

---

CSIRO PUBLISHING

---

# Marine & Freshwater Research

Volume 48, 1997  
© CSIRO Australia 1997

A journal for the publication of original contributions  
in physical oceanography, marine chemistry,  
marine and estuarine biology and limnology

**[www.publish.csiro.au/journals/mfr](http://www.publish.csiro.au/journals/mfr)**

All enquiries and manuscripts should be directed to

*Marine and Freshwater Research*

**CSIRO PUBLISHING**

PO Box 1139 (150 Oxford St)

Collingwood

Vic. 3066

Australia

Telephone: 61 3 9662 7618

Facsimile: 61 3 9662 7611

Email: [ann.grant@publish.csiro.au](mailto:ann.grant@publish.csiro.au)



Published by **CSIRO PUBLISHING**  
for CSIRO Australia and  
the Australian Academy of Science



## Recruitment strategies in lobsters and crabs: a comparison

J. Stanley Cobb<sup>AC</sup>, John D. Booth<sup>B</sup> and Michael Clancy<sup>A</sup>

<sup>A</sup>Department of Biological Sciences, University of Rhode Island, Kingston RI 02881, USA

<sup>B</sup>National Institute of Water and Atmospheric Research, PO Box 14-901, Wellington, New Zealand

<sup>C</sup>email: scobb@uriacc.uri.edu

**Abstract.** Early life-history characteristics that affect recruitment in spiny lobsters, clawed lobsters and crabs of the genus *Cancer* are reviewed. Spiny lobsters have many small eggs, a short period of parental care, and a long larval life that terminates in a swimming postlarva. *Cancer* species also have many small eggs, but have a longer period carrying eggs and a short larval life. Clawed lobsters have smaller clutches than the other two groups, long parental care and a short larval period. A cluster analysis on these and other characters in the 16 species considered shows that phylogeny dominates the clustering, because species of the same family group together. Within families, however, some possible environmental effects are seen. Spiny lobsters and *Cancer* crabs, with greater fecundity and presumably lower larval survival, may be predicted to have greater recruitment variability than clawed lobsters. The limited data available suggest that this is true.

### Introduction

This paper concerns factors affecting recruitment strength in several species of large decapod. Lobsters, and crabs of the genus *Cancer*, are important benthic omnivores in many temperate to tropical seas. The species abundant in shallower waters are usually heavily fished and closely regulated. The need for biological knowledge on which to base management decisions has prompted the collection of life-history information critical to understanding recruitment (the addition of new individuals) in these species, thereby providing an opportunity to compare recruitment tactics across families and among species.

Populations change size through four fundamental processes: births, deaths, immigration, and emigration. The first two are local processes whereas the others operate on a larger geographic scale, linking local populations through movement of benthic stages or larval dispersal. Early models of population dynamics often assumed that immigration and emigration were inconsequential, and larval dispersal was often not even considered. However, in lobsters and crabs, as in most marine species, the dispersive larval stage must be taken into account when considering population change for several reasons: larval dispersal may sever the link between reproductive success of adults and subsequent local population size; the magnitude of larval dispersal does not necessarily depend on local conditions; and dispersal is a consequence, at least in part, of hydrodynamic transport processes, not just of local population strength (Gaines and Lafferty 1995). Attempts to describe the dynamics of larval recruitment range from the modelling approach of fisheries biologists (Fogarty *et al.* 1991) to mechanistic studies of recruitment (Roughgarden *et al.* 1988; Katz *et al.* 1994).

Recruitment variability in marine animals with complex life cycles is strongly influenced during early life history by phenotypic traits and by stochastic environmental processes. The phenotypic traits are largely a consequence of adaptations to the environment and are exhibited through different levels of fecundity, different mechanisms for delivery of larvae, settlement in appropriate habitats, and different levels of post-settlement mortality. These adaptations, taken together, form recruitment strategies for dealing with variable environments. Recruitment strategies are shaped by constraints, and by trade-offs between phenotypic traits such as clutch size and ovum size on the one hand, and age at reproduction and longevity on the other. Life-history traits are, therefore, fundamental to population dynamics and hence important to evolutionary ecologists and fishery managers (Winemiller and Rose 1992). An understanding of the trade-offs helps us to formulate hypotheses about life-history strategies and may help us to understand how populations respond to fishing pressure. Many such traits have been studied in marine species, particularly in commercially valuable species. The relatively large amount of data now available may permit a comparative and evolutionary approach to understanding recruitment strategies. We take an adaptationist approach (*sensu* Harvey and Pagel 1991) and assume that the recruitment strategies of these decapods evolved largely as a result of the impact of different environments on growth, survival and fertility within phylogenetic constraints of body size and form, length of life and larval type. The decapod species examined here are similar in body size, they are iteroparous and they brood their eggs. They have pelagic, planktotrophic larvae and a dramatic metamorphosis at the end of the larval period followed by a postlarval stage that

makes the transition to the benthic habitat. These similarities in life history, present among phylogenetically separate taxa, permit a closer focus on other characteristics of the life history that are important to recruitment.

Pollock (1991, 1995) took a similarly comparative approach when attempting to understand the evolution of certain reproductive traits in lobsters. For spiny lobsters, Pollock (1995) suggested that a shift from deep to shallow-water habitats is correlated with greater protection of sperm, either by a hardened sperm packet or by internal fertilization, and with increased egg production. The selective forces driving these adaptations may be higher mortality and greater environmental variability in the shallower waters. For a clawed lobster, a freshwater crayfish and the spiny lobster genus *Jasus*, Pollock (1991) suggested that the important selective force was habitat limitation in nursery areas which led to density-dependent mortality and growth. It also led to differences in size at maturity due to density-dependent effects on juvenile moult increments. The present paper widens Pollock's approach by exploring reasons for, and consequences of, different recruitment strategies to species in three groups of large decapod occupying similar shallow-water niches: the Nephropidae, the Palinuridae and the Cancridae.

### Phylogeny and species considered

According to Holthuis (1991) for clawed and spiny lobsters and Rathbun (1930) for cancrid crabs, the family Nephropidae are part of Infraorder Astacidea (freshwater crayfishes and marine clawed lobsters), family Palinuridae are in Infraorder Palinura (which includes spiny, slipper and coral lobsters), and family Cancridae are among Infraorder Brachyura (true crabs). The Decapoda probably began to diversify in the Permian, about 250 million years ago. Schram's (1982) phylogenetic reconstruction suggests that the Palinura and the Astacidea separated from the ancestral stock at about that time. The Brachyura appear to have closer affiliations with the Palinura than they do with the Astacidea, as the Brachyura arose from the Palinura about 150 million years ago. The Astacidea may have closer affinities with Penaeidea (shrimps and prawns) than with other Macrura Reptantia, and probably have been a separate line since the Permian.

Forty-three species in 10 genera of clawed lobster occur on rock and mud substrata to depths of 3000 m in temperate to tropical seas (Holthuis 1991). Of these, only those in subfamily Nephropinae (five genera) found at depths of less than about 500 m are taken in any quantity. *Homarus americanus*, *H. gammarus* and *Nephrops norvegicus* are by far the most important commercially, and have the most information. The *Homarus* spp. are biologically very similar, and only *H. americanus* is considered here.

The nine genera of spiny lobster (Palinuridae) contain 48 species, the majority of which live in shallow water

(<100 m: Davie 1990; Holthuis 1991). Some of these species support major fisheries in temperate to tropical seas, where many are also important recreationally and traditionally. Most is known about the major commercial, shallow-water species, particularly *Panulirus* and *Jasus* spp.; of these we refer primarily to *P. argus*, *P. cygnus*, *P. homarus*, *P. penicillatus*, *J. edwardsii*, *J. lalandii* and *J. verreauxi*.

