

Larval dynamics of the sand crab, *Emerita analoga*, off the central Oregon coast during a strong El Niño period

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Populations of the sand crab, Emerita analoga, are well established on the California coast. However, populations in Oregon occur sporadically and appear to be restocked by larvae drifting north from California. Due to increased northward transport in winter during El Niño events, we would expect that larval recruitment to northern populations should be higher during these periods. This hypothesis was tested by comparing larval abundances between non-El Niño and El Niño years, 1997 and 1998, respectively. In 1997, larval abundances and seasonality were similar to historical data from 1969–71. First zoeal (Z1) stage larvae were present during these summers, but in low numbers, indicating that E. analoga spawned off the coast of Oregon. In 1998, strong larval recruitment from the south occurred, demonstrated by a large number of fifth zoeal stage (Z5) larvae collected off Oregon in April and May. The large numbers of Z1 found in summer 1998 indicate that the Z5, which arrived from California earlier that spring, successfully recruited to adulthood and reproduced. These data indicate that Oregon E. analoga populations are probably dependent on larvae travelling from California in the Davidson Current. It follows that this species could be used as an indicator of coastal current fluctuations such as those seen during El Niño events.

INTRODUCTION

The sand crab, *Emerita analoga* (Stimpson), (Anomura, Brachyura, Hippidae) is a filter feeder found in the wash zone of exposed sandy beaches. It is distributed along the temperate west coast of the Americas from Kodiak Island, Alaska to Magdalena Bay, Baja California, and from Salaverry, Peru to the Strait of Magellan and around Cape Horn to False Bay in Argentina (Efford, 1970). The life cycle of *E. analoga* consists of five planktonic zoeal stages (henceforth referred to as Z1–Z5) which hatch into the megalopal stage (Johnson and Lewis, 1942). Megalopae settle onto sandy beaches, where they moult and develop into juveniles after a few weeks, and then into adults. *Emerita analoga* reproduce in their first and second summers, and die in the autumn of their second year (Efford, 1976). Larvae remain planktonic for up to 4 months. According to laboratory studies, *E. analoga* moult into the megalopae 130 days after hatching (Efford, 1970). Johnson (Johnson, 1939) observed a pelagic larval stage

lasting 120 days. The long planktonic larval phase of this species implies a high dispersal potential, and coastal water transport is an important factor in determining its local and latitudinal distribution. Extended larval duration allows individuals to colonize new areas with suitable habitats, and is a mechanism to annually restock already existing populations (Tam *et al.*, 1996).

Emerita analoga populations are well established along the beaches of California. Although populations exist to the north of California, they are less common and are found only in patches between southern Oregon and Vancouver Island. These northern populations are thought to be maintained primarily by chance larval immigration from the populations in California via the mechanism of larval drift in the north-flowing Davidson Current. Larval transport plays a key role in determining this species' distribution because the direction of the coastal currents reverses on an interannual basis. The coastal component of the California Current flows southwards in the summer (April–September) but the coastal

current flows northwards as the Davidson Current from October until March (Hickey, 1989). In this transport pathway, larvae produced from eggs spawned during late summer and early fall in California coastal waters are transported north as pelagic zoeae. During their 4 month period of development, these larvae could easily reach the Oregon coast. *Emerita analoga* larval abundance in waters north of California almost certainly varies by year, and is probably dependent on the extent of spawning in California, larval survival and larval recruitment. These, in turn, are affected by physical factors such as current speed and direction, sea surface temperatures and inter-annual variations in upwelling strength.

In previous research off the coast of Newport, Oregon, the zooplankton were sampled for decapod larvae from June 1969 to April 1971 (Lough, 1975). A few *E. analoga* Z1 were found from August to November of 1970 and 1971 (fewer than 200 per 1000 m³). Z4 and Z5 were found only during the winter of 1969–70 (but not during winter 1970–71).

