies have evolved in response to this variability, enabling species to avoid extinction during sets of particularly adverse environmental conditions” (Pollock 1995).

The dramatic habitat shift from the cool, dark, calm, deep waters to the warmer, more turbulent, well lit coastal waters by the recent genera (George & Main 1967) have necessitated a whole range of adjustments to these new levels of salinity, turbidity,

temperatures, currents, and turbulence (wave action) (Pollock 1995), as well as light intensity, surge, and swell action. This paper extends the evolutionary study on three palinurid genera by Pollock (1995) and examines additional lifestyle changes throughout the family in morphology, reproductive characteristics, and migratory behaviour.

CLIMATE AND EVOLUTIONARY CHANGE

The inhabitants of the broad Tethys Sea would have been subjected to a Mesozoic climate of relatively mild wind systems, generally warm seas, and a gentle oceanic circulation system (Kennett 1982); in both the Stridentes and Silentes, the ancestral habitat of the Palinuridae is considered to be in the more stable, deeper water where, except for *Palinurellus*, the more primitive genera live today (George & Main 1967).

However, opposite views have been expressed by Feldmann & Tshudy (1989) who suggested that *Linuparus* arose in the shallow waters of Antarctica, radiating into deeper water, low latitude habitats, and by Davie (1990) who believed that George & Main's (1967) view may have been too simplistic. Davie (1990) suggested that the shallow water, primitive *Palinurellus* has survived by living in deep dark caves and thus avoiding the competition or predatory pressures which caused members of other genera to retreat into deeper water. Perhaps these opinions are also simplistic since they imply that there were no deeper-water competitors or predators and the "harassed" shallow-water fauna simply marched down into vacant deeper-water habitats unhindered, modifying their biological attributes as they went. It seems more likely that the relatively stable environmental conditions in the deeper waters supported biologically stable, ancestral stocks from which several series of experimental radiations have, over time, temporarily colonised the shallow-water environment.

Throughout geological time, this shallow zone has undergone more rapid changes in currents, temperature, sediment, salinity, wave action, and oxygen levels, all of which have been influential in determining the characteristics of the shallow and geologically-speaking, more recently evolved spiny lobster species. One would expect the shallow regions where primitive relict species abound, such as the Caribbean region, to have had a history of relative environmental stability. *Palinurellus* and

Panulirus argus could be good examples of spiny lobsters with long survival records.

EVOLUTION AND MORPHOLOGY IN PALINURIDAE

Within the Stridentes, morphological changes in the adult, in response to the evolution into high energy rocky shelters (*Panulirus*), include the adoption of a well-calcified, cylindrical exoskeleton, strong legs, and elevated eyes that are protected by large, erect, forwardly-curved supraorbital horns. *Palinurus* lives at deeper depths (70–400 m) and is regarded as a part-way genus in the evolutionary pattern (Baisre 1994). The eyes are laterally disposed and protected by large obliquely-elevated supraorbital horns, the legs are moderately strong, and the carapace is cylindrical. The ancestral-like genera that live on soft bottom at depth (*Linuparus*, *Puerulus*, and *Palinustus*) have poorly calcified, subcylindrical bodies, weak legs, and eyes sunken beneath low, flattened supraorbital horns (George & Main 1967). The rare, deepwater *Palibythus* has a cylindrical body, weak legs, and small eyes sunken beneath the rostral plate and is considered by Davie (1990) as an early Stridentes offshoot from a pemphicid ancestor.

The elongated eyestalks of larvae of some of the shallower water genera are considered a more recent specialisation (Baisre 1994) and this may be part of an adaptive response to levels of low light intensity, thus facilitating control by the larvae to retain a desired position in the upper water layers.

Phylogenetic morphological changes are also apparent for the larval stages in the two major lineages of *Panulirus* that have been recognised by Baisre (1994), McWilliam (1995), Ptacek et al. (2001), and Patek & Oakley (2003). The larvae of the deeper-water, more ancestral First Major Lineage, listed in Table 1, have less spinose pereopods (fewer ventral coxal, subexopodal, sternal, and dorsal coxal spines), have a shorter tapered apex to the antenna and a narrow cephalic shield compared with those of the shallower, more specialised, Second Major Lineage (see Table 1) which have spinose larvae with long, spatulate-tipped antennae and wide cephalic shields (McWilliam 1995). For the puerulus stages, McWilliam also concluded that these lineages show a similar specialised trend from less to more spinose (e.g., posterior sternal spines), from short and tapered to long and spatulate antennae and from long to short exopods on both the second and third maxillipeds.

Table 1 Comparative life cycle attributes of palinurid genera.

Species	Age (years) hatching to maturity	Egg size index	Broods per year	Incubation period (months)	No. of instars	Larval period (months)	Puerulus period (days)
STRIDENTES							
<i>Palinurus</i>							
<i>P. elephas</i>			1(22)	5–9(11)	10(22)	5–12(22) 4–5(30)	11–15(1)*
<i>P. delagoae</i>	c. 8(39)	200(37)	1(11)	5–6(11)		5–6(11)	
<i>P. gilchristi</i>	c. 8(39)	200(37)	1–2(38)				
<i>Panulirus</i>—First Major Lineage							
<i>P. a. argus</i>		800(3)	1–2(5)	1(27)		6–8(25)	5–10(6)
<i>P. a. westoni</i>			2(19)	4(19)			
<i>P. interruptus</i>	3–6(14)	400(3)	1(14)			7.75(1)	75(9)
<i>P. japonicus</i>	>3(16)		2(16)	1–2(27)	29(30)	9–10(24) 12(26) 8–13(24)*	>8(1) 12–15(1)*
<i>P. marginatus</i>			2(17)			6–11(1)	
<i>P. cygnus</i>	6–7(29)	400(3)	1–2(13)	0.5–2(27)	15(1)	9–11(1)	15(1)
<i>P. l. bispinosus</i>			1(15)	2–3(15)		9(26)	
<i>P. penicillatus</i>	3(32)		3–4(5)	1(27)		>7–8(1)	
<i>P. guttatus</i>		330(10)	>2(18)				
<i>Panulirus</i>—Second Major Lineage							
<i>P. polyphagus</i>	3(34)		2–5(34)	2–3(33)			>2–4(1)
<i>P. laevicauda</i>			2(19)	4(19)			
<i>P. gracilis</i>	c. 2(14)		3–4(5)	1(14)		7(14)	
<i>P. inflatus</i>	c. 2(14)		3–4(5)	1(14)	>25(6)	7(14)	
<i>P. h. homarus</i>	<3(35)	620(35)	2–4(35)	c.1(36)	18–19(35)	4–6 (35)*	
<i>P. h. rubellus</i>	<3(40)	800(3)	1–4(40)	1–2(40)		4–6(7)	
<i>P. ornatus</i>	2+(20)	720(35)	3(20)	c.1(35)	18–19(35)	4–7(21)	
<i>P. versicolor</i>		740(35)			8–19(35)	4–6(35)	
SILENTES							
<i>Sagmariasus</i>							
<i>S. verreauxi</i>	6–7(29)	500(3)	1(12)	3(4)	17(4)	8–12(1)	25(30) 20(1)*
<i>Jasus</i>							
<i>J. lalandii</i>	5–6(31)	500(3)	1(5)	4–6(5)	17(31)	9–10(1) 14–18(8) 10(30)*	>31(1)*
<i>J. novaehollandiae</i>	3.5–5(29)	400(3)	1(5)	4–6(5)		8–22(29)	
<i>J. edwardsii</i>	5–11(28)	300(3)	1(5)	4–6(5)	15–17(30)	12–22(28) 7–9(30)*	>70(2) 19(1)*
<i>J. frontalis</i>		400(3)	1(5)	4–6(5)			
<i>J. tristani</i>		300(2)	1(5)	3–4(8)			