*Cancer* contains 23 extant species, most of which are found in the Pacific Ocean (Nations 1979). The commercially important species include *C. magister* in the north-east Pacific and *C. pagurus* in the north-east Atlantic. We also consider the north-west Atlantic species *C. borealis* and *C. irroratus*, as well as others from the north-east Pacific, *C. antennarius*, *C. anthonyi*, *C. gracilis*, *C. oregonensis* and *C. productus*.

### Review and comparison

Here and in Table 1 we review aspects of the reproductive biology for each group then we compare, using cluster analysis, recruitment strategies among the groups.

#### Reproductive biology

Lobsters and crabs exhibit a variety of maturity schedules depending mainly on water temperature and latitude. Female *Homarus* mature between 55 mm and 110 mm carapace length (CL), at 5–9 years of age (Fogarty 1995; Waddy *et al.* 1995). *N. norvegicus* is smaller and so is the range of female size (18–32 mm CL) and age (2–3 years) at maturity (Sarda 1995). Warm-water spiny lobsters are younger (2–4 years) and smaller (40–75 mm CL) at maturity than cool-water species (5–7 years and 55–110 mm CL) (Chubb 1994; Kittaka and MacDiarmid 1994). Similarly, *Cancer* females mature earlier and at smaller sizes in warm than in cool waters. There is wide variation in size (10–130 mm carapace width (CW)), but less in age (1–3 years), at first reproduction (Shields 1991).

The number of eggs carried by the female varies with locality, egg size and body size. *Homarus* and *Nephrops* have much larger eggs (1.4–1.5 mm diameter) than do spiny lobsters (0.6–0.8 mm) or *Cancer* crabs (0.3–0.4 mm). Clutch size is smallest in the clawed lobsters (300–100 000: Estrella and Cadrin 1995; Sarda 1995), typically is 100 000–1 000 000 in the spiny lobsters, and is very high in most of the *Cancer* crabs (up to 3 000 000). Life-time fecundity is a function of clutch size and number of broods. The clawed lobsters spawn annually or every second year, spiny lobsters carry one (temperate species) to several (tropical species) clutches per year, and most *Cancer* crabs produce only one clutch per year (although *C. anthonyi* and *C. productus* may produce 3–4 broods per season) (Knudsen 1964; Shields 1991; Shields *et al.* 1991). Among these groups, the large, long-lived and fecund lobsters of the

**Table 1. Comparison of reproductive and early life-history characteristics among clawed lobsters, spiny lobsters, and *Cancer* crabs**

When more than one value was available, a value was chosen from near the centre of the geographic range of the species or, where appropriate, the median value. No. broods per lifetime (generally unknown) estimated (marked by ?) from longevity, age at maturity, and no. spawnings per year. Female size is carapace width (mm) for *Cancer* and carapace length (mm CL) for the others. Female maximum size taken from  $L_{\infty}$  of the von Bertalanffy equation. Female size at maturity is size at which 50% bear eggs. Pelagic period includes the pelagic postlarval (PL), puerulus or megalopal period. PL size is total length for both lobster groups and CL for *Cancer*. Characteristics in bold are those used in the cluster analysis

Species	Female maximum size (mm)	Female age at maturity (years)	Female size at maturity (mm)	Min. clutch size $\times 10^3$	Max. clutch size $\times 10^3$	Broods per year	Broods per life	Egg diameter (mm)	PL size (length, mm)	PL/egg ratio	Brood period (months)	Pelagic period (months)	Brood/pelagic ratio
<i>Homarus americanus</i>	240 <sup>1</sup>	5 <sup>2</sup>	90 <sup>1</sup>	5 <sup>1,36</sup>	100 <sup>1</sup>	0.5 <sup>2</sup>	15?	1.5 <sup>3</sup>	15 <sup>4</sup>	10	11 <sup>2</sup>	1 <sup>5</sup>	11
<i>Nephrops norvegicus</i>	60 <sup>8</sup>	2 <sup>9</sup>	24 <sup>9</sup>	0.3 <sup>8</sup>	3 <sup>8</sup>	1 <sup>8</sup>	10?	1.4 <sup>6</sup>	16 <sup>7</sup>	11.4	9 <sup>8</sup>	1 <sup>6</sup>	9
<i>Panulirus argus</i>	160 <sup>11</sup>	<4 <sup>16</sup>	75 <sup>12,13</sup>	160 <sup>13,14</sup>	1,630 <sup>13,14</sup>	2 <sup>15</sup>	≥20?	~0.6 <sup>16</sup>	15 <sup>17</sup>	25	1.5 <sup>13,15</sup>	6.5 <sup>23</sup>	0.2
<i>P. cygnus</i>	143 <sup>19</sup>	5 <sup>20</sup>	70 <sup>15,20</sup>	116 <sup>21</sup>	682 <sup>21</sup>	1 <sup>20</sup>	≥20?	~0.6 <sup>22</sup>	17 <sup>17</sup>	28.3	1.5 <sup>20</sup>	10 <sup>23</sup>	0.2
<i>P. homarus</i>	145 <sup>49</sup>	<3 <sup>49</sup>	43 <sup>49</sup>	100 <sup>50</sup>	900 <sup>50</sup>	2 <sup>15,49</sup>	≥30?	0.6 <sup>50</sup>	17 <sup>17</sup>	28.3	1.5 <sup>15,50</sup>	5 <sup>23</sup>	0.3
<i>P. penicillatus</i>	139 <sup>51,52</sup>	<3 <sup>52</sup>	69 <sup>52</sup>	150 <sup>52</sup>	575 <sup>52</sup>	2 <sup>15,52</sup>	≥30?	0.6 <sup>52</sup>	17 <sup>17</sup>	28.3	1 <sup>15,34</sup>	7.5 <sup>23</sup>	0.1
<i>Jasus edwardsii</i>	180 <sup>24</sup>	7 <sup>53</sup>	80 <sup>25</sup>	38 <sup>18,24</sup>	540 <sup>18,24</sup>	1 <sup>25</sup>	≥20?	0.8 <sup>24</sup>	25 <sup>26</sup>	31.3	3.5 <sup>27</sup>	18 <sup>23</sup>	0.2
<i>J. lalandii</i>	120 <sup>31</sup>	5 <sup>32</sup>	65 <sup>24</sup>	33 <sup>24</sup>	490 <sup>24</sup>	1 <sup>32</sup>	≥20?	0.8 <sup>24</sup>	25 <sup>33</sup>	31.3	4 <sup>34</sup>	15 <sup>23</sup>	0.3
<i>J. verreauxi</i>	240 <sup>28</sup>	<7 <sup>53</sup>	160 <sup>28</sup>	387 <sup>24</sup>	2,040 <sup>24</sup>	1 <sup>28</sup>	≥20?	0.6 <sup>24</sup>	25 <sup>29</sup>	41.7	3 <sup>30</sup>	10 <sup>23</sup>	0.3
<i>Cancer magister</i>	182 <sup>35</sup>	2 <sup>35</sup>	90 <sup>35</sup>	659 <sup>42</sup>	1,342 <sup>42</sup>	1.5 <sup>43</sup>	8 <sup>39</sup>	0.442 <sup>42</sup>	10.2 <sup>35</sup>	23.1	3.5 <sup>35</sup>	4 <sup>48</sup>	0.9
<i>C. gracilis</i>	106 <sup>35</sup>	2 <sup>35</sup>	54 <sup>35</sup>	189 <sup>42</sup>	789 <sup>42</sup>	1.5 <sup>43</sup>	4 <sup>39</sup>	0.329 <sup>42</sup>	2.8 <sup>35, 40</sup>	8.5	3 <sup>35</sup>	1 <sup>48</sup>	1.5
<i>C. productus</i>	167 <sup>35</sup>	2 <sup>35</sup>	70 <sup>35</sup>	559 <sup>42</sup>	1,036 <sup>42</sup>	1.5 <sup>43</sup>	6 <sup>39</sup>	0.367 <sup>42</sup>	4.0 <sup>35</sup>	10.9	4 <sup>35</sup>	1 <sup>48</sup>	1.3
<i>C. oregonensis</i>	47 <sup>35</sup>	1 <sup>35</sup>	10 <sup>35</sup>	0.78 <sup>42</sup>	82.5 <sup>42</sup>	1.5 <sup>43</sup>	12 <sup>39</sup>	0.383 <sup>42</sup>	4.2 <sup>35</sup>	10.9	3.5 <sup>35</sup>	1.5 <sup>48</sup>	2.3
<i>C. antennarius</i>	150 <sup>37</sup>	2 <sup>37</sup>	73 <sup>37</sup>	199 <sup>42</sup>	3,004 <sup>42</sup>	1.5 <sup>43</sup>	10 <sup>39</sup>	0.333 <sup>42</sup>	2.7 <sup>35</sup>	8.1	2 <sup>41</sup>	1 <sup>41</sup>	2
<i>C. anthonyi</i>	153 <sup>39</sup>	3.5 <sup>39</sup>	89 <sup>46</sup>	680 <sup>42</sup>	3,849 <sup>42</sup>	2.5 <sup>43</sup>	12 <sup>39</sup>	0.311 <sup>42</sup>	2.2 <sup>35</sup>	7.1	1.5 <sup>39</sup>	1 <sup>46</sup>	1.5
<i>C. pagurus</i>	242 <sup>10</sup>	3 <sup>10,44</sup>	133 <sup>10</sup>	606 <sup>42</sup>	3,000 <sup>10</sup>	2 <sup>43</sup>	9 <sup>39</sup>	0.396 <sup>42</sup>	3.3 <sup>35</sup>	8.3	8 <sup>10</sup>	2 <sup>10</sup>	4
<i>C. irroratus</i>	106 <sup>47</sup>	1 <sup>39</sup>	15 <sup>47</sup>	102 <sup>42</sup>	356 <sup>42</sup>	1 <sup>43</sup>	8 <sup>43</sup>	0.406 <sup>42</sup>	2.5 <sup>35</sup>	6.2	6 <sup>38</sup>	1 <sup>38</sup>	6
<i>C. borealis</i>	135 <sup>45</sup>	3 <sup>45</sup>	89 <sup>43,45</sup>	311 <sup>42</sup>	1,045 <sup>42</sup>	1 <sup>43</sup>	5 <sup>39</sup>	0.428 <sup>42</sup>	2.1 <sup>35</sup>	4.9	6 <sup>38</sup>	2 <sup>38</sup>	3