The purpose of our study was to determine how the *E. analoga* larval densities in coastal waters off central Oregon were affected by changes in oceanic conditions during the 1990s. We compared larval numbers observed in the late 1990s to those of Lough (Lough, 1975) from the early 1970s. This research topic arose from the observation that a general warming of the California Current in the 1990s resulted in northward expansions of a number of pelagic fish species. These include the Pacific hake (*Merluccius productus*), two species of mackerel (*Scomber japonicus* and *Trachurus symmetricus*) and Pacific sardines (*Sardinops sagax*) (McGowan *et al.*, 1998; Emmett and Brodeur, 2000). *E. analoga* were identified on northern Oregon beaches beginning in 1992 (T. Link, Oregon Department of Fish and Wildlife, Astoria, OR, personal communication). Large numbers of adult *E. analoga* carapaces had also been noted on the beaches of central Oregon from at least 1996 to the present, whereas they were rarely seen during the 1970s (W. Peterson, personal observation). This led to the question of whether or not individuals were reproducing and, if so, whether there were sufficient numbers of larvae to suggest that the local population was self-sustaining.

Our study took place during the El Niño of 1997–98, giving us the opportunity to examine the effects of this event on *E. analoga* recruitment. The environmental effects of El Niño events are well-known and include elevated sea surface heights in winter, decreased upwelling during summer, and increased sea surface temperatures in all seasons. In addition, the southward flow of the coastal component of the California Current generally decreases, whereas the northward flow of the Davidson Current increases. The northward flow of anomalously warm

water during the 1997–98 and past El Niños has led to well-documented poleward shifts in the distribution of many marine species, including exotic warm-water zooplankton (Keister *et al.*, in preparation), fish (Percy and Schoener, 1987; Percy, 2001) and birds (Mysak, 1986; Sharp, 1992). We expected that the 1997–98 El Niño would cause *E. analoga* to experience a northward habitat shift similar to that observed by other southern distributed species.

METHOD

Collection of larvae

Zooplankton samples were collected at a station 5 nautical miles (9 km) off Newport, Oregon (44.65°N, 124.18°W) (Figure 1) along the Newport Hydrographic (NH) line as part of a routine sampling programme. A total of 41 samples were collected between 24 February 1997 and 17 December 1998, using a 1 m diameter plankton net with 333 µm mesh and fitted with a TSK or General Oceanics flowmeter. The plankton net was fished by letting out 60 m of cable and then retrieving it while the vessel was travelling at 2 knots. Conductivity and temperature profiles were obtained using a Seabird SBE 19

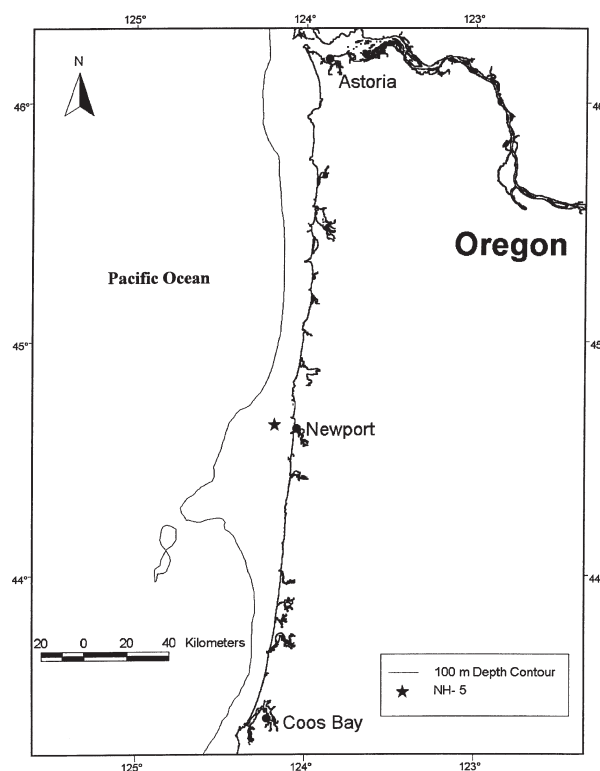


Fig. 1. Location of sampling site NH05, 5 nautical miles (9 km) off the coast of Newport, Oregon.

CTD (conductivity, temperature, depth) probe. Sea surface heights were obtained from the University of Hawaii Sea Level Center (Kilonsky, 1999).

Processing of plankton samples

Upon retrieval, plankton samples were immediately preserved in a 5–10% buffered formalin solution. In the laboratory, samples were sorted for *E. analoga*. In most cases, the entire sample was sorted, however, a Folsom splitter was used to subsample when high larval abundances made this impractical. *E. analoga* larvae were removed from each sample and identified to life-cycle stage according to Johnson and Lewis (Johnson and Lewis, 1942). Larval densities (number per 1000 m³) were calculated for each sample.

