Journal of Experimental Marine Biology and Ecology 372 (2009) 31–35

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Substrate preferences and redistribution of blue king crab *Paralithodes platypus* glaucothoe and first crab on natural substrates in the laboratory

Federico Tapella [a,*,1], M. Carolina Romero [a,1], Bradley G. Stevens [a,2], C. Loren Buck [b,3]

[a] National Marine Fisheries Service, Alaska Fisheries Science Center, Kodiak Fisheries Research Center, 301 Research Ct., Kodiak, AK 99615, United States
[b] Fishery Industrial Technology Center, School of Fisheries and Ocean Science, University of Alaska Fairbanks, 118 Trident Way, Kodiak, AK 99615, United States

ARTICLE INFO

Article history:
Received 27 October 2008
Received in revised form 2 February 2009
Accepted 3 February 2009

Keywords:
Habitat selection
Lithodids
Stock enhancement

ABSTRACT

Despite the importance of blue king crab (BKC) to the Bering Sea fishery, there has been no detailed study of juvenile habitat preferences. Such information is critical for understanding life history and for development of stock enhancement programs. The aims of this study were to determine the natural substrata that glaucothoe prefer to settle on, and whether they or subsequent crab 1 stage (C1) redistribute to different habitats over time. A laboratory experiment was performed in 24 round containers divided in four equal quadrants each filled with one of the following natural substrata: beach sand, gravel, shells and cobble. Containers were assigned to 8 groups of 3 replicates each and were kept at ~6–8 °C. Twenty five glaucothoe were released in each container on day 0, and one group of three replicates was removed for examination at each of the following intervals: 24 h, 7, 14, 21, 28, 35, 42 and 49 days. Numbers of swimming and settled specimens on each substrate and period were recorded. Glaucothoe began to settle immediately after being released since no swimming larvae were found during any sampling periods. Substrata complexity was important for the habitat selection and distribution of blue king crab glaucothoe and crab 1 stage. During the glaucothoe stage, beach sand was rejected and cobble, shell and gravel were chosen equally. After glaucothoe molted to crab 1 stage and became bigger, animals preferred cobble and shell instead of gravel and beach sand. Understanding habitat selection is useful not only for management of crab populations, but also for assessing the potential of various habitats for stock enhancement of blue king crabs.

1. Introduction

Recruitment of many marine decapod crustaceans is a complex process that involves the transition from a planktonic larval to a benthic juvenile phase. During this transition many factors (*e.g.*, current, tides, salinity, temperature, settling behavior, cannibalism, predation, competition, etc.) (Sulkin and Epifanio, 1984; Forward Jr., 1990; Phillips et al., 1991; Fernández et al., 1993; Hasek and Rabalais, 2001; Heck Jr. et al., 2001; Moksnes et al., 2003; Stevens, 2003; Van Montfrans et al., 2003) may affect recruitment success and significantly reduce the number of individuals that survive to adulthood (Wahle and Steneck, 1991; Rabalais et al., 1995). This demographic bottleneck effect is of special relevance for fisheries management and aquaculture (Wahle and Steneck, 1991; Rabalais et al., 1995). For example, the fishery quota for rock lobsters *Panulirus cygnus* in western Australia is based on the abundance of settled puerulus larvae measured 3 and 4 years earlier (Caputi et al., 2003).

Among factors that affect decapod recruitment, postlarval settlement behavior is important for the selection of an adequate substratum that provides shelter and food during critical early juvenile stages. Postlarval stages actively select substrata on which to settle before they undergo metamorphosis to the first juvenile instar (Wahle and Steneck, 1992; Stevens, 2003; Van Montfrans et al., 2003). Moreover, some species are able to delay metamorphosis in absence of suitable substratum (O'Connor, 1991; Harvey, 1993). In some species, such as *Petrolisthes cinctipes* (Jensen, 1991) and *Uca pugilator* (O'Connor, 1993), postlarvae select a settlement substrate occupied by adult conspecifics. Postlarvae may also orient toward nursery areas in response to chemical cues, as demonstrated for *Callinectes sapidus* (Forward Jr. et al., 2003). Decapod postlarvae often select structurally complex habitats for settlement, including those of American lobster *Homarus americanus* (Botero and Atema, 1982), Dungeness crab *Cancer magister* (Fernández et al., 1993), and red king crab *Paralithodes camtschaticus* (Stevens and Kittaka, 1998; Stevens, 2003; Stevens and Swiney, 2005).