*Denotes laboratory conditions.

References: (1) Booth & Phillips 1994; (2) Pollock & Goosen 1991; (3) Pollock 1995; (4) Kittaka et al. 1997; (5) Quackenbush 1994; (6) Phillips & Sastry 1980; (7) Berry 1974; (8) Roscoe 1979; (9) Serfling & Ford 1975; (10) Pollock 1997; (11) Berry 1973; (12) Booth 1986; (13) Chubb 2000; (14) Briones & Lozano 2000; (15) Gomez et al. 1994; (16) Minagawa 1997; (17) Polovina et al. 1995; (18) Losado-Tosteson et al. 2001; (19) Soares & Calvacante 1985; (20) Skewes et al. 1997; (21) Dennis et al. 2001; (22) Hunter 1999; (23) Pollock & Augustyn 1982; (24) Baisre 1994; (25) Silberman et al. 1994; (26) Inoue & Sekiguchi 2001; (27) MacDiarmid & Kittaka 2000; (28) Booth 2000; (29) Phillips et al. 2000; (30) Kittaka 2000; (31) Pollock 1986; (32) Plaut 1993; (33) Kagwade 1988a; (34) Kagwade 1988b; (35) Vijayakumaran pers. comm.; (36) Vijayakumaran 1990; (37) Pollock & Melville-Smith 1993; (38) Groeneveld & Rossouw 1995; (39) Groeneveld 2000; (40) Berry 1971.

Within the Silentes, from *Projasus* through *Sagmariasus* to *Jasus*, morphological changes that parallel those in the Stridentes accompany the evolutionary trend from deeper, calmer waters to shallower, more turbulent waters. The deep-water *Projasus* (175–880 m, Webber & Booth 1988; Baez & Ruiz 2000) is similar to the Stridentes *Puerulus* in having a poorly calcified, spinose ridged, subcylindrical carapace, weak legs, and eyes sunken below flattened supraorbital horns. The shallower-water *Sagmariasus* and *Jasus* have strongly calcified, evenly spinose cylindrical carapaces, strong legs, and moderately elevated eyes protected by moderately elevated supraorbital horns, somewhat similar to *Panulirus* (George & Main (1967). Following phylogenetic reviews of *Palinurellus* by Davie (1990) and Patek & Oakley (2003), *Palinurellus* is included here in the Silentes. The enigmatic *Palinurellus* is considered to represent the palinurid plesiomorphic condition for both the adult and larval characteristics but it lives in a shallow, perhaps relict, habitat (Davie 1990; Baisre 1994). It has a rounded carapace, small eyes, a broad rostrum, the forerunner of a stridulating organ, and moderately sturdy legs. Unfortunately, little is known of its life cycle characteristics.

SPERMATOPHORIC MASS

Berry & Heydorn (1970) discussed the selective forces that shaped the evolution of the spermatophoric mass. The most specialised condition is found in the most recently evolved Stridentes genus *Panulirus* where the ribbons of spermatophores are surrounded by a putty-like, granular mass that hardens in sea water and can be retained for minutes (10 min for *Panulirus japonicus*) or months (up to 69 days for *Panulirus cygnus*, MacDiarmid & Kittaka 2000) before the surface layers of the protective matrix are scraped away by the female when she chooses to fertilise her ripe eggs. For the more primitive Stridentes genera *Puerulus*, *Linuparus*, and *Palinurus*, the mass is gelatinous, does not disintegrate in sea water, and the female makes deep single scratches in the surface to release spermatozoa within a matter of days after deposition (Berry & Heydorn 1970). Berry & Heydorn concluded that the hardened spermatophoric mass of *Panulirus* is not a prerequisite for its invasion of shallow water but rather a strategy to control or prolong the interval between mating and oviposition. In the shallow waters, the ability of the female to

respond to seasonal and annual fluctuations in the environment and thus control the timing of egg-laying and subsequent larval release is a substantial advantage in enhancing the success of a species.

For the Silentes *Jasus*, the gelatinous spermatophoric mass contains a simple thread of spermatozoa that disintegrates in sea water and thus shows an unspecialised level of development that has changed little in the relatively stable environment of the southern temperate zone. Berry & Heydorn (1970) concluded that the spermatozoa are released immediately and are used to fertilise the ripe ova as they are exuded. This conclusion that egg laying immediately follows copulation is further supported by the experiments of MacDiarmid (1988).

LIFE CYCLE OF STRIDENTES

For the Stridentes, if we use what little natural history information we have on the deep water and primitive *Puerulus* and *Linuparus* as a guide, the ancestral genera probably lived in deep, dark basins where water temperatures were cooler than near the surface and stratification was less intense than today (Kennett 1982). The gelatinous spermatophoric mass remains intact for a few days (Berry & Heydorn 1970) and year-round spawning with prolonged incubation were likely in the constant conditions at those depths.

It is conjectured that the larvae of the deep-water genera circulated at depth since their larvae and pueruli are very rare in epipelagic (<200 m) plankton collections. For the pueruli of the deeper-water genera, Kancirik (1980) states "The puerulus stages of deep water species such as *Palinurus delagoae* (180–400 m), *Puerulus angulatus* (300 m), and *Linuparus* spp. (300 m) are not reported in shallow inshore areas. Presumably, they settle out at the greater depths characteristic of the adults". This concept of settlement of pueruli over wide distances is supported by the further observations of Berry (1974) and Chan (1997) who recorded pueruli of deep-water genera well outside their adult grounds. To recruit successfully, the juveniles must have the capability to migrate in the right direction to the adult grounds or they would be lost to the next generation.