RESULTS

Physical data

The 1997–98 El Niño event began to influence local wind and coastal circulation patterns in early May 1997. As a result, sea surface height anomalies increased, beginning in May 1997 and lasting through to June 1998 (Figure 2). The El Niño signal first appeared in late August 1997, when water 4–6°C warmer than average arrived on the beaches of Oregon (Figure 3). Sea surface temperatures for 1997 were, on average, 2°C higher than the 1969–72

average. Warm temperatures persisted through May 1998. It was not until mid-summer and autumn 1998 that sea surface temperatures were within normal ranges.

Larval abundances

Low densities (less than 200 per 1000 m³) of *E. analoga* larvae were observed off Newport, OR in 1997 (Figure 4). Z1 were found in June, October and December, but low numbers of all stages suggest low recruitment. During the winter and spring of 1997–98, when the El Niño was in full force, we found high larval densities (1–3 m⁻³), especially Z3 in January and Z4 and Z5 from January through June (Figure 5). These larvae were most likely transported north from California in the Davidson Current.

In summer 1998, densities of Z1 were more than an order of magnitude higher than in 1997. Z1 were found from May to September, but densities peaked in mid-July 1998. This peak indicated the production of a new cohort that was observed later as Z2 and Z3 in September–October, and as Z3 and Z4 in October–December. The time interval between peaks in Z1 and Z4 abundance was approximately 3–4 months. This is consistent with previous estimates of a larval duration of 4 months (Johnson, 1939; Efford, 1970).

It is also interesting to note that no *E. analoga* megalopae were found in any zooplankton samples. This supports the observations which predicted that *Emerita talpoida*, an East Coast species, settle while still fifth stage zoeae (Harvey, 1993).

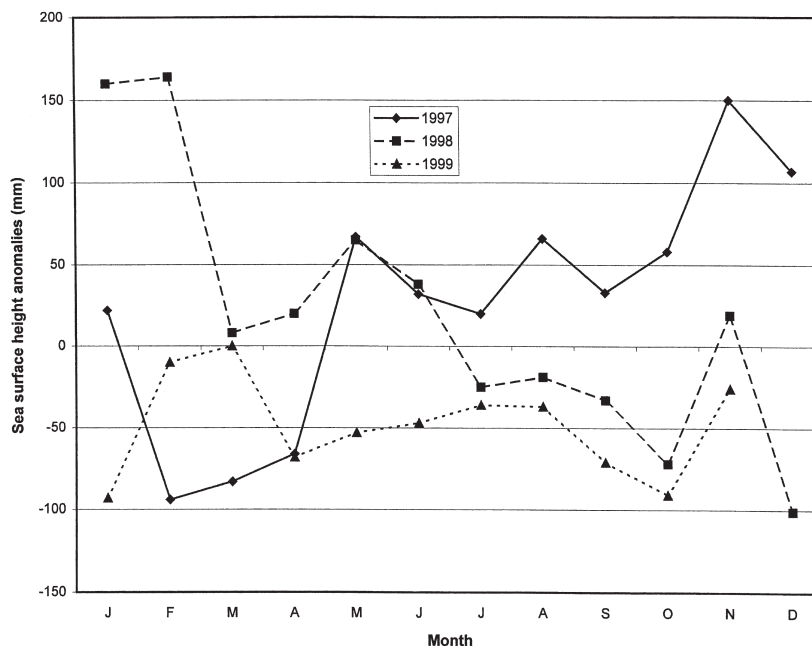


Fig. 2. Monthly sea surface height anomalies at Crescent City, California, 1997–99.