* Corresponding author. Current Address: Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Centro Austral de Investigaciones Científicas (CADIC), Houssay 200, V9410CAB, Ushuaia, Tierra del Fuego, Argentina. Tel.: +54 2901 422310; fax: +54 2901 430644.
E-mail address: ftapella@gmail.com (F. Tapella).
[1] Current Address: Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Centro Austral de Investigaciones Científicas (CADIC), Houssay 200, V9410CAB, Ushuaia, Tierra del Fuego, Argentina.
[2] Current Address: University of Massachusetts Dartmouth, School of Marine Science and Technology, 706 S. Rodney French Blvd., New Bedford, MA, 02740.
[3] Current Address: Biological Sciences Department, University of Alaska Anchorage, 3211 Providence Drive, Anchorage, Alaska, 99508.

0022-0981/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2009.02.003

Blue king crab *Paralithodes platypus* Brandt, 1850 (BKC) is an important commercially harvested crustacean that occurs in isolated populations around Alaska, as well as the western Pacific Ocean near Japan and Russia. Commercial fisheries for BKC were developed around the Pribilof Islands and St. Matthew Island during the 1960's and reached their peak harvest during the 1980's with annual landings of ~4500 t valued at US$ 9.6–25.6 million. Afterwards, the BKC fishery declined until it was closed for two periods (1988–1994 and 1995–2002), and was finally declared overfished in 2002 (NPFMC, 2002).

Blue king crab have a biennial spawning cycle (Jensen and Armstrong, 1989; Stevens et al., 2008b). During spring, females molt, mate, and extrude eggs which develop for approximately one year before hatching. Larvae hatch in late winter or early spring and develop through four pelagic zoeal stages, followed by a benthic postlarval (glaucothoe) stage which settles on the bottom before metamorphosis to the first juvenile crab (C1) stage (Sato, 1958; Hoffman, 1968).

Blue king crab distribution and habitat preference is related to their life history phase. Adult female BKC live primarily in rocky nearshore areas, whereas males tend to be farther offshore (Blau, 2000). Juveniles (<1 year old) occur in depths from 40 to 60 m in a habitat consisting of a mixture of dead but intact bivalve and snail shells, which usually occurred in pockets among rock, cobble, or gravel habitats (Armstrong et al., 1985). Despite the importance of the BKC fishery, little is known about the settlement habitat and distribution of glaucothoe and young-of-the-year-juveniles. This study was conducted to determine whether blue king crab glaucothoe exhibit a preference for one of four natural substrata commonly found at the Pribilof Islands and if the first crab stage redistributes among those substrata.

2. Methods

2.1. Animals

Adult female and male BKC were collected near St. Paul Island, at approximately 57° N, 169° 30' W in the eastern Bering Sea by trawls during July 2003, and by pots in October 2003 and July 2004. Crabs were wrapped in wet burlap and shipped in insulated containers to the Kodiak Fisheries Research Center (KFRC) in Kodiak, Alaska. Crabs were maintained in an 8000-L tank containing filtered running seawater at 6 °C and fed twice weekly ad libitum with a combination of squid (*Loligo* spp.), herring (*Clupea harengus*), Pacific cod (*Gadus macrocephalus*) or coho salmon (*Oncorhynchus kisutch*) cut into 2 cm chunks. During spring 2005, we facilitated mating to produce female crabs with embryos which developed during 2005 and hatched between February and March 2006. Just prior to releasing larvae, individual females were placed in 50-L plastic totes with filtered running seawater that were immersed in the chilled crab tanks.