The genus *Palinurus* is considered to have emerged "part-way" along the evolutionary line of the Stridentes (Forster 1973; Baisre 1994). On the basis of its biological attributes, the following scenario can be proposed. The adults grow slowly, are long-lived (>20 years), mature late (Table 1), and

aggregate once a year for seasonal mating (Pollock & Augustyn 1982; Hunter 1999; Groeneveld 2000; Pollock et al. 2000). When the oocytes are fully mature, the females attract the males via a mating call (Hunter 1999) and they receive a short-lived spermatophoric mass (Berry & Heydorn 1970) that almost immediately releases sperm for fertilisation of the ripe eggs (Hunter 1999).

The egg size given in Table 1 is an inverse index of egg size calculated by dividing the number of eggs in the brood by the body weight in grams over a wide range of body sizes (Pollock 1995). These calculations assume a constant weight and a constant size of an egg throughout development but Silberbauer (1971) and Pollock & Augustyn (1982) showed that egg diameter does increase with development for *Jasus lalandii* and *Palinurus gilchristi* respectively and Vijayakumaran (1990) found that the average egg of *Panulirus h. homarus* was c. 35% lighter and 20% smaller in the early stage of incubation than in the late stage. In spite of these possible variations, the egg indices given for the genera in Table 1; 200 for *Palinurus*, 300–500 for *Sagmariasus/Jasus* and, except for *Panulirus guttatus*, 400–800 for *Panulirus*, show very significant differences. Species of *Palinurus* produce a relatively low number of large eggs (Pollock & Melville-Smith 1993; MacDiarmid & Kittaka 2000) and incubate the eggs on the pleopods for a long period of 5–9 months (Hunter 1999). The newly hatched phyllosoma are relatively large, have well-formed, multi-spinose appendages and pass rapidly through only 10 instars to the relatively small final stage (Berry 1974; Baisre 1994; Kittaka 2000). Larvae probably inhabit mesopelagic depths (200–1000 m) in totally dark or extremely low light levels for 5–12 months (Berry 1974; Hunter 1999). The heavy, weak-swimming puerulus (Hunter 1999) is little more than a convenient morphological intermediate “transfer” phase from the last pelagic larval stage to their seabed settlement site (Pollock & Melville-Smith 1993) at depths similar to or deeper than that of the adults.

The most recent Stridentes genus, *Panulirus*, lives in the well-lit subtropical and tropical shelf waters in habitats that have been subjected to major environmental changes by tectonic plate movements over the past 20–30 million years. Two major lineages have been recognised (Ptacek et al. 2001). The biological attributes of the cool subtropical zone species (most species of the First Major Lineage) reflect an initial movement by the more primitive species into the seasonally changing shallow environments. They have slower growing (>3–7

years to maturity, see Table 1) long-lived adults and mate seasonally but the spermatophoric mass can be long lasting because of its insoluble outer coating. Females produce one or two batches of eggs each season (Booth 1986; Gomez et al. 1994; Quackenbush 1994). The eggs are smaller than *Palinurus* (Pollock 1995), incubation time is short (1–4 months) (Soares & Calvacante 1985; Gomez et al. 1994; MacDiarmid & Kittaka 2000) and the small sized, first stage larvae pass through many (15–27) instars (Booth & Phillips 1994; Kittaka 2000) over a relatively long time of 6–12 months (Baisre 1994; Booth & Phillips 1994; Inoue & Sekiguchi 2001) to reach the relatively large final stage (Baisre 1994; Table 1). Early stage phyllosomata rise to the epipelagic waters of the shelf even though they are relatively weak swimmers. The mid stages are stronger vertical swimmers and are carried by the prevailing currents into the offshore oceanic waters. The late stages are more abundant closer to the coast and accumulate near the shelf break (Phillips & Sastry 1980). After metamorphosis, the fast-swimming pueruli cross the shelf (Phillips & McWilliam 1986) to settle in their particular habitat which is shallower than that of the adult.

The Second Major Lineage represents a further radiation of *Panulirus* into a variety of shallow habitats in the tropical zone and the much warmer conditions have resulted in faster-growing (c. 3 years to maturity), shorter-lived, multiple-spawning species (2–>4) (Berry 1971; Soares & Calvacante 1985; Skewes et al. 1997; M. Vijayakumaran pers. comm.) with a shortened larval life of 4–7 months (Baisre 1994; Booth & Phillips 1994; McWilliam 1995; Dennis et al. 2001; Table 1).

LIFE CYCLE OF SILENTES

For the early genera of Silentes, the biological data is even more scanty (Berry 1974; Webber & Booth 1988; Baez & Ruiz 2000) than for the early Stridentes. The general biology of *Palinurellus* is unknown but the following scenario for *Projasus* is proposed.

Projasus occurs in all the major oceans at depths of 175–880 m (Baez & Ruiz 2000) on ridges, seamounts, oceanic volcanic islands, and continental slopes (Parin et al. 1997). *Projasus* is considered to be very close to the ancestral Silentes stock that probably originated in the deep, calm waters of the southern Tethys Sea, perhaps in the southern Indo-Pacific region off the northern coast of Gondwana.

The oceanic circulation was weak (Kennett 1982), spawning was probably year-round or very prolonged, the larvae probably lived at depth, and the pueruli probably settled at depth somewhere near the adults, as they do today (Webber & Booth 1988; Baez & Ruiz 2000). Subsequent intensification of ocean current systems has resulted in two widely distributed species. *Projasus bahamondei* inhabits the south-east Pacific, off Chile and *Projasus parkeri* is widespread from the south-east Atlantic, through the Indian Ocean to south-east Australia and New Zealand (Parin et al. 1997). Based on records in the Western Australian Museum, *P. Parkeri* also occurs off south-west Australia from C. Naturaliste (500 m), through C. Riche (400 m) to Esperance (540 m) (D. Jones pers. comm.). Parin et al. proposed that *P. bahamondei* dispersed eastwards across a major Pacific Ocean barrier from its *P. parkeri* ancestor. Just what evolutionary changes in the life cycle morphology and behaviour of these widely distributed *Projasus* populations occurred, as a result of the intensification of the currents must await further discoveries.

