Canadian Journal of Fisheries and Aquatic Sciences

OPEN ACCESS | Research Article

Blue king crab (*Paralithodes platypus*) and red king crab (*P. camtschaticus*) juvenile settlement to nearshore nursery habitats of Saint Paul Island, Pribilof Islands, Alaska

Jared D. Weems[a], **W. Christopher Long**[b], **Lauren M. Divine**[c], **and Ginny L. Eckert**[a]

[a]University of Alaska Fairbanks, College of Fisheries and Ocean Sciences, Juneau, AK 99801, USA; [b]National Oceanic and Atmospheric Administration, Alaska Fisheries Science Center, Kodiak, AK 99615, USA; [c]Aleut Community of Saint Paul Island Tribal Government, Ecosystem Conservation Office, Anchorage, AK 99503, USA

Corresponding author: **Jared D. Weems** (email: jared.weems@alaska.gov)

Abstract

The Pribilof Islands blue king crab (*Paralithodes platypus*) fishery collapsed over two decades ago, is considered overfished, and has not recovered in the absence of fishing. Red king crab (*Paralithodes camtschaticus*) abundance estimates have exceeded blue king crab for over three decades. We investigated the roles of larval recruitment and habitat availability as potential mechanisms limiting blue king crab recovery. We conducted young-of-year abundance and habitat assessments near Saint Paul Island from 2017 to 2019 and compared these results to 1983–1984 historical data to assess changes in larval supply and benthic substrates. Historically abundant blue king crab settlers were rarely encountered in our surveys. Red king crab settlers, once rare in historical surveys, are now more common throughout the region in low abundance. Benthic habitats did not change over time, as 90% of resampled sites had similar substrates. We conclude that larval supply and not benthic habitat is limiting juvenile recruitment. Our results could inform future fishery rebuilding efforts for blue king crab, which could include approaches to increase larval supply and juvenile recruitment through aquaculture.

Key words: blue king crab, red king crab, larval supply, benthic recruitment, Pribilof Islands

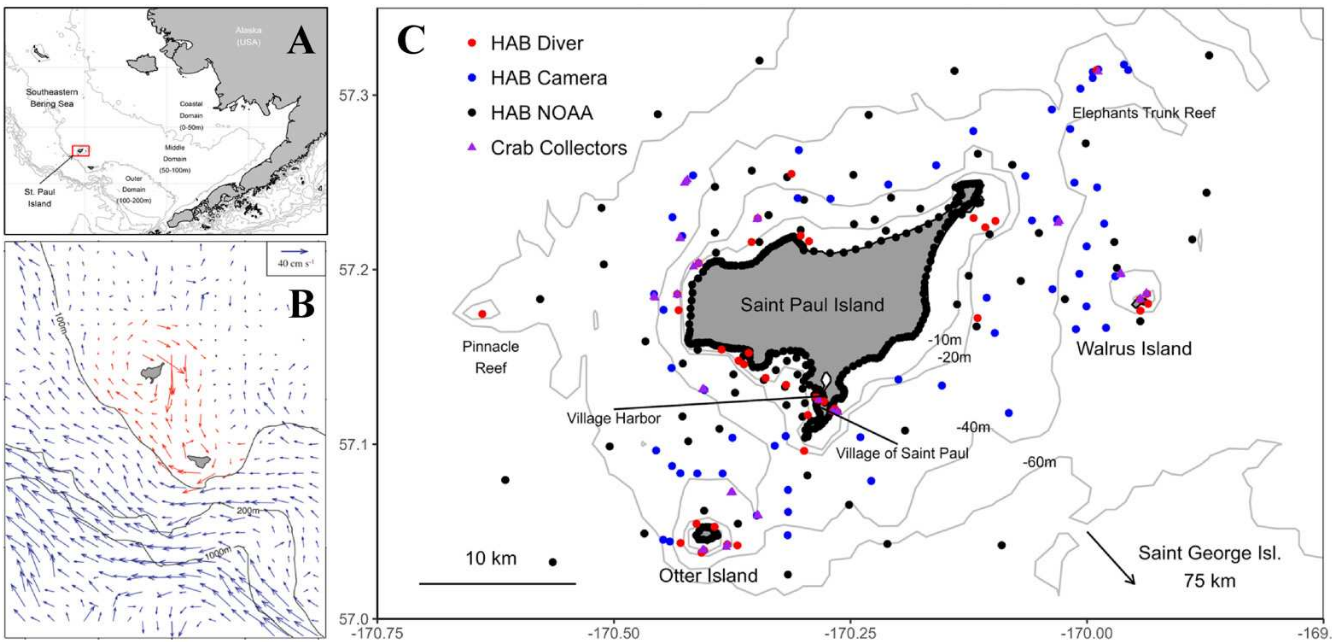
1. Introduction

Pribilof Islands blue king crab (*Paralithodes platypus* Brandt, 1850) once numbered in the tens of millions of crabs and produced millions of pounds of commercial harvests annually (Stockhausen 2023). Today, this stock is in an overfished and collapsed status and that has failed to rebuild in the absence of fishing. The stock was commercially fished from 1973 to 1989 and 1995 to 1998, closed in 1999, and declared overfished in 2002. The decades-long and thus far unsuccessful stock rebuilding effort limited targeted fishing and bycatch with little recovery (Salveson 2004; Foy et al. 2014). Pribilof Islands red king crab (*Paralithodes camtschaticus* Tilesius, 1815), on the other hand, were historically rare, increased in abundance in the late 1980s, and culminated in commercial co-harvesting of king crab species in the middle 1990s (Szuwalski 2022). Both species currently remain at low levels of abundance, though their stock assessments differ across status indicators. For example, blue king crab male mature biomass is estimated to be ~4% of total biomass necessary to maintain maximum sustainable yield (B_{msy}) while red king crab is ~227% (Szuwalski 2022; Stockhausen 2023). We investigated the role of blue and red king crab larval supply and benthic habitat as potential mechanisms limiting recovery by comparing historical surveys in the 1980s (Armstrong et al. 1985, 1987, 2015; Palacios et al. 1985) with contemporary surveys in 2017–2019.