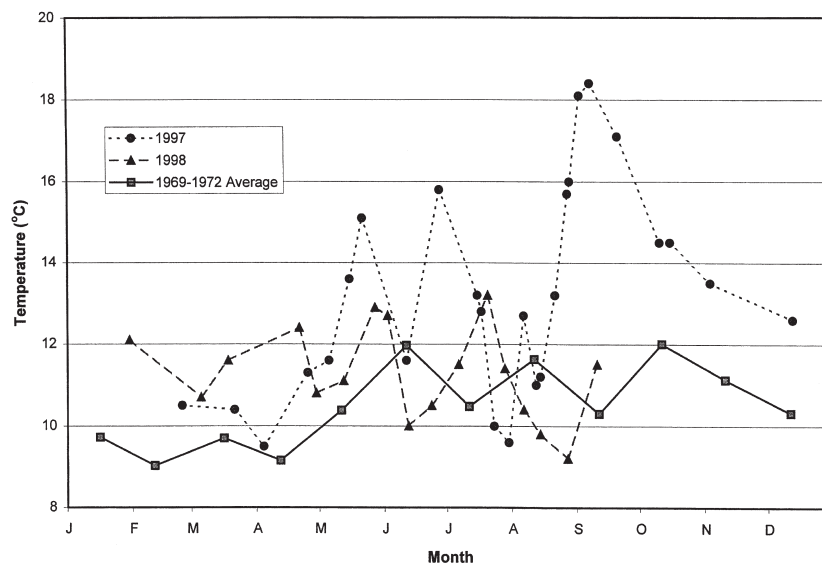


Fig. 3. Monthly sea surface temperatures 5 nautical miles (9 km) off the coast of Newport, Oregon, 1997–98, and average temperatures, 1969–72.

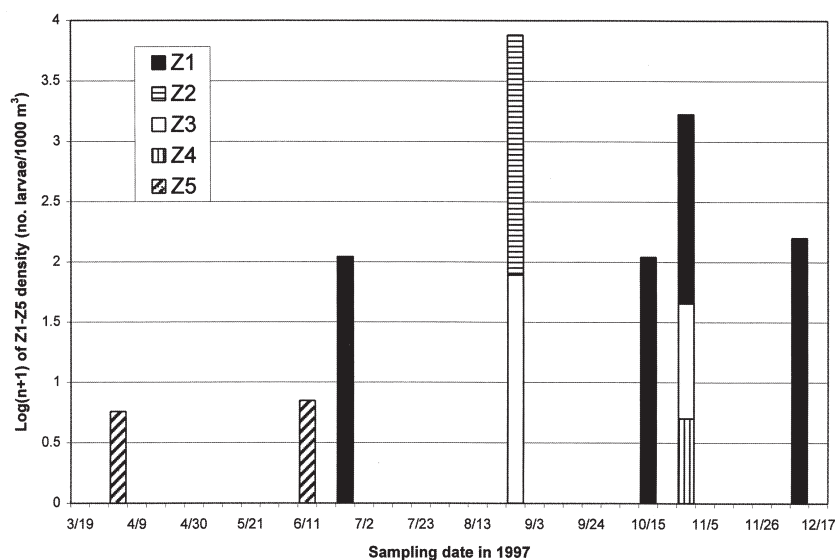


Fig. 4. Densities of *Emerita analoga* zoeae collected 5 nautical miles (9 km) off the coast of Newport, Oregon during 1997. (Zero values for 2/24, 3/21, 4/25, 5/05, 5/15, 5/28, 7/15, 7/18, 7/30, 8/06 and 8/12 are not shown.)

DISCUSSION

It is clear from our data, as well as those of Lough (Lough, 1975), that *E. analoga* populations off the central Oregon coast spawn during the summer in local waters, as evidenced by the presence of Z1 in the summers of 1997 and 1998. These Z1 could only have originated in either Oregon or a more northerly source because the transport of coastal and offshore waters is southerly in the spring and summer (Hickey, 1989). We observed pronounced

differences in Z1 densities in our 2 year study, with Z1 present from June to December in 1997, but only from July to September in 1998. Autumn of 1997 was anomalously warm due to the El Niño, suggesting that higher sea surface temperatures in 1997 resulted in a prolonged adult spawning season. Ocean temperatures returned to normal by August 1998 and this spawning season was correspondingly short (only 3 months), suggesting that spawning season length is temperature dependent.