The monotypic *Sagmariasus* has been elevated from a subgenus of *Jasus* to a full genus by Booth et al. (2002) and it is considered to be more primitive (Baisre 1994) and more fecund (Pollock 1997) than *Jasus*. It is the largest lobster in the family, also maturing at a large size and producing many small eggs "as strategies to boost egg production" (Pollock 1997). It may have lived in the subtropical region of the south-west Pacific in late Eocene and certainly in the Oligocene, as *Sagmariasus flemingi* (Glaessner 1969; George 1997). Each of the present two subpopulations of *Sagmariasus verreauxii* that live along the Australian and New Zealand east coasts have retained similar life histories despite their probable separation 10 million years ago (George 1997).

Seasonal regularity in both regions triggers a once-a-year spawning by females (Booth 1986) after a spring moulting and mating. Since the spermatophoric mass is probably short-lived, eggs are extruded synchronously and the sperm are used for almost immediate fertilisation. The small eggs (Pollock 1997) are incubated for 3 months in deeper water and the small larvae (Baisre 1994; Kittaka et al. 1997) hatch in summer with well-formed appendages except that the third maxilliped lacks an exopod until the final stages and an exopod bud does not develop on the fifth leg until the 4th instar of the 17 instar progression (McWilliam & Phillips 1987; Kittaka et al. 1997). During their 8–12 month pelagic life, the larvae may exhibit vertical migration to

control their direction of transport and are largely retained in the offshore eddies and gyres (Booth 1986). The pueruli swim strongly towards the coast, grasping onto seaweed as they settle along the coast well south of their natal region (Montgomery & Kittaka 1994). Because of this southern displacement, the subadults have evolved regular along-shore migrations up to 1700 km to recruit to the northern adult breeding grounds (Booth 1986). The very high fecundity probably evolved to counteract the high mortality loss of pueruli recruits since they have been carried far to the south of their optimal habitat, added to which are the predator risks associated with the long counter-current migrations to the adult grounds (Pollock 1997).

For *Jasus*, most is known about the *J. lalandii* clade. Males deposit a short-lived spermatophoric mass and the females immediately extrude the ripe eggs (MacDiarmid & Kittaka 2000). The females carry only one brood of small-sized eggs annually and after incubation for 3–6 months (Quackenbush 1994; Kittaka et al. 1997), the larvae begin a 9–22 month pelagic period (Roscoe 1979; Booth & Phillips 1994).

The behavioural attributes of the larvae of the continental species (*J. lalandii* clade) enable them to be retained in current systems that eventually concentrate the surviving late stages near the continental shelf break. For the South African *J. lalandii* and the New Zealand subpopulation of *Jasus edwardsii* (Booth 2000), larvae undergo stage-specific vertical migrations to c. 300 m depth but around Tasmania, Bruce et al. (1996) found "little evidence of a complicated, stage specific, pattern of vertical distribution. Larvae were primarily confined to the upper 100 m and were commonly at the surface, particularly at night." If this apparent lack of specific vertical movement by Tasmanian larvae is proven, it would support a conclusion that there are specific differences in each of the Australasian transport systems which assisted in the behavioural separation of the two subpopulations through larval evolution. The pueruli of both these continental species swim rapidly across the shelf to settle in shallow water (Booth 2001) and as subadults, they move to deeper water to join the adult stock. Counter-current movements by subadults of *Jasus* are limited and has only been demonstrated for *J. edwardsii* in the southern portion of its New Zealand range, where a small proportion migrate westwards around the Southland coast (Booth 1997).

Such limited movements by larvae and subadults may answer the question of how the southern

Australian subpopulation that stretches from Tasmania westwards across the Great Australian Bight to Cape Leeuwin is maintained. Perhaps the larvae are truly passive in the upper 100 m and simply rely on “random transport” and perhaps the pathways of the relatively weak currents (Bruce et al. 1996) are exceptionally reliable. This concept of reliable return near the point of origin might well be tenable if the complex tracks of the satellite-tracked drifters that remained within 500 km of the Tasmanian coast for 11–19 months, often returning to the point of release (Bruce et al. 1996), truly reflect the prime method of transport of the apparently passive larvae. Perhaps the larvae and pueruli in Tasmanian waters only need to respond weakly to the narrow temperature/salinity characteristics which clearly define the movements of the Subtropic Front (Bruce et al. 1996, fig. 34, 37–39) to effect their desired recruitment pathways via that water body.

For the species in the insular *Jasus frontalis* clade, egg size, incubation time and length of larval life are similar to the *J. lalandii* clade (Table 1) but little is known about their larval transport mechanisms. Their larval behaviour is more likely to be similar to that of the Australian subpopulation of *J. edwardsii* than to the other members of the *J. lalandii* clade since the local currents encompass isolated islands and/or seamounts and there are no wide continental shelves for the pueruli to swim across. The larvae and pueruli are probably passive and rely more on the strong island eddies and the seamount Taylor Columns for their local retention (George 1997).

EVOLUTION OF MIGRATION

Advantageous movements by palinurids pervade every phase in the life cycle and most movements are associated with the functions of feeding, sheltering, and reproduction. Herrnkind (1980) and Booth (1997) have given terms to the considerable variation in the benthic movement patterns by subadults and adults across the sea floor that may be associated with differing ecological and physiographic conditions. Here I expand their definitions and also consider the quite different transport methods that are used by the phyllosomata and pueruli during their pelagic and natant phases. An evolutionary approach is taken to assist in the evaluation of the importance of migrations at all phases in the life cycle during the evolutionary shifts

into the various shallower water habitats, particularly by *Panulirus*, *Sagmariasus*, and *Jasus*.

Migratory behaviour and adaptive movements

Light intensity appears to be extremely important in controlling the timing and direction of the various movements of palinurids (such as paddling, swimming, or walking) at each phase of their life. Many larvae respond to weak light values and migrate vertically as they paddle up and sink down diurnally; many pueruli swim horizontally near the surface and the benthic juveniles and adults walk along the bottom. The benthic phases mainly wander at night (nomadism) to forage for food or to seek new individual shelters as their life style changes with growth, particularly in the puerulus and early juvenile phases (Norman et al. 1994). Adults sometimes move seasonally for moulting and reproductive purposes or episodically to avoid short-term, adverse environmental conditions; they then return accurately to their original area (homing), often to the same den (Herrnkind 1980). Shelters of spiny lobsters usually consist of natural caves and crevices in firm, mostly rocky, substrates in contrast to the true lobsters that deliberately construct dens in soft substrates (Cooper & Unzmann 1980). Subadults of spiny lobsters may exhibit permanent, one-way movements (either onshore or offshore) from their settlement sites to the adult breeding areas, or longshore migrations against the current that had displaced their larvae downstream (contranant migration).