Environmental changes in the southeastern Bering Sea and Pribilof Islands over the past several decades have led to dramatic decreases in sea ice and increased seawater temperatures (Stabeno et al. 2007; Stabeno and Bell 2019). These changes reduce the extent and strength of the Bering Sea cold pool contributing to long-term ecosysptem changes (Hunt et al. 2008, 2011; Renner et al. 2012; Short et al. 2021). These climate-associated changes also have a variety of implications for crab, including changes in larval advection and survival (Rosenkranz et al. 2001; Orensanz et al. 2004; Richar et al. 2015; Daly et al. 2020), increases in disease prevalence (Morado et al. 2014; Ryazanova et al. 2016), and changing predator–prey and competitor dynamics (Livingston 1989; Burgos et al. 2013; Lyons et al. 2016).

Changes in pelagic or benthic communities and habitat structure could impact the survival of early benthic phase king crabs. Adult king crab females release larvae in nearshore habitats (Armstrong et al. 1987; Wainwright et al. 1992). In the Pribilof Islands, anticyclonic (clockwise) water flow (Kowalik and Stabeno 1999; Hunt et al. 2008) may promote local retention of larvae and early juvenile settlement in complex bottom habitats. Blue king crab settlers appear

Fig. 1. Study region and sampling locations for the assessment of blue king crab (*Paralithodes platypus*) and red king crab (*Paralithodes camtschaticus*) juvenile settlement dynamics at Saint Paul Island, Alaska, USA. (A) The southeast Bering Sea with the Pribilofs Islands located along the western-edge of Middle Shelf region. (B) Modelled seawater currents showing the Pribilof Islands oceanographic domain flow vectors (red vectors) relative to regional along-shelf and along-slope currents (blue vectors). Image adapted from Hunt et al. (2008). (C) Sampling locations for all 2017–2019 sausage-shaped artificial collector (crab collector, or SAC) deployments targeting age-0 blue and red king crab (purple triangles) and crab/habitat (HAB) assessment stations with SCUBA divers (red circles) and drop-cameras (blue circles). Additional US National Oceanic and Atmospheric Administration (NOAA) data were collected from various sources at intertidal and subtidal (black circles) locations to augment spatial habitat analyses.



to prefer complex cobble and intact shellhash substrates as nursery habitats (Armstrong et al. 1985; Palacios et al. 1985; Tapella et al. 2009; Lyons et al. 2016). Red king crab settlers prefer a wider variety of complex and epiphytic habitats (Loher and Armstrong 2000; Pirtle and Stoner 2010; Pirtle et al. 2012). Laboratory experiments suggest that interspecies interactions may favor red king crabs, but blue king crab may also reduce interactions when occupying complex habitats (i.e., shellhash) (Daly and Long 2014; Long et al. 2015; Lyons et al. 2016).

We investigated juvenile blue and red king crab settlement, availability of nearshore nursery habitats, and predation in the Pribilof Islands to better understand and identify if a population bottleneck is occurring at early life history stages. A companion study focused specifically on predation of newly-settled crab (Weems 2024). In this study, we hypothesize that a bottleneck exists in larval supply for blue king crab and that it is driven by low larval supply, changes to benthic settlement habitats, or both. We measure relative densities of blue and red king crab larvae and juveniles in nearshore habitats surrounding Saint Paul Island. We compare historical baselines of juvenile king crab settlement from 1983 to 1984 during peak fishing years to assess relative change over time (Armstrong et al. 1987, 2015). Historical and modern juvenile studies are contextualized relative to population assessments of adult spawner abundances (Zacher et al. 2023).

2. Methods

2.1. Study area and historical data

Saint Paul Island is the largest (110 km^2) and northernmost (57°N, 170°W) island in the Pribilof Islands group located in the southeastern Bering Sea (Fig. 1A). The Pribilof Islands are remote, supporting their own subarctic oceanographic and ecological domains (Fig. 1B) (Kowalik and Stabeno 1999; Hunt et al. 2008). Our study sites were selected near Saint Paul Island to assess juvenile king crab settlement, benthic substrate, and community structure between 2017 and 2019 (Table 1, Fig. 1C). We used a previous study, conducted during a time of relative health for the blue king crab stock, as a guide for sampling locations (Armstrong et al. 1985, 1987, 2015; Palacios et al. 1985). In that study, juveniles were sampled using beam trawls and rock dredges, and habitat observations were made through qualitative assessment of abiotic substrates collected and side-scan sonar results during three scientific cruises 1983–1984 (Table 1). Juvenile crab catch was higher for rock dredges compared to beam trawls; hence we selected only rock dredge catches of age-0 crab for comparison with this study. Seawater temperature and salinity were measured in both studies for comparing water mass characteristics. Sampling locations in this study were selected to resample historical stations with high 1983–1984 catches

Table 1. Study platforms and sampling efforts for the assessment of blue king crab (*Paralithodes platypus*) and red king crab (*Paralithodes camtschaticus*) settlement dynamics at Saint Paul Island, Alaska, USA.