2.2. Larval cultivation

In order to obtain a sufficient sample size of BKC glaucothoe for habitat selection experiments, 2000 stage I zoeae from two females were collected by dipping a glass beaker into the hatching totes during the peak hatching period (~10–30 ml larvae·day^{-1}). Larvae were distributed into 8 20-L culture containers (250 in each) filled with 14-L of filtered (5 µm) and UV-sterilized seawater and maintained at 6 °C in a cold room. Containers were aerated continuously to maintain oxygen saturation and keep larvae suspended in the water column. Water was changed and larvae were fed a combination of *Artemia* nauplii (3–5 nauplii·ml^{-1}) and *Thallasiosira nordenskioeldii* diatoms (1000–2000 cells·ml^{-1}) three times per week. Previous cultivation experiments (Stevens et al., 2008a) indicated that this diet was the best combination for larval survival. Dead larvae were removed during water changes. Daily observations were made to determine the occurrence of glaucothoe, when zoea IV stages were close to molting. Glaucothoe were removed from containers and used in the habitat selection experiment within 96 h of molting.

2.3. Habitat selection experiment

A seven week long experiment was conducted to determine the preferred natural substrata for settlement of glaucothoe and whether first instar crabs (stage C1) redistribute among different substrata. The experiment utilized twenty-four 12-L cylindrical containers (28 cm diameter and 19 cm height). The bottoms of the containers were divided in four equal sections by a white PVC strip 6 cm in height. Each section of the container was filled with one of the following natural substrata: 150 cm^3 of beach sand (<1 mm) (S), 150 cm^3 of gravel (2.8–4.8 mm) (G), 200 cm^3 of broken clam (*Saxidomus gigantea*) and cockle (*Clinocardium nuttallii*) shells (4.8–13 mm) (Sh) and 200 cm^3 of cobble (13–20 mm) (C). Before using substrata in experiments, they were rinsed three times with fresh water to remove naturally occurring organisms and dried at 70 °C for 36 h, except for beach sand which required 72 h to dry. In order to avoid location effects, substrata were arranged differently in each replicate as follows (in clock wise order): 1) C, S, G and Sh; 2) C, Sh, S and G; and 3) C, G, Sh and S. The surface of each substrate was ~3–4 cm below the upper lip of the PVC divider. This design allowed glaucothoe to settle in any substratum, but prevented changing substrata by random crawling; glaucothoe could only move between substrata by actively swimming over the divider.

Round containers were filled with 10-L filtered sea water and immersed in one of two water baths (12 in each) with ambient temperature seawater flowing around them; containers were randomly assigned to positions within either bath to eliminate location effects. Water bath tanks were covered with a layer of black plastic that partially blocked the fluorescent lab lighting. Temperature of each tank was recorded at 2 h intervals by an Onset Water-Temp Pro© electronic temperature logger (Onset Corporation, PO Box 3450, Pocasset, Massachusetts 02559).

On 5 May 2006, 25 glaucothoe were released in the center of each round container by pipette. During the course of the experiment, three replicate containers were analyzed and removed from the experiment after periods of 24 h, 7, 14, 21, 28, 35, 42 and 49 days (treatments), respectively. On each treatment date, swimming glaucothoe were counted in each container immediately after removing the black plastic cover. Then, water was siphoned down to the divider edge and live and dead specimens were recorded in each substrate. Individuals that occurred on dividers were recorded as being on "other" substrata. On day 22, dividers were removed because ~25% of glaucothoe had molted to crab stage 1 (C1) and a maximum of 27 days was required to molt to C1 (Stevens et al., 2008a). Thus, we expected that all animals would be stage C1 by day 28 and would no longer be able to swim. Water in the experimental containers was changed every three days by siphoning down to the divider edge and refilling to 10-L again. Glaucothoe were not fed since they do not eat (see review in Stevens and Kittaka, 1998) and C1 were fed ad libitum with "Cyclopeze" frozen copepods three times per week after the water was changed. Proportions of glaucothoe and C1 on each substrate were calculated on the basis of total live animals in each round container.