Very little is known about the cues for directional migration by spiny lobsters or indeed many invertebrates. However, for *Panulirus a. argus*, after geomagnetic manipulation and experimental displacement up to 30 km, juveniles “are capable of true navigation without relying on familiar surroundings, cues that emanate from the destination, or information collected during the outward journey” (Boles & Lohmann 2003). Boles & Lohmann concluded that the lobsters possess a magnetic map that allows them to “somehow derive sufficient positional information from the Earth’s magnetic field to determine the direction towards home”. How these displaced *P. a. argus* juveniles could acquire a geomagnetic map of an area they have only experienced as a first stage larvae remains a mystery. Biogenic magnetite has been suggested as a possible magnetoreceptor but the mechanism(s) remain mainly hypothetical (Alerstam 2003).

The following summary deals initially with some of the adaptive advantages of the various types of movements in the habitat shift to shallow water, first

presenting the life style of the shallow water coastal and shelf genera (*Panulirus*, *Sagmariasus*, and *Jasus*) and then the life style characteristics of the more ancestral outer shelf and deeper water genera.

Shallow-water genera

Phyllosoma phase

Like many other planktonic taxa, the larvae of spiny lobsters can move vertically in the water column and attain horizontal transport advantages by utilising the onshore and offshore currents and gyres that operate at those selected depths during their larval life. The directional offshore movement resulting from the behaviour of the early larvae is rapid and is gradually replaced by "circular retention" at deeper levels, in large eddies, mesoscale gyres, or oceanic currents. During the lengthy larval period of many months, each larval stage maintains a particular seasonal position within the dominant offshore current system, feeding on relatively soft-bodied zooplankters, such as fish larvae, cnidarians, salps, chaetognaths, and euphausiids (McWilliam & Phillips 1997) from which soft foods can be sucked by a pumping action (MacMillan et al. 1997).

The availability of these food types also varies seasonally and spatially within each current system and Cox & Johnston (2004) have described some of the digestive changes in the foregut that accompany larval growth. Cox & Johnston (2004) showed that the early larval stages of *S. verreauxi* possess simple digestive structures that are only equipped to deal with softer prey items like fish larvae and gelatinous zooplankton. However, the late larval stages develop a more complex filtering, sorting and mixing capacity that extends the range of diet to fleshier prey items like crustaceans. In their study of energy levels of phyllosoma and puerulus, McWilliam & Phillips (1997) concluded that, "For the late larval development and successful metamorphosis of *Panulirus cygnus*, the richest food resources seem to be located in the slope waters adjoining the shelf-break and the higher zooplankton and micronekton biomass found in this region may be related to the presence and strength of the Leeuwin Current."

Puerulus phase

The immediate post-larval pueruli can be strong horizontal swimmers, deliberately and directionally crossing the shelf. Some species settle very close to the adult grounds even though that may be on seamounts at 30 m depth (*Panulirus marginatus*, Polovina et al. 1995) or 45 m (*Jasus tristani*, Heydorn 1969). Those species live on steep volcanic

islands or banks and show limited movements thereafter because of depth limitations between suitable habitats, but other species like *P. cygnus* and *P. a. argus* settle in special shallow water habitats, and migrate offshore to the adult grounds. The successful survival of the non-feeding puerulus depends not only on its accumulated food reserves and its swimming prowess but also its ability to detect and settle in an area that provides individual protection, such as natural crevices or small-sized close-fitting holes that are often left in the solid substrate by dead borers such as pholad molluscs (Yoshimura & Yamakawa 1988; Jernakoff 1990; Norman et al. 1994). Booth (2001) concluded that "puerulus settlement of *Jasus edwardsii* is a process of active searching and habitat choice, at the small scale".

Juvenile phase

Short-distance movements of the fast-growing early post-puerulus are usually foraging forays in search of small food items such as tiny molluscs, worms, crustaceans, and epiphytes such as coralline algae. Following each moult and growth increment, the progressively larger juveniles must also search for and find larger, suitably-sized close-fitting holes or crevices for protection during these nomadic forays. Their survival also depends on the suitability of the environment to provide a range of shelter sizes as well as adequate food size, food quality and quantity. As the juveniles grow, they require larger-sized food items and must migrate to nearby suitable environmental grounds, eventually aggregating as two-year-olds (Kanciruk 1980) in large community dens. These deliberate movements are irreversible and have evolved to accommodate these dramatic changes in their requirements for particular feeding resources, physical habitats, and social characteristics.

Subadult phase

Most shallow water species emigrate from the juvenile habitat at or slightly before maturity (Kanciruk 1980). Only those individuals that deliberately march to the recognised breeding grounds can contribute genetically to the future cohorts of recruits. After an inshore moult, the adolescent "white" phase of *P. cygnus* migrates offshore and to the north-west, to join the adult stock. It is likely that such directional movements by the subadults also help to build up the reproductive stock in the northern regions and thus counteract the net southward transport of larvae (George 1958; Griffin et al. 2001).

If the local current systems consistently carry late stage larvae and pueruli beyond their natal grounds, subadults are naturally selected for their ability to emigrate and join the adult stock. Subadult *S. verreauxi* in both Australia and New Zealand migrate long distances to the north to reposition a recruitment stock upstream of the dominant south-flowing coastal currents which have carried the larvae far to the south of the acknowledged breeding grounds (Booth 1997; Phillips et al. 2000). Only small proportions of immature *J. edwardsii* migrate against the current, mainly in the Southland region (Booth 1997).

Sporadic adverse events associated with depleted oxygen levels along the south-west coast of South Africa force inshore movements of subadult *J. lalandii*, particularly of small females, and can result in devastating mass strandings (Cockcroft 2001).

Adult phase

Once the individuals have reached adulthood, migrations are quite short in distance and time (homing activities) and are associated with moulting in a more protected area, food gathering during nocturnal foraging, or finding a more environmentally comfortable position in another location when external conditions, such as winter storms and summer high temperatures (e.g., *P. a. argus* Herrnkind 1980) or oxygen depletion (e.g., *J. lalandii* Newman & Pollock 1974) force temporary emigration. The timing and extent of these migrations vary in each species and have been evolved in response to the particular characteristics of, and the seasonal changes in, the suite of environmental parameters that have controlled, and now determine its special habitat requirements.