Present study (North Pacific Research Board #1608)		2017 (19 May to 13 Aug.)		2018 (20 May to 14 Sep.)		2019 (4 June to16 Aug.)	
Gear type	Gear type description	Deployments	Retrieved	Deployments	Retrieved	Deployments	Retrieved
SAC: GN	Gillnet larval collectors deployed all years: horizontal depoloyment	54 [a]	72 [a]	134	68	96	76
SAC: GNSH	Gillnet and shell hash Type 1 larval collectors: 2017 only: horizontal deployment	54 [a]	32 [a]	–	–	–	–
HAB	Shallow sites: less than 18 m depths: full diver surveys and exploratory dives	27	–	13	–	–	–
HAB	Deep sites: 18–54 m depths: drop-camera video surveys to resample 1983–1984 sites	35	–	28	–	–	–
ZOOP	Ring net: 30 cm diameter frame: 333 μm mesh: upper water column oblique tows	6	–	8	–	–	–
SeaT	Temperature loggers: 15 min sampling interval at 35 m depth: 57.0591°N, 170.3489°W	4	3	4	3	4	3
Historical study (US MMS-OCSEAP; Armstrong et al. 1987, 2015) [b]		1983 (9–30 May)		1983 (19 Aug. to 7 Sep.)		1984 (11 Apr. to 4 May)	
Gear type	Gear type description	Deployments	Retrieved	Deployments	Retrieved	Deployments	Retrieved
BT	Beam Trawl: 3 m wide trawl: 6 mm codend mesh: ∼0.8 km / 10 min bottom tows	21	–	30	–	31	–
RD	Rock Dredge: 90 cm wide reinforced: 6 mm codend mesh: ∼0.4 km / 5 min bottom tows	4	–	52	–	24	–
HAB	Deep sites: BT / RD substrate bycatch observations used for study comparisons	9	–	42	–	24	–
ZOOP	Bongo net: twin 60 cm diameter frame: 505 μm mesh: full water column oblique tows	74	–	40	–	41	–
SeaT	CTD deployments: sea surface temperature point data nearest to 57.0591°N, 170.3489°W	8	–	4	–	5	–
Supplementary data							Data No.
HAB	NOAA Navigation Chart #16832 Edition #12 georeferenced subtidal sediment descriptions.						74
HAB	NOAA [c]: coastal/intertidal substrate descriptions ∼0.5 km or less separation of georeferenced points.						262
AirT	NOAA [d]: daily mean air temperatures: Saint Paul Airport National Weather Service Observation Center: Apr. to Sep. from 1983, 1984, 2016, 2017, 2018, and 2019.						915

Note: Gear types include (in order of appearance): sausage-shaped artificial collector (SAC) bags for juvenile crab including gillnet (GN) and gillnet/shellhash (GNSH) types, source-specific assessments for physical and biological benthic habitat (HAB), pelagic zooplankton tows for crab larvae (ZOOP), seawater temperature sensor deployments (SeaT), and historical-study bottom trawls (BT) and rock dredge trawls (RD) for crab, habitat, and community assessments. Additional data were collected from various US National Oceanic and Atmospheric Administration (NOAA) sources including daily mean air temperatures (AirT). CTD, conductivity–temperature–depth.

[a] SACs were deployed in pairs: 1-GN and 1-GNSH. Due to strong wave action, a subset of 2017 SACs lost their shellhash material through the outer mesh (deployed a GNSH: retrieved a GN).

[b] US Minerals Management Service, Outer Continental Shelf Environmental Assessment Program Saint Paul Island research area between 57–57.5 degrees North and 169.5–171 degrees West (Quadrants 1–4).

[c] NOAA/US Coast Guard 17th District. The Pribilof Islands: An Area of Extreme Environmental Sensativity. Map. Published August 1998.

[d] NOAA National Weather Service Forecast Office, Anchorage Alaska for Saint Paul Island. NOWData—NOAA Online Weather Data. https://w2.weather.gov/climate/xmacis.php?wfo=pafc.

Canadian Science Publishing

of juvenile blue king crab. We additionally selected shallow sites that were SCUBA diver-accessible (18 m depth or less).

Studies were conducted from small boat or by shore access. Data were maintained with Microsoft® Excel® 2016 and mapping and statistical analyses were carried out in R Version 4.2.2 (R Core Team 2022). Spatial visualizations of the Saint Paul Island area are Mercator projections (WGS84) of additional shoreline (Schnute et al. 2022) and bathymetric data (Pante et al. 2023). Field research and animal care guidelines were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee and conducted under protocol #1035800 from 18 April 2017 to 18 April 2020 (Weems 2024) in accordance with national standards (National Research Council 2011; Use of Fishes in Research Committee 2014). Field collections were allowed under Alaska Department of Fish and Game Aquatic Resource Permits CF 16-106/17-093/18-039/19-054 with special access to Walrus Island approved by NOAA's Office of Law Enforcement under the exemption for National Marine Fisheries Service research in critical habitats as described in 50 CFR 224.103 (https://www.ecfr.gov/current/title-50/part-224/section-224.103).

2.2. Field sampling

2.2.1. Settlement collectors

Crab settlement collectors were deployed annually at ten shallow (diver-accessible) sites and eight deep (27–54 m) historically sampled sites to create an index of juvenile crab settlement to the benthos. Sausage-shaped artificial collector bags, developed and used to sample settling king crab (Donaldson et al. 1992; Blau and Byersdorfer 1994), were constructed of 150 cm × 55 cm tubular-polyethylene netting with 2.5 cm diamond-mesh, weighted with an ∼0.5 kg rock, and filled with ∼0.25 kg recycled gillnet (1 mm diameter-nylon-multistrand monofilament). In 2017, a subset of collectors were assembled with gillnet and 0.5 kg cleaned oyster–clam–mussel shellhash (Taylor Shellfish Farms of Shelton, WA). Collectors were attached to individual moorings (all deep sites and 2018–2019 shallow sites) or longline mooring lines (2017 shallow sites) of 8 mm sinking groundline (three-strand-leaded-core polypropylene), anchored by 30 kg concrete pier-block moorings and marked with two surface buoys (36 cm foam-crab floats). Individual settlement collectors attached to the mooring lines averaged 60 cm in length, 18 cm in diameter, and laid horizontal upon the sea floor after deployment. Six settlement collectors were deployed at each site in June and recovered in August. Water currents, storm action, and mooring line failure prevented recovery of some settlement collectors (Table 1). Upon successful field collection, settlement collectors were placed in 92 cm × 62 cm screen bags (1 mm vinyl-coated-polyester mesh) and immersed in seawater until processing the same day.