<sup>1</sup>Fogarty (1995); <sup>2</sup>Waddy *et al.* (1995); <sup>3</sup>Herrick (1909); <sup>4</sup>Hadley (1906); <sup>5</sup>Ennis (1995); <sup>6</sup>Farmer (1975); <sup>7</sup>Santucci (1926); <sup>8</sup>Chapman (1980); <sup>9</sup>Sarda (1995); <sup>10</sup>Bennett (1995); <sup>11</sup>Olsen *et al.* (1975); <sup>12</sup>Warner *et al.* (1977); <sup>13</sup>Baisre and Cruz (1994); <sup>14</sup>Cruz (1980); <sup>15</sup>Chubb (1994); <sup>16</sup>Butler, M., pers. comm.; <sup>17</sup>Booth and Kittaka (1994); <sup>18</sup>Annala and Bycroft (1987); <sup>19</sup>Brown and Barker (1984); <sup>20</sup>Chittlborough (1976); <sup>21</sup>Morgan (1972); <sup>22</sup>Chubb, C., pers. comm.; <sup>23</sup>Booth and Phillips (1994); <sup>24</sup>Annala (1991); <sup>25</sup>Annala *et al.* (1980); <sup>26</sup>Booth (1979); <sup>27</sup>MacDiarmid (1989); <sup>28</sup>Booth (1984); <sup>29</sup>Montgomery and Kittaka (1994); <sup>30</sup>Booth (1986); <sup>31</sup>Heydorn (1969a); <sup>32</sup>Pollock (1986); <sup>33</sup>Kittaka (1988); <sup>34</sup>Kittaka and MacDiarmid (1994); <sup>35</sup>Orensanz and Gallucci (1988); <sup>36</sup>Estrella and Cadrin (1995); <sup>37</sup>Carroll (1982); <sup>38</sup>Sastry and McCarthy (1973); <sup>39</sup>Shields *et al.* (1991); <sup>40</sup>Ally (1975); <sup>41</sup>Roesijadi (1976); <sup>42</sup>Hines 1991; <sup>43</sup>Shields (1991); <sup>44</sup>Brown and Bennett (1980); <sup>45</sup>Wenner *et al.* (1992); <sup>46</sup>Anderson and Ford (1976); <sup>47</sup>Clancy (1995); <sup>48</sup>Sulkin and McKeen (1994); <sup>49</sup>Heydorn (1969b); <sup>50</sup>Berry (1971); <sup>51</sup>Plaut and Fishelson (1991); <sup>52</sup>MacDonald (1979); <sup>53</sup>NIWA unpubl. data.

temperate genus *Jasus* may have the greatest potential life-time fecundity. Long-lived temperate clawed lobsters (*Homarus*) have smaller clutches, but also have a high potential life-time fecundity because of the many spawnings possible. Unlike lobsters, it appears that most, and perhaps all, *Cancer* spp. have a terminal moult that limits the potential number of spawnings (Reilly and Saila 1978; Orensanz and Galluci 1988).

#### *Larvae and postlarvae*

Larval form is quite different among the three groups. The leaf-like phyllosoma larva of spiny lobsters is nearly transparent and is difficult to see in the water in contrast to the more heavily pigmented and solid nephropid mysis larva. Spiny lobster phyllosomata may reach large size (50 mm or more) after their many months in the plankton. Clawed lobster mysis larvae, the product of large eggs, start large and, along with spiny lobsters, have among the largest postlarvae in the Crustacea. In contrast, the zoea larvae of most *Cancer* species hatch at a small size and do not grow large. Within *Cancer*, the ratio of size increase from egg diameter to postlarval total length varies widely, from 5 to 23. The two species of clawed lobsters have ratios of 10–11, slightly larger than most of, but in the same range as, the ratios for *Cancer*. The values are highest for spiny lobsters, but they are also variable between species (25–42).

Clawed lobsters have three larval stages, which swim weakly and can control vertical position (Ennis 1986). Whereas *Homarus* larvae are generally found near the surface, *Nephrops* larvae are most abundant at 20–150 m (Nichols and Lovewell 1987). The larvae of both genera show some diel vertical migration (reviewed in Cobb and Wahle 1994). The larval period in *Homarus* and *Nephrops* lasts 3–7 weeks depending on water temperature (Cobb and Wahle 1994; Bennett 1995) so dispersion distances are relatively limited. Spiny lobster phyllosomata progress through 6–12 morphological stages, with at least as many instars, taking 5–24 months depending on species and temperature. The larvae hatch on the continental shelf, rise to the surface, and then migrate vertically between the surface at night and deeper waters during the day as they are carried offshore, presumably in the wind-driven surface layer (Rimmer 1980). In those species studied, mid- and late-stage larvae are found 10s to 100s of kilometres from their probable point of origin, and very seldom over the continental shelf. Phyllosoma larvae, unlike the larvae of clawed lobsters or crabs, may be able to moult repeatedly without changing stage ('mark-time moulting', Gore 1985), which could lead to greatly extended larval life in food-poor oceanic gyres (Pollock 1995). The zoea larvae of *Cancer* progress through five stages over 1–4 months. We expect larval advection to be less extensive than in spiny lobsters but similar to that in clawed lobsters because of this length

of the larval life. There is considerable variability both in the depth distribution and in distance of advection of larval *Cancer*, with *C. magister* probably advecting the furthest (Nichols and Thompson 1988; Jamieson *et al.* 1989; Hobbs and Botsford 1992; McConnaughey *et al.* 1992, 1994; Clancy 1995). *Cancer magister* and *C. oregonensis* megalopae are the dominant organisms in samples taken at night several hundred kilometres from shore, but other species that are sympatric as adults, such as *C. productus*, are rare in those same samples (Jamieson *et al.* 1989). *Cancer productus* larvae spend approximately 3 months in the plankton whereas *C. magister* and *C. oregonensis* spend 4 and 1.5 months in the plankton respectively, so spawning time, female behaviour, or larval behaviour must differ among these three species to account for the difference in planktonic abundance patterns (Jamieson *et al.* 1989).