Deeper-water genera

In some of the outer shelf and slope genera (*Puerulus* and *Palinurus*), their pueruli appear to settle downstream and/or in deeper water, i.e., well outside the preferred range of the adults (e.g., *Puerulus*, Berry 1974; Chan 1997) and the evolution of deliberate subsequent migrations by subadults to the adult grounds must be an obvious selective advantage. Compensatory migrations by subadults from deep to shallower water, as well as alongshore against the prevailing current, to the adult breeding grounds have also been evolved in *Palinurus gilchristi* and *P. delagoae* (Groeneveld 2002; Groeneveld & Branch 2002). In *Palinurus*, short-term offshore-onshore homing movements also facilitate successful individual participation in reproduction, particularly in the processes of mating, incubation, and larval release

(e.g., *P. elephas*, Hunter 1999 and *P. delagoae* Cockcroft et al. 1995; Groeneveld 2002).

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REFERENCES

- Alerstam, T. 2003: The lobster navigators. *Nature* 421: 27–28.
- Baez, P.; Ruiz, R. 2000: Puerulus y postpuerulus de *Projasus bahamondei* George 1976 (Crustacea Decapoda Palinuridae). *Investigaciones Marinas Valparaiso* 28: 15–26.
- Baisre, J. A. 1994: Phyllosoma larvae and the phylogeny of Palinuroidea (Crustacea; Decapoda): a review. *Australian Journal of Marine and Freshwater Research* 45: 925–944.
- Berry, P. F. 1971: The spiny lobsters (Palinuridae) of the coast of southern Africa: distribution and ecological notes. *South African Association for Marine Biological Research Report* 27: 1–23.
- Berry, P. F. 1973: The biology of the spiny lobster *Palinurus delagoae* Barnard, off the coast of Natal, South Africa. *Investigation Reports of the Oceanographic Research Institute of South Africa* 31: 1–27.
- Berry, P. F. 1974: Palinurid and scyllarid lobster larvae of the Natal coast, South Africa. *South African Association of Marine Biological Research, Investigation Report* 34: 1–44.
- Berry, P. F.; Heydorn, A. E. F. 1970: A comparison of the spermatophoric mass and mechanisms of fertilisation in South African spiny lobsters (Palinuridae). *Investigation Reports of the Oceanographic Research Institute of South Africa* 25: 1–18.
- Boles, L. C.; Lohmann, K. L. 2003: True navigation and magnetic maps in spiny lobsters. *Nature* 421: 60–63.
- Booth, J. D. 1986: Recruitment of packhorse rock lobster *Jasus verreauxii* in New Zealand. *Canadian Journal of Fisheries and Aquatic Sciences* 3: 2212–2220.
- Booth, J. D. 1997: Long-distance movements in *Jasus* spp. and their role in larval recruitment. *Bulletin of Marine Science* 61(1): 111–128.

- Booth, J. D. 2000: New Zealand's rock lobster fisheries. In: Phillips, B. F.; Kittaka, J. ed. Spiny lobsters: fisheries and culture. 2nd ed. London, Fishing News Books. Pp. 78–89.
- Booth, J. D. 2001: Habitat preferences and behaviour of newly settled *Jasus edwardsii* (Palinuridae). *Marine and Freshwater Research* 52(8): 1055–1066.
- Booth, J. D.; Phillips, B. F. 1994: Early life history of spiny lobster. *Crustaceana* 66(3): 271–294.
- Booth, J. D.; Webber, R.; Kittaka, J.; Ovenden, J. 2002: *Jasus (Sagmariasus) verreauxi* has a name change. *Lobster Newsletter* 15(1): 17–18.
- Briones-Forzan, P.; Lozano-Alvarez, E. 2000: The spiny lobster fisheries in Mexico. In: Phillips, B. F.; Kittaka, J. ed. Spiny lobsters: fisheries and culture. 2nd ed. London, Fishing News Books. Pp. 169–199.
- Bruce, B.; Bradford, R.; Griffin, D.; Gardner, C.; Young, J. 1996: A synthesis of existing data on larval rock lobster distribution in southern Australia. *Fisheries Research and Development Corporation Report 96/107*: 1–57.
- Chan, T. Y. 1997: Crustacea Decapoda: Palinuridae, Scyllaridae and Nephropsidae collected in Indonesia by the Karubar cruise, with an identification key for the species of *Metanephrops*. *Resultats des Campagne Musorstom* 16: 410–430.
- Chubb, C. F. 2000: Reproductive biology: issues for management. In: Phillips, B. F.; Kittaka, J. ed. Spiny lobsters: fisheries and culture. 2nd ed. London, Fishing News Books. Pp. 245–275.
- Cockroft, A. C. 2001: *Jasus lalandii* 'walkouts' or mass strandings in South Africa during the 1990s: an overview. *Marine and Freshwater Research* 52(8): 1085–1094.
- Cockroft, A. C.; Groeneveld, J. C.; Cruywagen, G. C. 1995: The influence of depth, latitude and width of the continental slope on the size distribution and availability of spiny lobster *Palinurus delagoae* off the east coast of South Africa. *South African Journal of Marine Science* 16: 149–160.
- Cooper, R. A.; Unzmann, J. R. 1980: Ecology of juvenile and adult *Homarus*. In: Phillips, B. F.; Kittaka, J. ed. Spiny lobsters: fisheries and culture. 2nd ed. London, Fishing News Books. Pp. 349–408.
- Cox, S. L.; Johnston, D. L. 2004: Developmental changes in foregut functioning of packhorse lobster *Jasus (Sagmariasus) verreauxi* (Decapoda: Palinuridae) phyllosoma larvae. *Marine and Freshwater Research* 55: 145–153.
- Davie, P. J. F. 1990: A new genus and species of marine crayfish, *Palibythus magnificus*, and new records of *Palinurellus* (Decapoda: Palinuridae) from the Pacific Ocean. *Invertebrate Taxonomy* 4: 685–695.
- Dennis, D. M.; Pitcher, C. R.; Skewes, T. D. 2001: Distribution and transport pathways of *Panulirus ornatus* (Fabricius, 1776) and *Panulirus* spp. larvae in the Coral Sea, Australia. *Marine and Freshwater Research* 52: 1175–1185.
- Feldmann, R. M.; Tshudy, D. M. 1989: Evolutionary patterns in macrurus decapod crustaceans from Cretaceous to early Cenozoic rocks of the James Ross Island region, Antarctica. In: Crame, J. D. ed. Origins and evolution of the Antarctic biota. *Geological Society Special Publication No. 47*: 183–195.
- Forster, R. 1973: Untersuchungen an oberjurassischen Palinuridae (Crustacea, Decapoda) *Mitterlungen Bayerische Staatsammlung für Palaeontologie und historische Geologie* 13: 31–46.
- George, R. W. 1958: The status of the white crayfish in Western Australia. *Australian Journal of Marine and Freshwater Research* 9: 573–585.
- George, R. W. 1997: Tectonic plate movements and the evolution of *Jasus* and *Panulirus* spiny lobsters (Palinuridae). *Marine and Freshwater Research* 48: 1121–1130.
- George, R. W.; Main, A. R. 1967: The evolution of spiny lobsters (Palinuridae): a study of evolution in the marine environment. *Evolution* 21: 803–820.
- Glaessner, M. F. 1969: Decapoda. In: Moore, R. ed. Treatise on invertebrate palaeontology. Part R, Arthropoda. Pp. 217–340.
- Gomez, E. D.; Juinio, M. A. R.; Bermas, N. A. 1994: Reproduction of *Panulirus longipes longipes* in Calatagan, Batangas, Philippines. *Crustaceana* 67(1): 110–120.
- Griffin, D. A.; Wilkin, J. L.; Chubb, C. F.; Pearce, A. F.; Caputi, N. 2001: Ocean currents and the larval phase of Australian western rock lobster, *Panulirus cygnus*. *Marine and Freshwater Research* 52: 1187–1199.
- Groeneveld, J. C. 1997: Growth of the spiny lobster *Palinurus gilchristi* (Decapoda: Palinuridae) off South Africa. *South African Journal of Marine Science* 18: 19–29.
- Groeneveld, J. C. 2000: Stock assessment, ecology and economics as criteria for choosing between trap and trawl fisheries for spiny lobster *Palinurus delagoae*. *Fisheries Research* 48: 141–155.
- Groeneveld, J. C. 2002: Long-distance migration of the rock lobster *Palinurus delagoae* off South Africa and Mozambique. *South African Journal of Marine Science* 24: 395–400.
- Groeneveld, J. C.; Branch, G. M. 2002: Long-distance migration of South African deep-water rock lobster *Palinurus gilchristi*. *Marine Ecological Progress Series* 232: 225–238.