Small crabs, fish, and other invertebrates were washed from the settlement collectors, sieved over 1 mm mesh, and sorted. Juvenile blue and red king crab were measured for carapace length (CL) and either retained live for later predation experiments (Weems 2024) or fixed in 5% formalin (v/v borax-buffered formaldehyde and seawater). Individual king crabs were classified based on measured CL as either age-0 (C1–C5, ∼2–5 mm CL) or age-1 juvenile stages (C6–C10, ∼6–13 mm CL) (Table 2; Fig. A1). Stage counts and catch-per-unit-effort (CPUE, mean count per collector) were calculated by station. All other juvenile crab and fish specimens were similarly fixed and retained for community analyses.

2.2.2. Benthic surveys

Crab recruits, benthic habitat, and community structure of invertebrates and fishes were surveyed by SCUBA divers (40 sites) and drop cameras (63 sites) (Fig. 1C). Benthic SCUBA surveys were conducted at shallow (<18 m depth) sites. At full dive survey sites (n = 19), juvenile king crab and benthic habitat were characterized along a 50 m transect line. Percent cover of physical substrate, algae, and sessile invertebrates and counts of macroinvertebrates and demersal fishes were made in five 1 m × 1 m quadrat surveys (at 0, 12.5, 25, 37.5, and 50 m). Additionally, 0.5 m × 0.5 m quadrats (n = 4–10 site^{-1}) were placed in complex microhabitats thought to be ideal for juvenile king crab near the transect and searched for small crabs. Data were averaged for each species and substrate at each site. Exploration dives were conducted at an additional 21 sites by shore or boat to identify benthic substrate type.

Drop camera images were used to characterize benthic substrate at all deep settlement collector sites, as well as other historically sampled sites with positive blue king crab catch (18–55 m depths). A stereo-vision waterproof housing with dual GoPro Hero3+ Black Edition cameras (Schmidt and Rzhanov 2012) and three Light & Motion Sola 800 underwater lights were mounted inside a constructed frame consisting of two stacked and de-netted Dungeness crab pots (round-reinforced-sport pots, 76 cm diameter, 57 cm total height). The downward-looking cameras were centrally located 55 cm above the bottom of the frame, and the survey area measured directly under the camera was 0.245 m^2. At each site, the recording cameras and frame were deployed once with three successive drops to the seafloor. Once bottom contact was confirmed, 15 s video clips were recorded of the seafloor prior to resuspending the instrument. Surface currents were sufficient to move the boat between drops to achieve three unique video clips per site. One stable image was captured from each video clip and used to estimate mean percent cover or mean cover m^{-2} of substrate and individuals m^{-2} of organisms at each site. Substrate categories from diver surveys and drop cameras were identical to those assigned in the historical study: bedrock (contiguous rock), boulder (>258 mm), cobble (64–257 mm), gravel (2–63 mm), sand (0.06–2 mm), mud (<0.06 mm), green mud, shellhash Type 1 (cobble-gravel-sized intact shell pieces and live mollusks), and shellhash Type 2 (pulverized and crushed pieces of shell material) (Armstrong et al. 1985, 1987; Palacios et al. 1985).

2.2.3. Oceanography and zooplankton

Onset® HOBO® TidbiT v2 temperature loggers were deployed on four settlement collector moorings during 2017–

Can. J. Fish. Aquat. Sci. **82**: 1–21 (2025) | dx.doi.org/10.1139/cjfas-2024-0227

Table 2. Pribilof Islands blue king crab (*Paralithodes platypus*) and red king crab (*Paralithodes camtschaticus*) abundance indices for larvae and early juvenile stages near Saint Paul Island for 2017–2019.