In all groups, the end of the larval period is marked by a dramatic metamorphosis to a postlarva which appears similar to the adult in many ways. Unlike many other groups with larval stages (e.g. insects or anurans) in which habitat transition occurs at the same time as metamorphosis, metamorphosis and settlement are decoupled in these crustaceans. In clawed lobsters, timing of metamorphosis (and thus the duration of the larval period) appears to be controlled largely by the action of water temperature and nutrition on the term of three otherwise fixed larval stages. In spiny lobsters, the larval period is more variable, with metamorphosis apparently taking place near the edge of the continental shelf (Booth and Phillips 1994), suggesting that an environmental cue may be the trigger. Pollock (1990, 1992) hypothesized that the cues for metamorphosis are chemical and physical and differ according to 'home' environments.

An important difference between spiny lobsters and the other two groups, and a crucial subject for research, is the possibility that phyllosoma larvae can delay metamorphosis until conditions are suitable (Kanciruk 1980; Pollock and Melville-Smith 1993; Baisre 1994). This ability could, in combination with mark-time moulting, lead to a highly variable larval period.

The postlarva swims strongly enough to allow long-distance movement in all three groups. In *H. americanus*, the postlarva swims approximately nine body lengths per second (Rooney and Cobb 1991; Ennis 1995). In southern New England (USA), northerly oriented swimming combined with wind-driven circulation may allow individuals hatched  $\geq 100$  km offshore to reach inshore areas (Cobb *et al.* 1989; Katz *et al.* 1994). The pueruli of spiny lobsters can swim about  $9 \text{ cm s}^{-1}$  (see Booth and Phillips 1994). Because they have seldom been taken seaward of the continental slope in plankton sampling, it appears that pueruli do not disperse randomly after metamorphosis but move shoreward, suggesting an ability to navigate. The cues for orientation are

not known. Directed, rapid swimming has been observed in megalopae of two species of *Cancer*, but the orientation of swimming (towards the sun at all times of day) did not seem likely to provide shoreward transport (Shanks 1995).

#### *Pelagic–benthic transition*

*Homarus* postlarvae settle to the bottom in the mid to late postlarval period (Herrick 1909; Cobb *et al.* 1989; Incze and Wahle 1991). Negative phototaxis, downward swimming and passive sinking are all involved, with no apparent correlation with the lunar cycle. The postlarvae of *Homarus* and *Nephrops* are quite specific in their choice of substratum. *Homarus* postlarvae settle primarily in cobble (Botero and Atema 1982; Hudon 1987; Wahle and Steneck 1991), with the odour of predators possibly affecting timing and choice of location (Boudreau *et al.* 1993a, 1993b). *Nephrops* postlarvae appear to require the same fine mud as adults, and may even be found in the burrows of adults (Chapman 1980).

The pueruli of spiny lobsters settle in a range of habitats including algal clumps, seagrass beds, crevices, holes and indentations (reviewed in Herrnkind *et al.* 1994; Phillips and Booth 1994). Significant settlement by at least some species takes place to depths of at least 50 m and up to several kilometres from shore. Puerulus settlement is not uniform along coasts; wide variation within and between sites in levels of monthly and annual settlement is common and settlement is usually seasonal (*see* Booth and Phillips 1994). Pueruli settle mainly at night or near dawn, and in some *Panulirus* spp. pueruli settle near the time of the new moon. Environmental factors, from local wind-driven currents and intermittent cross-shelf circulation to much larger-scale El Niño–Southern Oscillation (ENSO) events, can affect strength of settlement (MacDonald 1986; Pearce and Phillips 1988; Polovina and Mitchum 1992).

*Cancer* megalopae settle in a wide variety of habitats — shell habitats to featureless sand or mud substrata (Winn 1985; Clancy 1995; Eggleston and Armstrong 1995) — and with no apparent link with ENSO events (Hobbs and Botsford 1992). In at least *C. magister*, settlement and year-class strength in the fishery varies inversely with alongshore transport, suggesting strong pelagic–benthic coupling (McConnaughey *et al.* 1992, 1994). *C. magister* megalopae swim directionally and are highly selective at settlement, with habitat-specific behaviours enhancing juvenile survival (Fernandez *et al.* 1993, 1994; Eggleston and Armstrong 1995). Clancy (1995) presented evidence for pelagic–benthic coupling of *C. irroratus*, although on much shorter (hours to days) time-scales than for *C. magister*. Megalopae and juveniles of *C. irroratus* were uniformly distributed across habitats in laboratory tanks and field settings, suggesting a lack of the habitat-specific behaviours that are found in congeners (Clancy 1995). There appears to be a similar absence of habitat selection by *C. antennarius* megalopae, whereas *C. anthonyi* prefers sand (Winn 1985). Habitat choice

at settlement appears, therefore, to be more variable in *Cancer* than in either lobster group, perhaps because *Cancer* megalopae and juveniles are more efficient in their use of a variety of benthic habitats, especially featureless sediments such as sand.

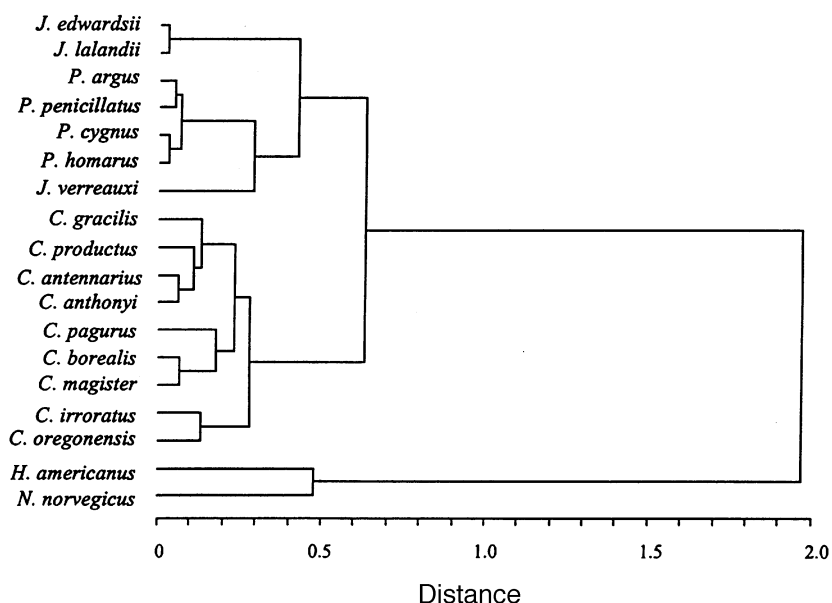
#### *Cluster analysis*

To determine if recruitment tactics exhibited by the three groups of decapods show similarities that might help us to understand the selective forces shaping them, a cluster analysis was performed on the variables indicated in Table 1. This used the unweighted pair-group method with arithmetic averages (UPGMA) in which the Euclidean distance between two clusters is calculated as the average distance between pairs of observations for different species (Krebs 1989; Anon. 1990). The resulting dendrogram is shown in Fig. 1.