- Groeneveld, J. C.; Rossouw, G. J. 1995: Breeding period and size in the South Coast rock lobster, *Palinurus gilchristi* (Decapoda: Palinuridae). *South African Journal of Marine Science* 15: 17–23.
- Herrnkind, W. F. 1980: Spiny lobsters: patterns of movement. In: Phillips, B. F.; Kittaka, J. ed. Spiny lobsters: fisheries and culture. 2nd ed. London, Fishing News Books. Pp. 349–407.
- Heydorn, A. E. F. 1969: The south Atlantic rock lobster *Jasus tristani* at Vema Seamount, Gough Island and Tristan da Cunha. *Investigational Report, South African Division of Sea Fisheries* 73: 1–20.
- Hunter, E. 1999: Biology of the European spiny lobster, *Palinurus elephas* (Fabricius, 1787) (Decapoda, Palinuridae). *Crustaceana* 72: 545–565.
- Inoue, N.; Sekiguchi, H. 2001: Distribution of late-stage larvae of *Panulirus japonicus* in the Kuroshio subgyre. *Marine and Freshwater Research* 52: 1201–1209.
- Jernakoff, P. 1990: Distribution of newly settled western rock lobster *Panulirus cygnus*. *Marine Ecological Progress Series* 66: 63–74.
- Kagwade, P. V. 1988a: Reproduction in the spiny lobster *Panulirus polyphagus* (Herbst). *Journal of the Biological Association of India* 30: 37–46.
- Kagwade, P. V. 1988b: Fecundity in the spiny lobster *Panulirus polyphagus* (Herbst). *Journal of the Biological Association of India* 30: 114–120.
- Kanciruk, P. 1980: Ecology of juvenile and adult Palinuridae (Spiny lobsters). In: Phillips, B. F.; Kittaka, J. ed. Spiny lobsters: fisheries and culture. 2nd ed. London, Fishing News Books. Pp. 59–96.
- Kennett, J. P. 1982: Marine geology. Edgewood Cliffs, NJ, Prentice-Hall.
- Kittaka, J. 2000: Culture of spiny lobsters. In: Phillips, B. F.; Kittaka, J. ed. Spiny lobsters: fisheries and culture. 2nd ed. London, Fishing News Books. Pp. 508–532.
- Kittaka J.; Ono, K.; Booth, J. D. 1997: Complete development of the green rock lobster *Jasus verreauxi* from egg to juvenile. *Bulletin of Marine Science* 61(1): 57–71.
- Losado-Tosteson, V.; Posado, J. M.; Losado, F. 2001: Size and reproductive status of fished spotted spiny lobster, *Panulirus guttatus* in Morrocoy National Park, Venezuela: a preliminary report. *Marine and Freshwater Research* 52: 1599–1603.
- MacDiarmid, A. B. 1988: Experimental confirmation of external fertilisation in the southern temperate rock lobster *Jasus edwardsii* (Hutton) (Decapoda:Palinuridae). *Journal of Experimental Marine Biology and Ecology* 120: 277–285.
- MacDiarmid, A. B.; Kittaka, J. 2000: Breeding. In: Phillips, B. F.; Kittaka, J. ed. Spiny lobsters: fisheries and culture. 2nd ed. London, Fishing News Books. Pp. 485–507.
- MacMillan, D. L.; Sandow, S. L.; Wickley, D. M.; Frisher, S. 1997: Feeding activity and the morphology of the digestive tract in stage–1 phyllosoma larvae of the rock lobster *Jasus edwardsii*. *Marine and Freshwater Research* 48: 19–26.
- McWilliam, P. S. 1995: Evolution in the phyllosoma and puerulus phases of the spiny lobster genus *Panulirus* White. *Journal of Crustacean Biology* 15: 542–557.
- McWilliam, P. S.; Phillips, B. F. 1987: Distinguishing the phyllosoma larvae of rock lobster species of the genus *Jasus* (Decapoda, Palinuridae) in the waters of Australia and New Zealand. *Crustaceana* 52(1): 1–24.
- McWilliam, P. S.; Phillips, B. F. 1997: Metamorphosis of the final phyllosoma and secondary lecithotrophy in the puerulus of *Panulirus cygnus* George: a review. *Marine and Freshwater Research* 48: 783–790.
- Minagawa, M. 1997: Reproductive cycle and size-dependent spawning of female spiny lobsters (*Panulirus japonicus*) off Oshima Island, Tokio, Japan. *Marine and Freshwater Research* 48: 869–874.
- Montgomery, S. S.; Kittaka, J. 1994: Occurrence of pueruli of *Jasus verreauxi* (H. Milne-Edwards, 1851) (Decapoda, Palinuridae) in waters off Cronulla, New South Wales, Australia. *Crustaceana* 67(1): 65–70.
- Newman, G. G.; Pollock, D. E. 1974: A mass stranding of rock lobsters *Jasus lalandii* at Elands Bay, South Africa. *Crustaceana* 26: 1–4.
- Norman, C. P.; Yamakawa, H.; Yoshimura, T. 1994: Habitat selection, growth rate and density of juvenile *Panulirus japonicus* (Von Siebold, 1824) (Decapoda, Palinuridae) at Banda, Chiba Prefecture, Japan. *Crustaceana* 66(3): 366–383.
- Patek, S. N.; Oakley, T. H. 2003: Comparative tests of evolutionary trade-offs in a palinurid lobster acoustic system. *Evolution* 57(9): 2082–2100.
- Phillips, B. F.; McWilliam, P. S. 1986: The pelagic phase of spiny lobster development. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 2153–2163
- Phillips, B. F.; Sastry, A. N. 1980: Larval ecology. In: Phillips, B. F.; Kittaka, J. ed. Spiny lobsters: fisheries and culture. 2nd ed. London, Fishing News Books. Pp. 11–57.
- Phillips, B. F.; Chubb, C. F.; Melville-Smith, R. 2000: The status of Australia's rock lobster fisheries. In: Phillips, B. F.; Kittaka, J. ed. Spiny lobsters: fisheries and culture. 2nd ed. London, Fishing News Books. Pp. 45–77.