Emerita analoga populations in Oregon do not appear to

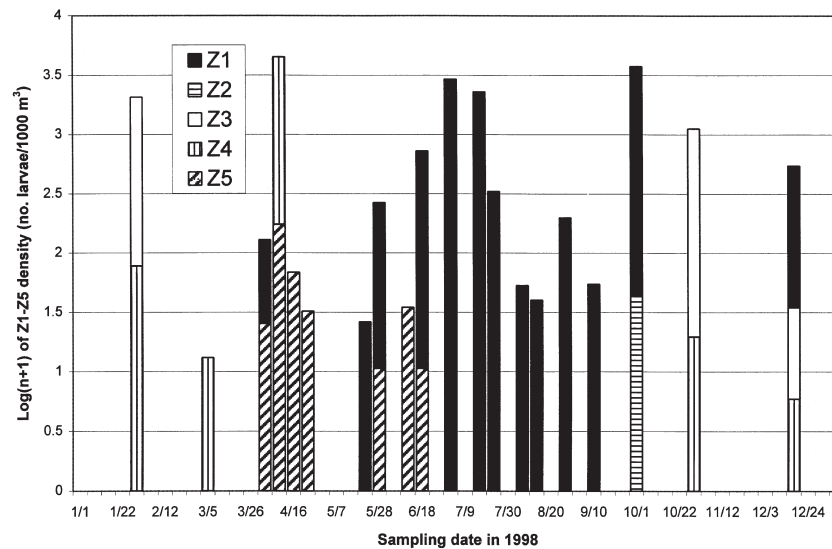


Fig. 5. Densities of *Emerita analoga* zoeae collected 5 nautical miles (9 km) off the coast of Newport, Oregon during 1998. (Zero values for 3/18, 5/12 and 7/14 are not shown.)

be self-sustaining owing to larval transport away from suitable settling habitats. They are probably maintained by larval drift arriving from California and augmented during El Niño events. In 1997 there were very few Z1 seen, indicating limited local spawning. However, an extraordinarily large number of late larvae were found in spring of 1998 due to strong northward transport during El Niño. We suggest that these larvae settled and matured on the Oregon coast in June 1998, and became the adults which, in turn, produced the high numbers of Z1 in July 1998. It remains an open question whether the central Oregon coast *E. analoga* populations can persist during non-El Niño years. Even though these populations are capable of reproduction, it is unclear whether their planktonic progeny contribute to future generations. Thus, northern populations probably depend almost entirely upon recruitment from California populations.

The 1997–98 El Niño event probably had several effects on the local *E. analoga* populations. First, as noted above, warm water that persisted through autumn 1997 may have allowed prolonged spawning. Second, enhanced northward transport during the winter of 1997–98 carried high numbers of late-stage larvae to Oregon from California, resulting in high settlement rates in June. *Emerita analoga* were previously observed in Washington and British Columbia during the 1957–58 El Niño event (Radovich, 1961) and during the 1982–83 El Niño (Schoener and Fluharty, 1985). The observed relationship between *E. analoga* abundances in Oregon and climatic conditions is related to their long planktonic larval stage and dispersal in oceanic currents. Based on a pelagic larval stage of 120 days (Johnson, 1939) and a northward

flow rate of 20 km day⁻¹ for the Davidson Current (Efford, 1970), Z4 and Z5 larvae could drift upwards of 3000 km north of the beach from which they were released. Hart (Hart, 1982) suggested that the individuals observed north of Oregon were a ‘temporary’ result of northward planktonic drift. A similar scenario to explain the northern spread of the European green crab (*Carcinus maenas*), which appeared in Oregon, Washington and British Columbia during the summer of 1998, has also been presented (Behrens Yamada and Hunt, 2000).

We suggest that at some northern geographic point, perhaps off northern Oregon or Washington, *E. analoga* recruitment only occurs during El Niño events, when northward flows are strongest. Regular monitoring of adult *E. analoga* on beaches would be a useful means of tracking the strength of El Niño events and of wintertime poleward flows. Years of high northward flows should result in higher numbers of *E. analoga* the following summers. Such a programme could result in a valuable index of ocean conditions. For example, we learned from T. Link (Oregon Department of Fish and Wildlife, Astoria, OR, personal communication), who walks the beaches of the northern Oregon coast, that *E. analoga* were not found off these beaches in the late 1980s and early 1990s. They appeared during the summer of 1992 and have persisted until the present. This appearance of *E. analoga* occurred while El Niño conditions prevailed throughout the California Current system, zooplankton biomass within the current was at extraordinarily low levels (Roemmich and McGowan, 1995), and typically southerly distributed pelagic fishes became abundant off Oregon and Washington (Emmett and Brodeur, 2000).

Large and persistent populations of *E. analoga* off the Oregon coast appear to be indicators of weak upwelling and low biological production in the California Current. We suggest that *E. analoga* larvae and adult population sizes are useful biological indicators of Northeast Pacific oceanic conditions.

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