Phylogeny clearly dominates the clustering. At the family level, clawed lobster species group together, as do the spiny lobster species and the *Cancer* species, suggesting that phylogenetic constraints on the characters used in this analysis are significant and outweigh the effects of recent history in different environments. The two clawed lobster genera cluster together at a position well removed from the other two groups because of the greatly different egg and brood sizes. This matches the phylogeny suggested by Schram (1982) in which the Palinura and the Brachyura have closer affinities with each other than with the Nephropidae.

All *Panulirus* spp. clustered together, but were joined by *J. verreauxi*. *Jasus* has seven species, six of them in the ‘*lalandii*’ group. *J. verreauxi*, the most warm-water species, is the only member of an apparently ancestral group (Holthuis 1991, Baisre 1994) which is distinguished from the other *Jasus* species by having, among other features, larger broods, smaller eggs, shorter incubation period and a shorter larval life.

Within *Cancer*, *C. gracilis*, *C. antennarius* and *C. anthonyi* clustered. These three occur at the southern end of the north-east Pacific range, have several broods per year and have the smallest eggs. *Cancer irroratus* and *C. borealis*, with largely overlapping distributions throughout much of their ranges in the north-west Atlantic (and sympatric with *H. americanus*), do not cluster together (nor with *H. americanus*), probably because of differences in size at maturity and clutch size. Also, *C. borealis* is found in deeper water than *C. irroratus*, and hatches eggs later in the year (Wenner *et al.* 1992). On the other hand, *C. oregonensis* and *C. irroratus*, found on opposite sides of North America, group together, probably because of the shared characteristics of small size at maturity and relatively high number of broods per life-time; they also have among the largest eggs. Within the *Cancer* group, except for the *gracilis*–*antennarius*–*anthonyi* subcluster, there appears not



**Fig. 1.** Dendrogram resulting from the cluster analysis on the life-history characteristics of three groups of decapod identified in Table 1.

to be the correlation between grouping and geographic location that might have been expected if recruitment strategies depended largely on environmental constraints.

### Discussion

Classification of species as *r*-selected or *K*-selected (Pianka 1970) is a useful initial approach to understanding life-history strategies. Along the *r*-*K* continuum, the *Cancer* spp. are clearly *r*-strategists (having high potential for population increase), clawed lobsters are closer to a *K* strategy (where potential for population increase is more modest and more closely related to the carrying capacity of the environment), and spiny lobsters lie somewhere between. These classifications are relative, since even the least fecund lobster we considered, *Nephrops*, with multiple clutches of up to 3000 eggs each, is difficult to regard as *K*-selected when compared with species that produce only 10s to 100s of offspring. Others have suggested triangular continua that have three end-points, such as *r*-*K*-adversity resistant (Southwood 1977) or opportunistic-periodic-equilibrium (Winemiller and Rose 1992). Southwood (1997) argued that habitats, especially the way they vary temporally and spatially, are critical to a life-history strategy. In the present analysis, sympatric species did not deal with the environment (i.e. by having different recruitment tactics) in the same manner, especially the spiny lobsters and *Cancer* (Fig. 1). In the continuum of Winemiller and Rose (1992) above, all the species we considered would be considered periodic strategists since, among the crustaceans, they are large, highly fecund, and long-lived.

Fecundity is a major contributor to fitness. The number of offspring can be increased by having a greater number of broods per lifetime, by increasing the number of eggs per brood, or both. There are trade-offs and constraints in each case. An increase in the number of broods per lifetime achieved by early maturity may be balanced by smaller adult body size and increased vulnerability to predators after maturity. An increase in the number of eggs per brood (without an increase in body size) must result in smaller eggs and larvae. Smaller larvae, in turn, may require longer in the plankton to reach settling size, and may experience increased predation (Werner 1986; but *see* Hart 1995). All lobsters and brachyuran crabs brood their eggs, and this involves another trade-off, that between incubation time and time in the plankton. A longer incubation period may mean lower mobility and feeding rates for the adult, and a longer time in the plankton again increases vulnerability to predation and increases risk of advective loss. There are several possible ways to confront mortality in the plankton: (a) a short planktonic period; (b) a larger size, achieved either by rapid growth from small eggs or by starting at a large size from large eggs; (c) morphological or behavioural adaptations (e.g. spines or migration); or (d) production of many eggs. A strategy for confronting planktonic mortality is subject to environmental constraints. A major environmental constraint is likely to be productivity of the sea: species whose larvae live in temperate coastal waters encounter a relatively food-rich environment, whereas for tropical oceanic species the food is likely to be more sparse. Faster growth can be expected in better nutritional

environments. Another important environmental factor is the pattern of the wind-driven and geostrophic currents that determine delivery of larvae to suitable settlement habitat and thus constrain the potential larval duration.

We can summarize the strategies as follows. Clawed lobsters, found in temperate coastal waters, have three larval instars and a relatively short larval period. Because of their short planktonic duration, larvae remain in coastal waters, where both productivity and predation risk is high. Delivery to settlement areas depends on local conditions such as winds and fronts as well as on larval and postlarval behaviour. Clawed lobsters invest heavily in each ovum by producing relatively few large eggs, brooding them for a long period, and producing large, short-lived larvae. Spiny lobsters, particularly those in the tropics and subtropics, have many and variable numbers of larval instars and a long larval period. The clear waters of the pelagic oceanic environment have low productivity, but the density of predators is also likely to be lower. Delivery to settlement areas depends on large-scale oceanic circulation as well as behaviour of the phyllosoma and puerulus. The strategy adopted by tropical spiny lobsters is to invest in many relatively small eggs, brood them for a short time, and produce many small larvae which remain pelagic for a long time while growing large. *Cancer* crabs are similar to clawed lobsters in their temperate distribution, few and fixed number of instars, and presence in waters of high productivity and high predation risk. The phylogenetic constraint of few larval stages limits the duration in the plankton, generally confining zoeae to near the coast. As in clawed lobsters, delivery to appropriate settlement habitat is due to coastal advective processes and larval and megalopal behaviour. The early life-history strategy is quite different from that of clawed lobsters, however: *Cancer*, with a shorter life span, invests in fewer broods of many, tiny eggs, broods them for an intermediate period, and produces many small larvae which remain pelagic for a short time (relative to spiny lobsters); larvae never attain the final size of larvae of spiny or clawed lobsters and thus remain vulnerable to a larger suite of predators.

The differing strategies of the three groups lead to testable predictions as suggested by Fogarty *et al.* (1991). We might predict, for instance, that clawed lobsters would have the lowest loss to predation and advection during the relatively short larval period, leading to relatively low recruitment variability measured at the time of settlement. In spiny lobsters we might expect relatively low proportional losses to predation during the long larval period, high losses to advection, and higher recruitment variability. *Cancer*, with a coastal distribution and larval period intermediate in length between clawed and spiny lobsters, might experience higher losses to predation than the other two groups while advective losses might be equal to or greater than those for

clawed lobsters. Recruitment variability in *Cancer* is likely to be equal to or higher than that in spiny lobsters.

We have no good data on predation or advective loss during the larval period, but there are some data on settlement variability. In a six-year record the abundance of recently settled *C. magister* varied by a factor of 45 — a high level of variability (McConnaughey *et al.* 1994, 1995). Similarly, *Panulirus cygnus* settlement in Western Australia from 1969 to 1996 varied greatly, from 15 to nearly 300 pueruli per collector, a factor of 20 (C. Chubb, B. F. Phillips, personal communication). For *J. edwardsii* in New Zealand, annual levels of pueruli and early juveniles on collectors between 1980 and 1996 varied by factors of 5 at Castlepoint to 80 in Kaikoura (Booth 1994, and unpublished); similar variability has been seen in the settlement levels of this species in southern Australia (R. Kennedy, J. Prescott, personal communication). Six years of settlement data for *P. argus* on collectors in the Caribbean varied by a factor of only 3 (Briones-Fourzán 1994), but the numbers of animals taken were much lower. *Homarus* settlement showed densities in Maine (USA) between 1989 and 1996 to range from 0.4 to 1.7 recently-settled juveniles m<sup>-2</sup>, a factor of 4 (Incze *et al.* 1997). These data provide support, albeit weak, to the prediction that recruitment variability is higher among the species with higher fecundity, smaller eggs and longer larval life.