2.4. Data analysis

Proportions of glaucothoe and C1 on each substrate are presented as means ± 1 SD. In order to determine the preference of glaucothoe and crab I for a natural substrata, analysis of variance (one-way ANOVAs) were performed separately for each of the eight experimental periods. Data were arcsine transformed and assessed for normality and homogeneity of variances by Kolmogorov–Smirnov and Levene tests, respectively (Sokal and Rohlf, 1995). Significant

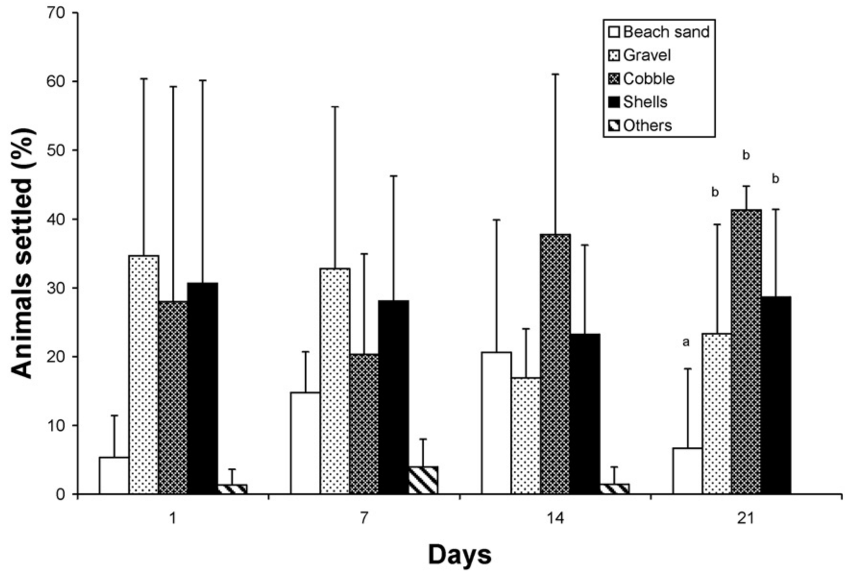

Fig. 1. Percentage of blue king crab (*Paralithodes platypus*) glaucothoe stage on natural substrates in different development periods. Vertical lines indicate standard deviation. Different letters above deviation lines indicate significant differences at $P<0.05$. For details on substrates and sampling periods see Methods.

differences ($P<0.05$) were compared using the Tukey post-hoc test (Sokal and Rohlf, 1995).

3. Results

Hatching to first glaucothoe duration was 37.6 ± 0.5 days and survival rate of blue king crab larvae was $83.7 \pm 5.1\%$. Water temperature increased from 5.6 to 8.3 °C (mean 7.2 ± 0.9 °C) over the course of the experiment. A total of 675 glaucothoe were released into the aquaria, and 4.4 and 24.1% died during the glaucothoe and C1 stages, respectively. No glaucothoe were observed swimming during any observation periods, so that the category was removed from analysis.

Blue king crab glaucothoe preferred to settle on complex substrata. Glaucothoe selected for cobble, broken shell and gravel, although there were no significant differences in the proportion of settled glaucothoe among substrata during the three first sampling periods (1, 7 and 14 days) (Fig. 1 and Table 1). By day 21, settlement of glaucothoe on complex substrates such as cobble, shell and gravel was significantly greater than on beach sand (Fig. 1 and Table 1). There were no statistical differences among G, C, or Sh.

Stage 1 crabs redistributed to those substrata with higher levels of complexity. During all four later sampling periods (days 28–49), the proportion of C1 crabs was significantly different among substrates (Fig. 2 and Table 1). Cobble and shell were always significantly preferred over gravel, and gravel was significantly preferred over sand on days 28 and 49 (but not on days 35 and 42). The proportion on shell exceeded that on cobble on days 28, 35, and 42 but was not significant. Stage C1 crabs did not select for beach sand as a substratum, similar to the glaucothoe stage (Figs. 1 and 2).