				2017–2019 Study—Saint Paul Island Area											Literature Information			
				Carapace Length		Crab Abundance Indices									Carapace Length	Intermolt Period	Temperature Range	
	Stage/Molt	Approx.	Occupied			2017			2018			2019						
Species	Number	Age Class	Habitat(s)	mm	SD	N	ind./m^3	SE	N	ind./m^3	SE	N	ind./m^3	SE	mm	days	°C	Literature Cited [a]
Blue king crab *Paralithodes platypus*	Zoea 1	age-0	Pelagic	–	–	0	–	–	0	–	–	0	–	–	1.20	6–15	4.5–8.5	H68, S13a
	Zoea 2	age-0	Pelagic	–	–	0	–	–	0	–	–	0	–	–	1.30	7–14	4.5–8.5	H68, S13a
	Zoea 3	age-0	Pelagic	–	–	0	–	–	0	–	–	0	–	–	1.60	7–15	4.5–8.5	H68, S13a
	Zoea 4	age-0	Pelagic	–	–	0	–	–	1	0.010	0.010	0	–	–	2.00	10–17	4.5–8.5	H68, S13a
	Glaucothoe	age-0	Pel. / Ben.	–	–	0	–	–	1	0.010	0.010	0	–	–	1.80–1.90	9–20	4.5–8.5	H68, S13a
	Total					0	–	–	2	–	–	0	–	–				
							ind./SAC			ind./SAC			ind./SAC					
	Instar C1	age-0	Benthic	–	–	0	–	–	0	–	–	0	–	–	1.90–2.62	24–30+	1–12	S13a, St13, L17
	Instar C2	age-0	Benthic	2.64	0.10	2	0.019	0.013	4	0.050	0.028	0	–	–	1.89–2.98	21–30+	1–12	S13a, St13, L17
	Instar C3	age-0	Benthic	3.26	0.02	0	–	–	2	0.048	0.048	0	–	–	2.34–3.64	26–30+	1–10	St13, L17
	Instar C4	age-0	Benthic	–	–	0	–	–	0	–	–	0	–	–	2.04–5.16	30–60+	1–10	St13, L17
	Instar C5	age-0	Benthic	–	–	0	–	–	0	–	–	0	–	–	3.28–5.73	30–60+	1–10	L17
	Total					2	0.019	0.013	6	0.098	0.052	0	–	–				
							count			count			count					
	Instar C6	age-1	Benthic	–	–	0	–	–	0	–	–	0	–	–	3.60–6.25	30–60+	1–10	L17
	Instar C7	age-1	Benthic	–	–	0	–	–	0	–	–	0	–	–	5.34–6.25	30–60+	1–10	L17
	Instar C8	age-1	Benthic	–	–	0	–	–	0	–	–	0	–	–				
	Instar C9	age-1	Benthic	–	–	0	–	–	0	–	–	0	–	–				
	Instar C10	age-1	Benthic	–	–	0	–	–	0	–	–	0	–	–				
	Instar C11+	age-1+	Benthic	–	–	0	–	–	0	–	–	0	–	–				
	Total					0	–	–	0	–	–	0	–	–				

Canadian Science Publishing

Table 2. (*concluded*).

				2017–2019 Study—Saint Paul Island Area											Literature Information			
				Carapace Length		Crab Abundance Indices									Carapace Length	Intermolt Period	Temperature Range	
						2017			2018			2019						
Species	Stage/Molt Number	Approx. Age Class	Occupied Habitat(s)	mm	SD	N	ind./m^3	SE	N	ind./m^3	SE	N	ind./m^3	SE	mm	days	°C	Literature Cited [a]
Red king crab *Paralithodes camtschaticus*	Zoea 1	age-0	Pelagic	–	–	0	–	–	4	0.023	0.023	–	–	–	1.18–1.39	4–10	7–11	ST49, E06, S13b
	Zoea 2	age-0	Pelagic	–	–	0	–	–	1	0.006	0.006	–	–	–	1.38–1.63	4–10	7–11	ST49, E06, S13b
	Zoea 3	age-0	Pelagic	–	–	0	–	–	0	–	–	–	–	–	1.45–1.83	5–9	7–11	ST49, E06, S13b
	Zoea 4	age-0	Pelagic	–	–	8	0.247	0.227	2	0.011	0.011	–	–	–	1.53–2.07	7–10	7–11	ST49, E06, S13b
	Glaucothoe	age-0	Pel. / Ben.	–	–	3	0.142	0.088	2	0.021	0.021	–	–	–	1.80–1.85	14–35	5–12	ST49, E06, S13b
	Total					11	–	–	9	–	–	0	–	–				
							ind./SAC			ind./SAC			ind./SAC					
	Instar C1	age-0	Benthic	2.22	0.20	73	0.700	0.173	1	0.012	0.012	26	0.313	0.088	1.80–2.18	17–77	1.5–12	D92, St10, S13b
	Instar C2	age-0	Benthic	2.85	0.16	6	0.056	0.056	7	0.095	0.042	26	0.322	0.095	2.30–2.84	21–60+	1.5–10	D92, St10, S13b
	Instar C3	age-0	Benthic	3.50	0.18	0	0	0	5	0.095	0.052	1	0.022	0.022	3.30–3.76	19–60+	1.5–10	D92, St10, S13b
	Instar C4	age-0	Benthic	–	–	0	–	–	0	–	–	0	–	–	3.86–4.85	30–60+	1.5–10	D92, St10, S13b
	Instar C5	age-0	Benthic	–	–	0	–	–	0	–	–	0	–	–	5.00–5.64	30–60+	1.5–10	D92, St10
	Total					79	0.754	0.212	13	0.202	0.063	53	0.658	0.146				
							count			count			count					
	Instar C6	age-1	Benthic	6.82	0.19	1	–	–	1	–	–	0	–	–	6.00–6.67	30–60+	1.5–10	D92, St10
	Instar C7	age-1	Benthic	8.86	0.22	0	–	–	4	–	–	2	–	–	8.00	30–60+		D92
	Instar C8	age-1	Benthic	10.08	0.51	0	–	–	7	–	–	7	–	–	9.50	30–60+		D92
	Instar C9	age-1	Benthic	11.47	0.46	0	–	–	10	–	–	3	–	–	11.20	30–60+		D92
	Instar C10	age-1	Benthic	12.61	0.48	0	–	–	7	–	–	1	–	–				
	Instar C11+	age-1+	Benthic	34–43	0.56	0	–	–	4	–	–	0	–	–				
	Total					1	–	–	33	–	–	13	–	–				

Note: Raw counts (N) and abundance by stage with standard error (SE) for larvae (individuals/m^3), age-0 juveniles (mean ind./sausage-shaped artificial collector, SAC), and age-1 juveniles (total number observed) were calculated for assigned stage classes based on best available taxonomic description or developmental study. Literature range estimates or mean values are provided for stage carapace length (mm), intermolt period or duration (days), and temperature regimes (degrees celsius) informing all stage assignments.