### Acknowledgments

Our thanks to two referees who suggested improvements to earlier drafts of this manuscript. J.S.C. and M.C. thank the Rhode Island Sea Grant Program and the URI/NOAA Cooperative Marine Education and Research Program for support of their research.

### References

- Ally, J. R. R. (1975). A description of the laboratory-reared larvae of *Cancer gracilis* Dana, 1852 (Decapoda, Brachyura). *Crustaceana* **28**, 231–46.
- Anderson, W. R., and Ford, R. F. (1976). Early development, growth and survival of the yellow crab *Cancer anthonyi* Rathbun (Decapoda, Brachyura) in the laboratory. *Aquaculture* **7**, 267–79.
- Annala, J. H. (1991). Factors influencing fecundity and population egg production of *Jasus* species. In 'Crustacean Egg Production'. (Eds A. Wenner and A. Kuris.) pp. 301–15. (A. A. Balkema: Rotterdam.)
- Annala, J. H., and Bycroft, B. L. (1987). Fecundity of the New Zealand rock lobster, *Jasus edwardsii*. *New Zealand Journal of Marine and Freshwater Research* **21**, 591–7.
- Annala, J. H., McKoy, J. L., Booth, J. D., and Pike, R. B. (1980). Size at the onset of sexual maturity in female *Jasus edwardsii* (Decapoda: Palinuridae) in New Zealand. *New Zealand Journal of Marine and Freshwater Research* **14**, 217–27.
- Anon. (1990). SAS/STAT User's Guide. Version 6. 4th Edn. (SAS Institute: Cary, NC.)
- Baisre, J. A. (1994). Phyllosoma larvae and the phylogeny of Palinuroidea (Crustacea : Decapoda): a review. *Australian Journal of Marine and Freshwater Research* **45**, 925–44.



- Baisre, J. A., and Cruz, R.** (1994). The Cuban spiny lobster fishery. In 'Spiny Lobster Management'. (Eds B. F. Phillips, J. S. Cobb and J. Kittaka.) pp. 119–32. (Blackwell Scientific: Cambridge.)
- Bennett, D. B.** (1995). Factors in the life history of the edible crab (*Cancer pagurus* L.) that influence modelling and management. *International Council for the Exploration of the Sea Marine Science Symposia* **199**, 89–98.
- Berry, P. F.** (1971). The biology of the spiny lobster *Panulirus homarus* (Linnaeus) off the east coast of southern Africa. Oceanographic Research Institute Investigational Report No. 28.
- Booth, J. D.** (1979). Settlement of the rock lobster, *Jasus edwardsii* (Decapoda : Palinuridae), at Castlepoint, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **13**, 395–406.
- Booth, J. D.** (1984). Size at onset of breeding in female *Jasus verreauxi* (Decapoda : Palinuridae) in New Zealand. *New Zealand Journal of Marine and Freshwater Research* **18**, 159–69.
- Booth, J. D.** (1986). Recruitment of packhorse rock lobster *Jasus verreauxi* in New Zealand. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 2212–20.
- Booth, J. D.** (1994). *Jasus edwardsii* larval recruitment off the east coast of New Zealand *Crustaceana* **66**, 295–317.
- Booth, J. D., and Kittaka, J.** (1994). Growout of juvenile spiny lobster. In 'Spiny Lobster Management'. (Eds B. F. Phillips, J. S. Cobb and J. Kittaka.) pp. 424–45. (Blackwell Scientific: Oxford.)
- Booth, J. D., and Phillips, B. F.** (1994). Early life history of spiny lobster. *Crustaceana* **66**, 271–94.
- Botero, L., and Atema, J.** (1982). Behavior and substrate selection during larval settling in the lobster *Homarus americanus*. *Journal of Crustacean Biology* **2**, 59–69.
- Boudreau, B., Bourget, E., and Simard, Y.** (1993a). Behavioural responses of competent lobster postlarvae to odor plumes. *Marine Biology* **117**, 63–9.
- Boudreau, B., Bourget, E., and Simard, Y.** (1993b). Effect of age, injury, and predator odors on settlement and shelter selection by lobster *Homarus americanus* postlarvae. *Marine Ecology Progress Series* **93**, 119–29.
- Briones-Fourzán, P.** (1994). Variability in postlarval recruitment of the spiny lobster *Panulirus argus* (Latreille, 1804) to the Mexican Caribbean coast. *Crustaceana* **66**, 326–40.
- Brown, R. S., and Barker, E. H.** (1984). The Western rock lobster fishery 1977–1978. Department of Fisheries and Wildlife Western Australia Report No. 64.
- Brown, C. G., and Bennett, D. B.** (1980). Population and catch structure of the edible crab (*Cancer pagurus*) in the English Channel. *Journal du Conseil. Conseil International pour l'Exploration de la Mer* **39**, 88–100.
- Carroll, J. C.** (1982). Seasonal abundance, size composition, and growth of rock crab, *Cancer antennarius* Stimpson, off central California. *Journal of Crustacean Biology* **2**, 549–61.
- Chapman, C. J.** (1980). Ecology of juvenile and adult *Nephrops*. In 'The Biology and Management of Lobsters'. (Eds J. S. Cobb and B. F. Phillips.) pp. 143–78, Vol.2. (Academic Press: New York.)
- Chittleborough, R. G.** (1976). Breeding of *Panulirus longipes cygnus* George under natural and controlled conditions. *Australian Journal of Marine and Freshwater Research* **27**, 499–516.
- Chubb, C. F.** (1994). Reproductive biology: issues for management. In 'Spiny Lobster Management'. (Eds B. F. Phillips, J. S. Cobb and J. Kittaka.) pp. 181–212. (Blackwell Scientific: Oxford.)
- Clancy, M.** (1995). Recruitment of the rock crab, *Cancer irroratus*. Ph.D. Thesis, University of Rhode Island.
- Cobb, J. S., and Wahle, R. A.** (1994). Early life history and recruitment processes of clawed lobsters. *Crustaceana* **67**, 1–25.
- Cobb, J. S., Wang, D., Campbell, D. B., and Rooney, P.** (1989). Speed and direction of swimming by postlarvae of the American lobster. *Transactions of the American Fisheries Society* **118**, 82–6.
- Cruz, R.** (1980). Fecundidad y madurez sexual en la langosta comercial *Panulirus argus* (Latreille, 1804) (Crustacea : Palinuridae) en Cuba. *Revista Cubana de Investigaciones Pesqueras* **5**, 1–27.
- 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**, 685–95.
- Eggleston, D. B., and Armstrong, D. A.** (1995). Pre- and post-settlement determinants of estuarine Dungeness crab recruitment. *Ecological Monographs* **65**, 193–216.
- Ennis, G. P.** (1986). Swimming ability of larval American lobsters, *Homarus americanus*, in flowing water. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 2177–83.
- Ennis, G. P.** (1995). Larval and postlarval ecology. In 'Biology of the Lobster *Homarus americanus*'. (Ed. J. Factor.) pp. 23–46. (Academic Press: San Diego.)
- Estrella, B. T., and Cadrin, S. X.** (1995). Fecundity of the American lobster (*Homarus americanus*) in Massachusetts coastal waters. *International Council for the Exploration of the Sea Marine Science Symposia* **199**, 61–72.
- Farmer, A. S. D.** (1975). Synopsis of biological data on the Norway lobster *Nephrops norvegicus* Linnaeus, 1758). FAO Fisheries Synopsis No. 112.
- Fernandez, M., Iribarne, O., and Armstrong, D.** (1993). Habitat selection by young-of-the-year Dungeness crab *Cancer magister* and predation risk in intertidal habitats. *Marine Ecology Progress Series* **92**, 171–7.
- Fernandez, M., Iribarne, O., and Armstrong, D.** (1994). Ecdysial rhythms in megalopae and first instars of the Dungeness crab *Cancer magister*. *Marine Biology* **118**, 611–5.
- Fogarty, M. J.** (1995). Populations, fisheries and management. In 'Biology of the Lobster *Homarus americanus*'. (Ed. J. Factor.) pp. 111–38. (Academic Press: San Diego.)
- Fogarty, M. J., Sissenwine, M. P., and Cohen, E. B.** (1991). Recruitment variability and the dynamics of exploited marine populations. *Trends in Ecological Evolution* **6**, 241–6.
- Gaines, S. D., and Lafferty, K. D.** (1995). Modeling the dynamics of marine species: the importance of incorporating larval dispersal. In 'Ecology of Marine Invertebrate Larvae'. (Ed. L. McEdward.) pp. 389–412. (CRC Press: Boca Raton.)
- Gore, R. H.** (1985). Molting and growth in decapod larvae. In 'Crustacean Issues 2'. (Ed. F. R. Schram.) (A. A. Balkema: Rotterdam.) 66 pp.
- Hadley, P. B.** (1906). Regarding the rate of growth of the American lobster (*Homarus americanus*). *Annual Report of the Rhode Island Commissioner of Inland Fisheries* **36**, 153–235.
- Hart, M. W.** (1995). What are the costs of small egg size for a marine invertebrate with feeding planktonic larvae? *The American Naturalist* **146**, 415–26.
- Harvey, P. H., and Pagel, M. D.** (1991). 'The Comparative Method in Evolutionary Ecology.' (Oxford University Press: Oxford.)
- Herrick, F. H.** (1909). Natural history of the American lobster. *Bulletin of Bureau of Fisheries (US)* **29**, 149–408.
- Herrnkind, W. F., Jernakoff, P., and Butler, M. J.** (1994). Puerulus and post-puerulus ecology. In 'Spiny Lobster Management'. (Eds B. F. Phillips, J. S. Cobb and J. Kittaka.) pp. 213–29. (Blackwell Scientific: Oxford.)
- Heydorn, A. E. F.** (1969a). The rock lobster of the South African west coast *Jasus lalandii* (H. Milne-Edwards) 2. Population studies, behaviour, reproduction, moulting, growth and migration. Division of Sea Fisheries Investigational Report No. 71. (Republic of South Africa Department of Industries.)