4. Discussion

Blue king crab glaucothoe actively select complex natural substrata for settlement. Our results suggest that BKC glaucothoe prefer cobble, broken shell and gravel equally and avoid sand as a substrate. This selection pattern may be an adaptive behavior that reduces mortality rates by predation, since complex habitats have a high fraction of interstitial space that offers shelter to glaucothoe and first juvenile stages (Stevens and Swiney, 2005). Selection of structurally complex habitats has been reported for several decapod species. For example, stage IV larvae of the lobster *Homarus americanus* display a strong preference for algal-covered rock and rocky substrata for settlement (Botero and Atema, 1982). Megalopae of the Dungeness crab *Cancer magister* select habitats that provide the lowest risk of mortality (shell) over those (mud) where the probability of mortality is high (Fernández et al., 1993). Similarly, *Carcinus maenas* megalopae and first instar shore crabs are more abundant on structurally complex habitats such us filamentous algae, eelgrass and mussel beds than on open sand (Moksnes, 2002). Glaucothoe of the red king crab *Paralithodes camtschaticus*, another Lithodid species from Alaskan water, exhibit a strong association with complex substrata, either artificial (mesh) (Stevens and Kittaka, 1998) or biological (hydroids and red algae) (Stevens, 2003), in which they are able to grip and hide among small interstitial spaces.

Our results suggest that cobble, broken shell (*i.e.*, “shell hash”, *sensu* Armstrong et al., 1985) and gravel substrata are suitable habitats for BKC settlement. In our experiments, no swimming glaucothoe were observed during any observation period and all glaucothoe settled within 24 h after release into the aquaria (Fig. 1). Moreover, even though there were no significant differences in the proportion of glaucothoe on different substrata until day 14, a clear tendency to avoid sand was observed from the beginning of the experiments

Table 1
Result of one-way analysis of variance (ANOVAs) conducted to test the effect of different substrates on the settled blue king crab (*Paralithodes platypus*) glaucothoe and crab 1 stage in each sample period. References: F, F-statistic; *df*, degree of freedom and MS, mean square. For details on substrates and period samples see Methods.

Stage	Source	*df*	MS	F	*P*
Glaucothoe	Period 24 h	4	600.71	2.59	0.10
	Error	10	231.86		
	Period 7 days	10	257.57	2.19	0.14
	Error	10	125.57		
	Period 14 days	4	443.66	2.91	0.08
	Error	10	152.59		
	Period 21 days	3	524.57	4.98	0.031
	Error	8	105.22		
Crab 1	Period 28 days	3	683.51	15.12	0.001
	Error	8	45.21		
	Period 35 days	3	6592.12	4.62	0.037
	Error	8	128.30		
	Period 42 days	3	299.18	53.00	<0.001
	Error	8	5.64		
	Period 49 days	3	597.40	10.27	0.004
	Error	8	58.16		

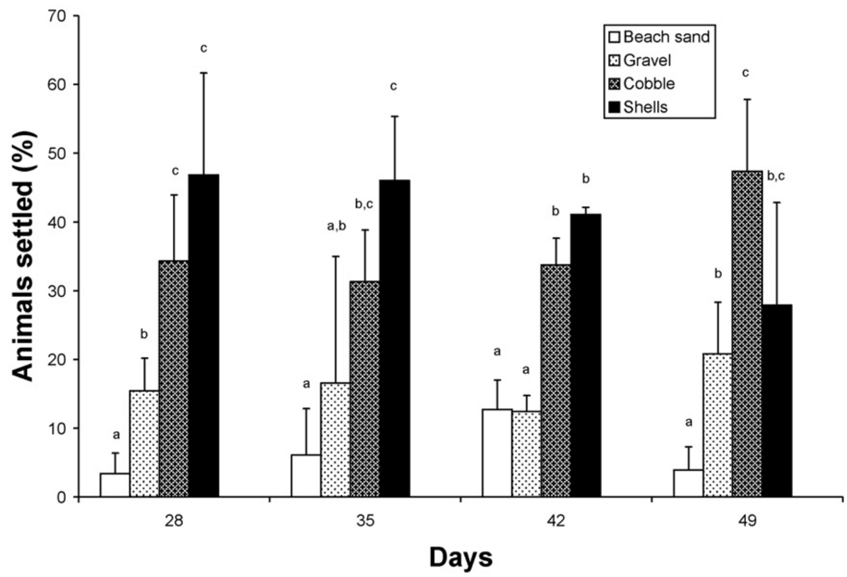

Fig. 2. Percentage of blue king crab (*Paralithodes platypus*) crab 1 stage on natural substrates in different development periods. Vertical lines indicate standard deviation and different letters above deviation lines indicates significant differences at $P<0.05$. For details on substrates and sampling periods see Methods.