[a] Blue king crab literature cited: H68 (Hoffman 1968), S13a (Swingle et al. 2013*a*), L17 (Long et al. 2017; ambient treatment), St13 (Stoner et al. 2013); and red king crab literature cited: ST49 (Sato and Tanaka 1949), E06 (Epelbaum et al. 2006), S13b (Swingle et al. 2013*b*), D92 (Donaldson et al. 1992), St10 (Stoner et al. 2010).

2019 sampling seasons. Temperature data from only one site, northeast of Otter Island at 35 m depth, is presented as daily averages calculated from raw 15 min logging intervals. Historical sea surface temperatures were collected with a RBR*brevio*[3] conductivity–temperature–depth recorder and data were restricted to locations near the Otter Island site for comparison.

Zooplankton samples ($n = 14$) were collected with a 2.25 kg weighted 30 cm ring frame net with 333 µm mesh by conducting oblique tows of the upper half of the water column. A calibrated General Oceanics Inc. mechanical flowmeter was fixed and centered in the net mouth and used to estimate seawater filtrate volume. Nets were rinsed, and the sieved codend samples were fixed in 1 L jars with 5% formalin. Laboratory processing employed sequential Folsom sample splitting methods, and larvae were sorted and identified to species and stage (Table 2) (Sato and Tanaka 1949; Kurata 1963; Makarov 1967; Hoffman 1968; Haynes 1973, 1984; Donaldson et al. 1992; Jensen et al. 1992; Konishi and Shikatani 1999; Kittaka et al. 2002; Epelbaum et al. 2006; Stoner et al. 2010, 2013; Daly and Swingle 2013; Long et al. 2017). All species and stages were counted and CPUE (ind. m^{-3} filtrate) estimated for each successful tow. Historical larvae CPUE (ind. m^{-3}) was summarized for the Saint Paul Island area.

2.3. Data analyses

2.3.1. Blue and red king crab catch index comparisons

Juvenile age-0 king crab counts per station were mapped for the Saint Paul Island area for 1983–1984 rock dredge and 2017–2019 settlement collector sampling. Gear selectivity was assumed to be similar for blue and red king crabs for each gear type. To determine changes in relative abundances (ratio of blue to red king crab), counts of age-0 blue and red king crab at all stations for each survey (i.e., gear type) were summed and the proportion of each species contributed to the total catch was calculated. Annual settlement collector CPUE was analyzed with an ANOVA with year (2017, 2018, and 2019), station location, gear type (with or without shellhash), and depth stratum (shallow, deep) as factors and pairwise comparisons were conducted using post hoc Tukey's tests. Age-1 blue and red king crab qualitative observations are noted.

Larval supply may be associated with spawning stock abundance. Adult Pribilof Island female blue king crab and female red king crab abundance from the summer NOAA Eastern Bering Sea (EBS) bottom trawl survey database for 1975–2023 (Zacher et al. 2023) were graphed in comparison to juvenile settlers. Mature-sized females (synonymous with spawners) were defined as ≥100 mm CL for blue king crab and ≥90 mm CL for red king crab (Stockhausen 2023; Szuwalski 2022). No mature-sized female red king crab were caught in 1975 and 1985 and no survey occurred in 2020; therefore, we excluded those years. Using mean abundance estimates, we calculated female spawner ratios (blue king crab/red king crab) for each EBS survey year. Ratios were log transformed to achieve homogeneity of variances and data symmetry around zero. For comparison, log transformed age-0 catch ratios were calculated for historical (dredge catch) and modern (settlement collector catch) studies.

2.3.2. Benthic substrate comparisons and interpolation

Benthic substrate composition was qualitatively compared by site between the 1983–1984 and 2017–2019 periods. Changes in composition were characterized as either no change in substrate (at least one common substrate type) or changed substrate (no common substrates). Additional substrate data were sourced from published literature for subtidal (NOAA Office of Coast Survey 2020) and intertidal areas (Gundlach et al. 1999). For these comparisons, we aggregated substrates from all data sources into four groups at each site: rocks (includes bedrock, boulder, and cobbles), grains (includes gravel, sand, mud, and green mud), intact shellhash Type 1 (Shell T1), and crushed shellhash Type 2 (Shell T2) and percent cover was estimated for each site. Substrate cover was interpolated using kriging to account for spatial autocorrelation in arcsine transformed mean cover using the "gstat" package (Oliver and Webster 2014; Gräler et al. 2016). Exponential variogram model range, sill, partial sill, and nugget were estimated separately for each substrate group. A too-far prediction limit was set at 0.045 decimal degrees (~5 km). Model performance was assessed using local neighbor 5-fold cross-validation. Mean error (ME ~ 0), mean square normalized error (MSNE ~ 1), and correlation coefficients between prediction and observed values (1 = perfect relationship, 0 = no relationship) were calculated and variance was visualized.