- Heydorn, A. E. F. (1969b). Notes on the biology of *Panulirus homarus* and on length/weight relationships of *Jasus lalandii*. Division of Sea Fisheries Investigational Report No. 69. (Republic of South Africa Department of Industries.)
- Hines, A. H. (1991). Fecundity and reproductive output in nine species of *Cancer* crabs (Crustacea, Brachyura, Cancridae). *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 265–75.
- Hobbs, R. C., and Botsford, L. W. (1992). Influence of hydrographic conditions and wind forcing on the distribution and abundance of Dungeness crab, *Cancer magister*, larvae. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 1379–88.
- Holthuis, L. B. (1991). Marine lobsters of the world. FAO Fisheries Synopsis No. 125 FIR/S125 Vol. 13. 292 pp.
- Hudon, C. (1987). Ecology and growth of postlarval and juvenile lobster, *Homarus americanus*, off Iles de la Madeleine (Quebec). *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 1855–69.
- Incze, L. S., and Wahle, R. A. (1991). Recruitment from pelagic to early benthic phase in lobsters (*Homarus americanus*). *Marine Ecology Progress Series* **79**, 77–87.
- Incze, L. S., Wahle, R. A., and Cobb, J. S. (1997). Quantitative relationships between postlarval production and benthic recruitment in lobsters, *Homarus americanus*. *Marine and Freshwater Research* **48**, 729–43.
- Jamieson, G. S., Phillips, A. C., and Huggett, W. S. (1989). Effects of ocean variability on the abundance of Dungeness crab (*Cancer magister*) megalopae. *Canadian Special Publication Fisheries and Aquatic Sciences* **108**, 305–25.
- Kanciruk, P. (1980). Ecology of juvenile and adult Palinuridae (spiny lobsters). In 'The Biology and Management of Lobsters'. (Eds J. S. Cobb and B. F. Phillips.) pp. 59–96, Vol. 2. (Academic Press: New York.)
- Katz, C. H., Cobb, J. S., and Spaulding, M. (1994). Larval behavior, hydrodynamic transport, and potential offshore-to-inshore recruitment in the American lobster *Homarus americanus*. *Marine Ecology Progress Series* **103**, 265–73.
- Kittaka, J. (1988). Culture of the palinurid *Jasus lalandii* from egg stage to puerulus. *Nippon Suisan Gakkaishi* **54**, 87–93.
- Kittaka, J., and MacDiarmid, A. B. (1994). Breeding. In 'Spiny Lobster Management'. (Eds B. F. Phillips, J. S. Cobb and J. Kittaka.) pp. 384–401. (Blackwell Scientific: Oxford.)
- Knudsen, J. W. (1964). Observations of the reproductive cycles and ecology of the common Brachyura and crablike Anomura of Puget Sound, Washington. *Pacific Science* **18**, 3–33.
- Krebs, C. J. (1989). 'Ecological Methodology'. (Harper and Row: New York.)
- MacDiarmid, A. B. (1989). Moulting and reproduction of the spiny lobster *Jasus edwardsii* (Decapoda : Palinuridae) in northern New Zealand. *Marine Biology* **103**, 303–10.
- MacDonald, C. D. (1979). Final report to the Western Pacific Regional Fishery Management Council on management aspects of the biology of the spiny lobsters, *Panulirus marginatus*, *P. penicillatus*, *P. versicolor* and *P. longipes femoristriga* in Hawaii and the western Pacific. Contract No. WP-78–204.
- MacDonald, C. D. (1986). Recruitment of the puerulus of the spiny lobster, *Panulirus marginatus*, in Hawaii. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 2118–25.
- McConnaughey, R. A., Armstrong, D. A., Hickey, B. M., and Gunderson, D. R. (1992). Juvenile Dungeness crab (*Cancer magister*) recruitment variability and oceanic transport during the pelagic larval phase. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2028–44.
- McConnaughey, R. A., Armstrong, D. A., Hickey, B. M., and Gunderson, D. R. (1994). Interannual variability in coastal Washington Dungeness crab (*Cancer magister*) populations: larval advection and the coastal landing strip. *Fisheries Oceanography* **3**, 22–38.
- McConnaughey, R. A., Armstrong, D. A., and Hickey, B. M. (1995). Dungeness crab (*Cancer magister*) recruitment variability and Ekman transport of larvae. *International Council for the Exploration of the Sea Marine Science Symposia* **199**, 167–74.
- Montgomery, S. S., and 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**, 65–70.
- Morgan, G. R. (1972). Fecundity in the western rock lobster *Panulirus longipes cygnus* (George) (Crustacea : Decapoda : Palinuridae). *Australian Journal of Marine and Freshwater Research* **23**, 133–41.
- Nations, D. (1979). The genus *Cancer* and its distribution in time and space. *Bulletin of the Biological Society of Washington* **3**, 153–87.
- Nichols, J. H., and Lovewell, S. J. (1987). Lobster larvae (*Homarus gammarus* L.) investigations in Bridlington Bay. Can quantitative sampling be confined to the neuston layer? *Journal of Natural History* **21**, 825–41.
- Nichols, J. H., and Thompson, B. M. (1988). Quantitative sampling of crustacean larvae and its use in stock size estimation of commercially exploited species. In 'Aspects of Decapod Crustacean Biology'. (Eds A. A. Fincham and P. S. Rainbow.) Vol.59. (Clarendon Press: Oxford.)
- Olsen, D. A., Herrnkind, W. F., and Cooper, R. A. (1975). Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus*, of St. John, U.S.V.I.: (1) Introduction and general population characteristics. In 'Results of the Tektite Program: Coral Reef Invertebrates and Plants'. (Eds S. A. Earle and R. J. Lavenberg.) pp. 11–6. Natural History Museum of Los Angeles County Science Bulletin No. 20.
- Orensanz, J. M., and Gallucci, V. F. (1988). Comparative study of postlarval life-history schedules in four sympatric species of *Cancer* (Decapoda : Brachyura : Cancridae). *Journal of Crustacean Biology* **8**, 187–220.
- Pearce, A. F., and Phillips, B. F. (1988). ENSO events, the Leeuwin Current, and larval recruitment of the western rock lobster. *Journal du Conseil. Conseil International pour l'Exploration de la Mer* **45**, 13–21.
- Phillips, B. F., and Booth, J. D. (1994). Design, use, and effectiveness of collectors for catching the puerulus stage of spiny lobsters. *Reviews in Fisheries Science* **2**, 255–89.
- Pianka, E. R. (1970). On *r*- and *K*- selection. *The American Naturalist* **104**, 592–97.
- Plaut, I., and Fishelson, L. (1991). Population structure and growth in captivity of the spiny lobster *Panulirus penicillatus* from Dahab, Gulf of Aqaba, Red Sea. *Marine Biology* **111**, 467–72.
- 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**, 2107–17.
- Pollock, D. E. (1990). Palaeoceanography and speciation in the spiny lobster genus *Jasus*. *Bulletin of Marine Science* **46**, 387–405.
- Pollock, D. E. (1991). Population regulation and stock recruitment relationships in some crayfish and lobster populations. In 'Crustacean Issues'. (Eds A. Wenner and A. Kuris.) pp. 247–66, Vol.7. (Balkema: Rotterdam.)
- Pollock, D. E. (1992). Palaeoceanography and speciation in the spiny lobster genus *Panulirus* in the Indo-Pacific. *Bulletin of Marine Science* **51**, 135–46.
- Pollock, D. E. (1995). Evolution of life-history patterns in three genera of spiny lobsters. *Bulletin of Marine Science* **57**, 516–26.
- Pollock, D. E., and Melville-Smith, R. (1993). Decapod life histories and reproductive dynamics in relation to oceanography off southern Africa. *South African Journal of Marine Science* **13**, 205–12.
- Polovina, J. J., and Mitchum, G. T. (1992). Variability in spiny lobster *Panulirus marginatus* recruitment and sea level in the Northwestern Hawaiian Islands. *Fishery Bulletin* **90**, 483–93.