(Fig. 1). Based on other habitat selection studies, postlarval stages keep swimming until they find a suitable habitat for settlement. Red king crab glaucothoe that found complex substrate settled onto them rapidly and remained stationary, whereas those that were provided only with sand continued swimming and settled there as last resort (Stevens, 2003). Similarly, settlement of lobster *Homarus americanus* larvae was delayed for 2 weeks in the absence of an appropriate substratum, such as when only flat sand was offered (Botero and Atema, 1982).

Redistribution of stage C1 blue king crabs among substrata may be related to apparent differences in the availability of interstitial space of appropriate size. Glaucothoe at day 21 (~5 days before molting, Stevens et al., 2008a), settled on cobble, shell and gravel equally and only avoided sand (Fig. 1). However, after glaucothoe molted and consequently increased in size, stage 1 crabs were found mainly on shell and cobble substrates, whereas gravel was rejected almost as strongly as sand (Fig. 2). During every sampling period for glaucothoe, it was necessary to remove the gravel substrate to find and count animals because they were hiding in the interstitial spaces. However, during C1 stage sampling periods, animals which occurred on gravel were found and counted at first sight without removing the substrate. Similar to studies on *Carcinus maenas* (Moksnes, 2002) and *Callinectes sapidus* (Etherington and Eggleston, 2000), these results suggest that BKC glaucothoe and young juveniles would have different requirements for shelter that result in a post-settlement movement and an ontogenetic shift in habitat use among several structurally complex habitats. Redistribution of juveniles to other habitats shortly after metamorphosis has been proposed as a strategy to reduce intra-specific interactions such as cannibalism and competition (Moksnes, 2002; Blackmon and Eggleston, 2001; Moksnes et al., 2003).

The preferences of BKC glaucothoe and C1 stages for structurally complex substrata support the hypothesis that the distribution of BKC juveniles surrounding the Pribilof Islands is limited by the complexity of substrate (Armstrong et al., 1985). Blue king crab juveniles (<30 mm CL) were restricted to near shore areas around the Pribilof Islands and the bulk of the population occurred within 10–15 km of St. Paul and east of St. George (Armstrong et al., 1985). They also found a strong association between juveniles and complex substrata composed of cobble, gravel, and shell with an ephipytic covering of diatoms, bryozoans and algae. These biologically complex habitats are scarce in the Bering Sea (Stevens, 2003) and seem to be the preferred habitats of juvenile king crabs. Similar to BKC, juvenile red king crabs in the Bering Sea commonly occur among such epifauna as sea stars, polychaete tubes, sponges, bryozoans, hydroids and mussel colonies that are attached to dispersed hard substrata such as gravel and shell debris (Stevens, 2003).

In summary, substrate complexity plays a key role in the habitat selection and distribution of glaucothoe and juvenile stages of the blue king crab in the Bering Sea. Our experiments indicate that BKC glaucothoe select natural complex substrate for settlement and, after molting to crab stage 1 (and becoming larger), redistribute to substrata with larger interstitial spaces. The availability of complex substrata for settlement of BKC glaucothoe in the Bering Sea is limited and thus may create a bottleneck effect on recruitment (*sensu* Wahle and Steneck, 1991), limiting the number of settlers that can survive there. Future studies should evaluate the preference of glaucothoe and C1 crabs for natural biological assemblages and their natural mortality (by predation and cannibalism) within those habitats. Such knowledge would be extremely useful not only for management of crab populations, but also for assessing the potential of various habitats for stock enhancement of both red and blue king crabs.

Acknowledgements

We are grateful to S. Persselin, S. Van Sant and K. Swiney for laboratory assistance and to those people from the Kodiak Fisheries Research Center (KFRC) and the Fishery Industrial Technology Center (FITC) for their friendly relationship with MCR and FT. This project was supported by grant N° R0507 from the North Pacific Research Board (NPRB) to CLB and BGS. We also wish to thank the University of Alaska Sea Grant Program for supplementary funding. MCR and FT thank to Consejo Federal Pesquero and Gobierno of Tierra del Fuego from Argentina providing the air tickets from Ushuaia to Kodiak. [SS], [RH] and [ST].