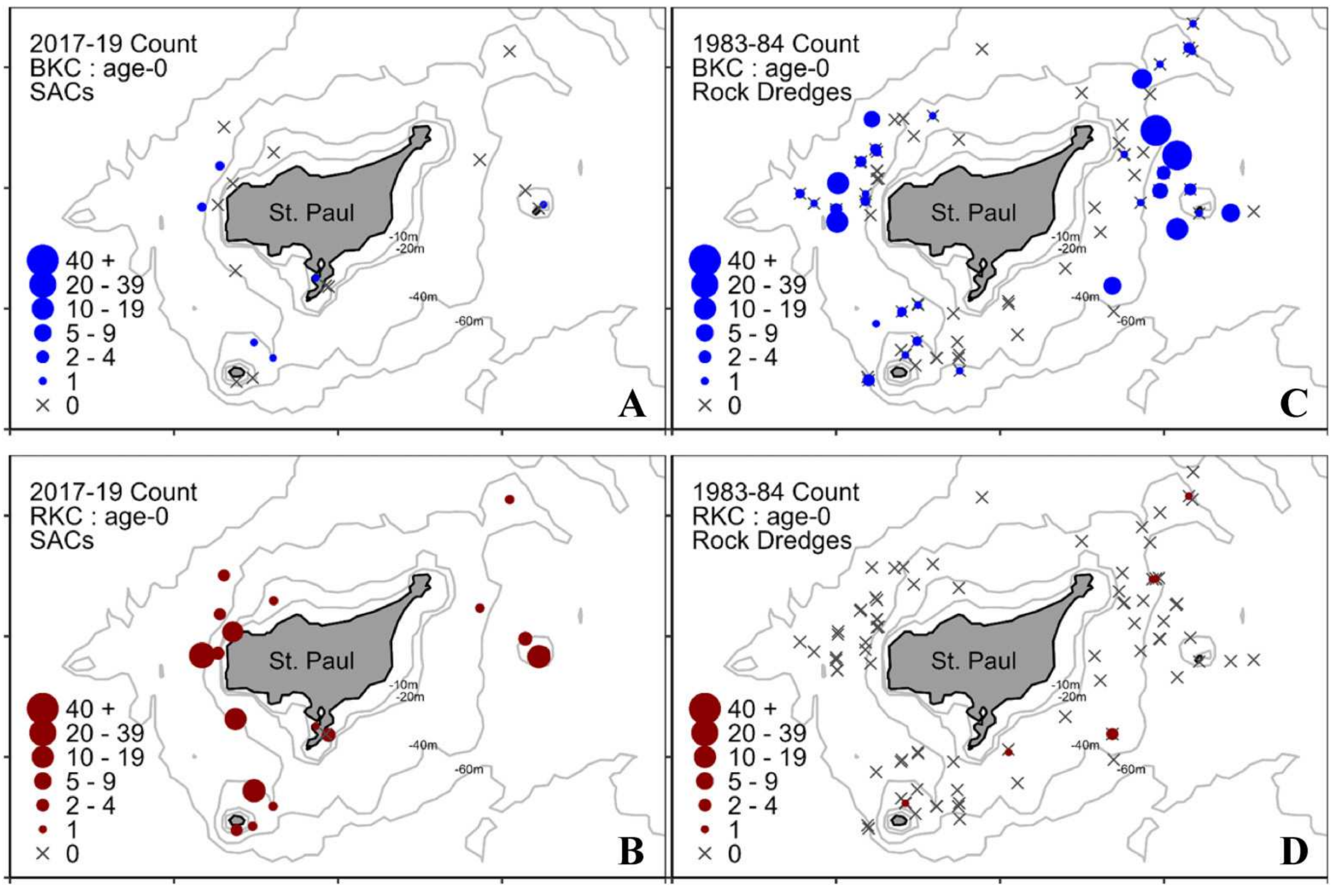
2.3.3. Benthic juvenile crab association to nearby benthic substrates

Non-linear generalized additive modeling (GAM) was employed to assess relationships between nearby substrate cover and red king crab catch using the "mgcv" package (Wood 2017). We modeled the settlement collector counts of age-0 red king crab across stations as a function of percent cover of each of the four substrate types separately (rocks, grains, Shell T1, Shell T2). Only mooring locations were used in this analysis and counts were modeled as arising from either a Poisson or a negative binomial process with a log link:

$$\log(\text{red king crab count})_i = \alpha + s\,(\text{substrate}_i)$$

where red king crab count_i is the summed count of red king crab at site i, α is the intercept, and the $s(_i)$ is a smooth function of the predictor substrate variable (percent cover). One-dimensional smooth function knots were set to a maximum of $k = 4$ to avoid overfitting (Wood 2004). For model comparisons, Poisson and negative binomial models were initially fit via maximum likelihood and the best fitting models were refit using restricted maximum likelihood. Blue king crab

Fig. 2. Counts of age-0 blue king crab (BKC, *Paralithodes platypus*) and red king crab (RKC, *Paralithodes camtschaticus*) caught in 2017–2019 and 1983–84 to assess settlement of crabs in nearshore nursery habitats of Saint Paul Island, Alaska. (A) BKC and (B) RKC were sampled using benthic sausage-shaped artificial collectors (SAC), individual sizes were measured (age-0 ∼2–5 mm carapace length), and counts were summed by station for 2017–2019. Historical catch of (C) BKC and (D) RKC were sampled with a small rock dredge, similarly measured, and counts were summed by station for 1983–1984 (Table A1).



modeling was not attempted due to the small number of positive observations.

2.3.4. Seasonal stage development of age-0 king crab relative to temperature

Larval and juvenile ontogeny were estimated and visualized by pooling data across years and gear types to quantify the proportional contribution of each stage at a given time of year. Blue and red king crab counts were combined to boost sample sizes among years. Thus, for this analysis we assume stage-specific developmental rates are temperature-dependent (Hartnoll 2001) and relatively similar between species (Epelbaum et al. 2006; Stevens 2006*a*; Stoner et al. 2013; Westphal et al. 2014), though optimal thermal ranges for juvenile king crab are different (Long and Daly 2017). Crab stage-specific counts were calculated for each 2-week period beginning 1 April through 7 September. Crab catch data includes all 2017–2019 larvae (Zoeae 1–4), post-larval glaucothoe (PL), and benthic juveniles (C1–5, CL $\leq$ 5 mm) observed. Data from 1983 to 1984 include a subset of larval catches (Zoeae 1–4, PL) collected east of Otter Island. The total number of individual crab in each stage, Z1-C5, was used to calculate the proportion by stage for each positive catch day. The mean proportional contribution by stage was then calculated for biweekly time bins and visualized.