- Rathbun, M.** (1930). The cancroïd crabs of America of the families Euryalidae, Portanidae, Atelecyclidae, Cancridae and Xanthidae. Bulletin of the US National Museum No. 152, 609 pp.
- Reilly, P. N., and Saila, S. B.** (1978). Biology and ecology of the rock crab, *Cancer irroratus* Say, 1817, in southern New England waters (Decapoda, Brachyura). *Crustaceana* **34**, 121–40.
- Rimmer, D. W.** (1980). Spatial and temporal distribution of early-stage phyllosoma of western rock lobster, *Panulirus cygnus*. *Australian Journal of Marine and Freshwater Research* **31**, 485–97.
- Roesijadi, G.** (1976). Descriptions of the prezoeae of *Cancer magister* Dana and *Cancer productus* Randall and the larval stages of *Cancer antennarius* Stimpson (Decapoda, Brachyura). *Crustaceana* **31**, 275–95.
- Rooney, P., and Cobb, J. S.** (1991). Effects of time of day, water temperature, and water velocity on swimming by postlarvae of the American lobster, *Homarus americanus*. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 1944–50.
- Roughgarden, J., Gaines, S., and Possingham, H.** (1988). Recruitment dynamics in complex life cycles. *Science* **241**, 1460–6.
- Santucci, R.** (1926). Lo sviluppo e l'ecologia post-embryonali dello 'scampo' (*Nephrops norvegicus* (L.)) nel Tirreno e nei Mari Nordici. *Memoria Regio Comitato Talassografico Italiano* **125**.
- Sarda, F.** (1995). A review (1967–1990) of some aspects of the life history of *Nephrops norvegicus*. In 'Shellfish Life Histories and Shellfishery Models'. (Eds D. E. Aiken, S. L. Waddy and G. Y. Conan.) *International Council for the Exploration of the Sea Marine Science Symposia* **199**, 78–88.
- Sastry, A. N., and McCarthy, J. F.** (1973). Diversity in metabolic adaptation of pelagic larval stages of two sympatric species of Brachyuran crabs *Netherlands Journal of Sea Research* **7**, 434–46.
- Schram, F.R.** (1982). The fossil record and evolution of crustacea. In 'Systematics, the Fossil Record, and Biogeography'. (Ed. L. Abele.) *The Biology of Crustacea* Vol. 1, 93–147. (Academic Press: New York.)
- Shanks, A. L.** (1995). Orientated swimming by megalopae of several eastern North Pacific crab species and its potential role in their onshore migration. *Journal of Experimental Marine Biology and Ecology* **186**, 1–16.
- Shields, J. D.** (1991). The reproductive ecology and fecundity of *Cancer* crabs. In 'Crustacean Egg Production'. (Eds A. M. Wenner and A. M. Kuris.) *Crustacean Issues*. Vol.7, pp.193–213. (Balkema: Rotterdam.)
- Shields, J. D., Okazaki, R. K., and Kuris, A. M.** (1991). Fecundity and the reproductive potential of the yellow rock crab, *Cancer anthonyi*. *Fishery Bulletin (US)* **89**, 299–305.
- Southwood, T. R. E.** (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology* **46**, 337–65.
- Sulkin, S. D., and McKeen, G.** (1994). Influence of temperature on larval development of four co-occurring species of the brachyuran genus *Cancer*. *Marine Biology* **118**, 593–600.
- Waddy, S. L., Aiken, D. E., and de Kleijn, D. P. V.** (1995). Control of growth and reproduction. In 'Biology of the Lobster *Homarus americanus*'. (Ed. J. R. Factor.) pp. 217–66. (Academic Press: San Diego.)
- Wahle, R. A., and Steneck, R. S.** (1991). Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? *Marine Ecology Progress Series* **69**, 231–43.
- Warner, R. E., Combs, C. L., and Gregory, D. R.** (1977). Biological studies of the spiny lobster, *Panulirus argus* (Decapoda; Palinuridae), in south Florida. *Proceedings of the Gulf and Caribbean Fisheries Institute* **29**, 166–83.
- Wenner, E. L., Barans, C. A., and Ulrich, G. F.** (1992). Population structure and habitat of Jonah crab, *Cancer borealis* Stimpson 1859, on the continental slope off the southeastern United States. *Journal of Shellfish Research* **11**, 95–103.
- Werner, E. E.** (1986). Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *The American Naturalist* **128**, 319–41.
- Winemiller, K. O., and Rose, K. A.** (1992). Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2196–218.
- Winn, R. N.** (1985). Comparative ecology of three cancroïd crab species (*Cancer anthonyi*, *C. antennarius* and *C. productus*) in marine subtidal habitats in southern California. Ph.D. Thesis, University of Southern California.