References

Armstrong, D.A., Armstrong, J.L., Palacios, R., Williams, G., Jensen, G.C., 1985. Early life history of juveniles blue king crab, *Paralithodes platypus*, around the Pribilof Islands. Proceedings of the International King Crab Symposium. University of Alaska Sea Grant, Anchorage, AK, USA, pp. 211–230.

Blackmon, D.C., Eggleston, D.B., 2001. Factors influencing planktonic, post-settlement dispersal of early juvenile blue crabs (*Callinectes sapidus Rathbun*). J. Exp. Mar. Biol. Ecol. 257, 183–203.

Blau, S.F., 2000. Nearshore blue king crab survey: St. Matthew Island, 1999. Regional Information Report. Alaska Department of Fish and Game, Division of Commercial Fisheries, ADF&G Westward Regional Office, 211 Mission Rd, 99615 Kodiak, Alaska, USA. 30 pp.

Botero, L., Atema, J., 1982. Behavior and substrate selection during larval settling in the lobster *Homarus americanus*. J. Crustac. Biol. 2, 59–69.

Caputi, N., Chubba, C., Melville-Smith, R., Pearce, A., Griffinc, D., 2003. Review of relationships between life history stages of the western rock lobster, *Panulirus cygnus*, in Western Australia. Fish. Res. 65, 47–61.

Etherington, L.L., Eggleston, D.B., 2000. Large-scale blue crab recruitment: linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. Mar. Ecol. Prog. Ser. 204, 179–198.

Fernández, M., Iribarne, O., Armstrong, D., 1993. Habitat selection by young-of-the-year Dungeness crab *Cancer magister* and predation risk in intertidal habitats. Mar. Ecol. Prog. Ser. 92, 171–177.

Forward Jr., R.B., 1990. Behavioral responses of crustacean larvae to rates of temperature change. Biol. Bull. 178, 195–204.

Forward Jr., R.B., Tankersley, R.A., Smith, K.A., Welch, J.M., 2003. Effects of chemical cues on orientation of blue crab, *Callinectes sapidus*, megalopae in flow: implications for location of nursery areas. Mar. Biol. 142, 747–756.

Harvey, A.W., 1993. Larval settlement and metamorphosis in the sand crab *Emerita talpoida* (Crustacea: Decapoda: Anomura). Mar. Biol. 117, 575–581.

Hasek, B.E., Rabalais, N.N., 2001. Settlement patterns of Brachyuran megalopae in a Louisiana estuary. Estuaries 24, 796–807.

Heck Jr., K.L., Coen, L.D., Morgan, S.G., 2001. Pre- and post-settlement factors as determinants of juvenile blue crab *Callinectes sapidus* abundance: results from the north-central Gulf of Mexico. Mar. Ecol. Prog. Ser. 222, 163–176.

Hoffman, E.G., 1968. Description of laboratory-reared larvae of *Paralithodes platypus* (Decapoda, Anomura, Lithodidae). J. Fish. Res. Board. Can. 25, 439–455.

Jensen, G.C., 1991. Competency, settling behavior, and postsettlement aggregation by porcelain crab megalopae (Anomura: Porcellanidae). J. Exp. Mar. Biol. Ecol. 153, 49–61.

Jensen, G.C., Armstrong, D.A., 1989. Biennial reproductive cycle of blue king crab, *Paralithodes platypus*, at the Pribilof Islands, Alaska and comparison to a congener, *P. camtschatica*. Can. J. Fish. Aquat. Sci. 46, 932–940.

Moksnes, P.-O., 2002. The relative importance of habitat-specific settlement, predation and juvenile dispersal for distribution and abundance of young juvenile shore crabs *Carcinus maenas* L. J. Exp. Mar. Biol. Ecol. 271, 41–73.