- Plaut, I. 1993: Sexual maturity, reproductive season and fecundity of the spiny lobster *Panulirus penicillatus* from the Gulf of Eilat (Aqaba), Red Sea. *Australian Journal of Marine and Freshwater Research* 44: 527–535.
- Pollock, D. E. 1986: Review of the fishery for and biology of the cape rock lobster *Jasus lalandii* with notes on larval recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 2107–2117.
- Pollock, D. E. 1995: Evolution of life history patterns in three genera of spiny lobsters. *Bulletin of Marine Science* 57(2): 516–526.
- Pollock, D. E. 1997: Egg production and life history strategies in some clawed and spiny lobster populations. *Bulletin of Marine Science* 61(1): 97–110.
- Pollock, D. E.; Augustyn, C. J. 1982: Biology of the rock lobster *Palinurus gilchristi* with notes on the South African fishery. *Fisheries Bulletin of South Africa* 16: 57–73.
- Pollock, D. E.; Goosen, P. C. 1991: Reproductive dynamics of two *Jasus* species in the south Atlantic region. *South African Journal of Marine Science* 10: 141–147.
- Pollock, D. E.; Melville-Smith, R. 1993: Decapod life histories and reproductive dynamics in relation to oceanography off southern Africa. *South African Journal of Marine Science* 13: 205–212.
- Pollock, D. E.; Cockroft, A. C.; Groeneveld, J. C.; Schoeman, D. S. 2000: The commercial fisheries for *Jasus* and *Palinurus* species in south-east Atlantic and south-west Indian oceans. In: Phillips, B. F.; Kittaka, J. ed. *Spiny lobsters: fisheries and culture*. 2nd ed. London, Fishing News Books. Pp. 105–120.
- Polovina, J. J.; Haight, W. R.; Moffit, R. B.; Parrish, F. A. 1995: The role of benthic habitat, oceanography and fishing on the population dynamics of the spiny lobster, *Panulirus marginatus* (Decapoda, Palinuridae) in the Hawaiian Archipelago. *Crustaceana* 68(2): 203–212.
- Ptacek, M. B.; Sarver, S. K.; Childress, M. J.; Herrnkind, W. F. 2001: Molecular phylogeny of the spiny lobster genus *Panulirus* (Decapoda: Palinuridae). *Marine and Freshwater Research* 52: 1037–1048.
- Quackenbush, L. S. 1994: Lobster reproduction: a review. *Crustaceana* 67(1): 82–94.
- Roscoe, M. J. 1979: Biology and exploitation of the rock lobster *Jasus tristani* at the Tristan da Cunha Islands, South Atlantic, 1949–1976. *Investigational Report, South African Division of Sea Fisheries* 118: 1–47.
- Serfling, S. A.; Ford, R. A. 1975: Ecological studies of the puerulus larval stage of the California spiny lobster, *Panulirus interruptus*. *Fishery Bulletin* 73(2): 360–377.
- Silberbauer, B. I. 1971: The biology of the South African rock lobster *Jasus lalandii* (H. Milne-Edwards) 1. Development. *Investigational Report, South African Division of Sea Fisheries* 92: 1–90.
- Silberman, J. D.; Sarver, S. K.; Walsh, P. J. 1994: Mitochondrial DNA variation in seasonal cohorts of spiny lobster (*Panulirus argus*) postlarvae. *Molecular Marine Biology and Biotechnology* 3(3): 165–170.
- Skewes, T. D.; Dennis, D. M.; Pitcher, C. R.; Long, B. G. 1997: Age structure of *Panulirus ornatus* in two habitats in Torres Strait, Australia. *Marine and Freshwater Research* 48: 745–750.
- Soares, C. N. C.; Cavalcante, P. P. L. 1985: Caribbean spiny lobster (*Panulirus argus*) and smoothtail spiny lobster (*Panulirus laevicauda*) reproductive dynamics on the Brazilian northeastern coast. *Food and Agriculture Organisation of the United Nations Fisheries Report No. 327*. Supplement. Pp. 200–217.
- Vijayakumaran, M. 1990: Energetics of a few marine crustaceans. Unpublished PhD thesis, Cochin University of Science and Technology, Kochi, India. 138 p.
- Webber, W. R.; Booth, J. D. 1988: *Projasus parkeri* (Stebbing, 1902) (Decapoda, Palinuridae) in New Zealand and description of a *Projasus* puerulus from Australia. *National Museum of New Zealand Records* 3: 81–92.
- Yoshimura, T.; Yamakawa, H. 1988: Microhabitat and behaviour of settled pueruli and juveniles of the Japanese spiny lobster *Panulirus japonicus* at Kominato, Japan. *Journal of Crustacean Biology* 8: 524–531.