Moksnes, P.-O., Hedvall, O., Reinwald, T., 2003. Settlement behavior in shore crabs *Carcinus maenas*: why do postlarvae emigrate from nursery habitats? Mar. Ecol. Prog. Ser. 250, 215–230.

NPFMC (North Pacific Fishery Management Council), 2002. Stock assessment and fishery evaluation report for the king and tanner crab fisheries of the Bering Sea and Aleutian Islands Regions. North Pacific Fishery Management Council, 605 W. 4th Ave., #306, 99501 Anchorage, Alaska, USA.

O'Connor, N.J., 1991. Flexibility in timing of the metamorphic molt by fiddler crab megalopae *Uca pugilator*. Mar. Ecol. Prog. Ser. 68, 243–247.

O'Connor, N.J., 1993. Settlement and recruitment of the fiddler crabs *Uca pugnax and U. pugilator* in a North Carolina, USA, Salt Marsh. Mar. Ecol. Prog. Ser. 93, 227–234.

Phillips, B.F., Pearce, A.F., Litchfield, R.T., 1991. The Leeuwin Current and larval recruitment to the rock (spiny) lobster fishery off Western Australia. J. Roy. Soc. West. Aust. 74, 93–100.

Rabalais, N.N., Burditt, F.R., Coen, L.D., Cole, B.E., Eleuterius, C., Heck, K.L., McTigue, T.A., Morgan, S.G., Perry, H.M., Truesdale, F.M., Zimmer-Faust, R.K., Zimmerman, R.J., 1995. Settlement of *Callinectes sapidus* megalopae on artificial collectors in four Gulf of Mexico estuaries. Bull. Mar. Sci. 57, 855–876.

Sato, S., 1958. Studies on larval development and fishery biology of king crab, *Paralithodes camtschatica* (Tilesius). Bull. Hokkaido. Natl. Fish. Res. Lab. 17, 1–102.

Sokal, R.R., Rohlf, F.J., 1995. Biometry, The principles and practice of statistics in biological research. W.H. Freeman and Co., N.Y. New York. 887 pp.

Stevens, B.G., 2003. Settlement, substratum preference, and survival of red king crab *Paralithodes camtschaticus* (Tilesius, 1815) glaucothoe on natural substrata in the laboratory. J. Exp. Mar. Biol. Ecol. 283, 63–78.

Stevens, B.G., Kittaka, J., 1998. Postlarval settling behavior, substrate preference, and time to metamorphosis for red king crab *Paralithodes camtschaticus*. Mar. Ecol. Prog. Ser. 167, 197–206.

Stevens, B.G., Swiney, K.M., 2005. Post-settlement effects of habitat type and predator size on cannibalism of glaucothoe and juveniles of red king crab *Paralithodes camtschaticus*. J. Exp. Mar. Biol. Ecol. 321, 1–11.

Stevens, B.G., Persselin, S., Matweyou, J., 2008a. Survival of blue king crab *Paralithodes platypus* Brandt, 1850, larvae in cultivation: effects of diet, temperature and rearing density. Aquac. Res. 39, 390–397.

Stevens, B.G., Swiney, K.M., Buck, C.L., 2008b. Thermal effects on embryo development and hatching for blue king crab *Paralithodes platypus* held in the laboratory, and a method for predicting dates of hatching. J. Shellfish Res. 27, 1255–1263.

Sulkin, S., Epifanio, C., 1984. A conceptual model for recruitment of the blue crab *Callinectes sapidus* Rathburn, to estuaries of the middle Atlantic Bight. In: Jamieson, G. S., Bourne, N. (Eds.), North Pacific Workshop on Stock Assessment and management of Invertebrates. Can. Spec. Publ. Fish. Aquat. Sci., 92, pp. 117–123.

Van Montfrans, J., Clifford, H.R., Orth, R.J., 2003. Substrate selection by blue crab *Callinectes sapidus* megalope and first juvenile instars. Mar. Ecol. Prog. Ser. 260, 209–217.

Wahle, R.A., Steneck, R.S., 1991. Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? Mar. Ecol. Prog. Ser. 69, 231–243.

Wahle, R.A., Steneck, R.S., 1992. Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. J. Exp. Mar. Biol. Ecol. 157, 91–114.