Daily mean seawater temperatures (Otter Island Tidbit sensors) and air temperatures (National Weather Service, Saint Paul Island Airport) were computed and visualized to assess changes in pelagic habitat occurring over the course of spring and summer seasons and potential impacts on crab settlement.

3. Results

3.1. Juvenile crab abundance indices

In 2017–2019, total age-0 king crab catch from settlement collectors consisted of 5.2% blue king crab ($n = 8$, Fig. 2A) and 94.8% red king crab ($n = 145$, Fig. 2B). In contrast, 1983–1984 total age-0 king crab catch from rock dredges was composed of 96.3% blue king crab ($n = 309$, Fig. 2C) and 3.7% red king crab ($n = 12$, Fig. 2D) (Table A1).

3.1.1. Blue king crab

Mean CPUE (ind. per settlement collector) per year was 0.02 in 2017, 0.09 in 2018, and 0 in 2019 (Table 2). Individual crabs were caught at stations west of Saint Paul Island ($n = 4$), Otter Island ($n = 2$), Walrus Island ($n = 1$), and inside the village harbor ($n = 1$). Crab CL ranged from 2.55 to 3.34 mm (juvenile stages C2 and C3). Current settlement sites match the historical distribution.

3.1.2. Red king crab

Total combined catch from 2017 to 2019 of juvenile red king crab was 192, with 145 age-0 and 47 age-1 individuals. All age-0 individuals were found in settlement collectors and divers caught all but one age-1 crab. Mean CPUE (ind. per collector) per year differed among years (one-way, mean parameterized ANOVA: df = 3, $F = 15.77$, $p < 0.0001$) at 0.75 in 2017, 0.20 in 2018, and 0.66 in 2019 (Table 2). In post hoc comparisons, catches were significantly higher in 2017 versus 2018 (Tukey's test, $p = 0.0389$) and no significant differences were observed between 2017–2019 or 2018–2019. In 2017, collectors with Shell T1 had a higher mean CPUE of juvenile red king crab (GNSH; $N = 33$, CPUE = 0.99 ind./collector, SE = 0.27) than gillnet collectors (GN; $N = 46$, CPUE = 0.72, SE = 0.23) (df = 2, $F = 11.34$, $p = 0.0002$). Crab CL from settlement collections ranged from 1.45 to 3.67 mm for age-0 stages C1–C3. Age-1 crab CL ranged from 6.67 to 13.57 mm for stages C6–C13. Four larger juveniles were found on dock pilings in Village Harbor, ranging from 34.36 to 44.07 mm CL.

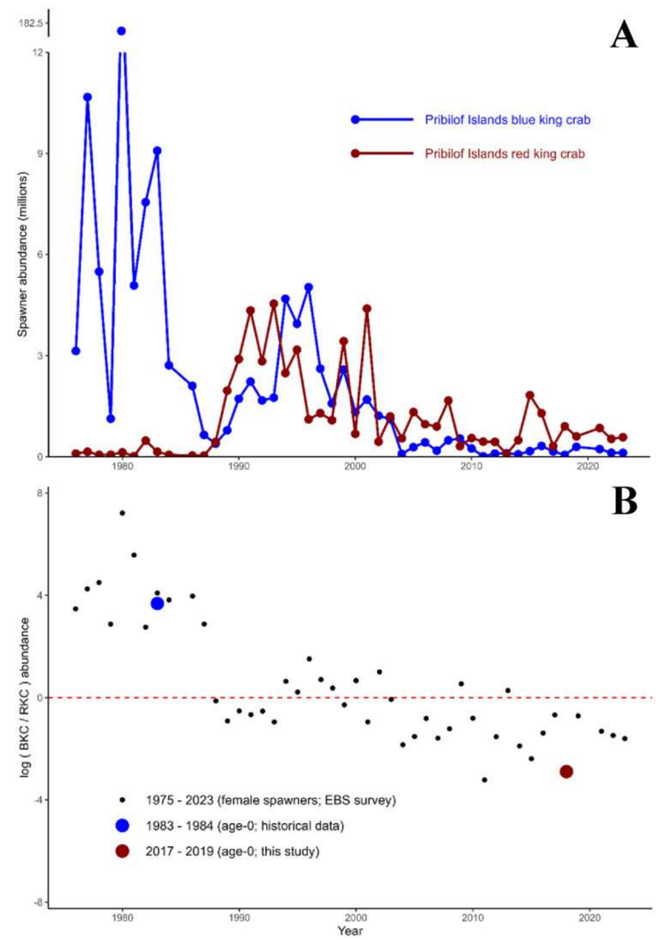
3.1.3. SCUBA observations of king crab

No juvenile blue king crab and three age-1 red king crab (6–13 mm CL) were found during intensive quadrat surveys. Opportunistic roving diver searches (<5 per min dive) observed higher abundances of age-1 red king crab in 2018 ($n = 33$) and 2019 ($n = 13$), as compared to 2017 ($n = 1$). Most juvenile red king crab were observed on top of large boulders among complex encrusting epifauna communities or near large macroinvertebrates such as anemones and sea stars. Anecdotal evidence suggests crabs' typical response to divers was to stay motionless and cling to the substrate. No adult king crabs were observed.

3.1.4. Spawner abundance relative to juveniles

EBS survey abundance estimates from 1976 to 1985 and from 2013 to 2023 show that mean blue king crab mature-sized female abundance declined from ~23 to ~0.16 million individuals. In contrast, mean red king crab mature-sized female abundance increased from ~0.13 to ~0.75 million individuals. Blue king crab females were 180 times more abundant than red king crab in 1976–1985 but were four times less abundant than red king crab in 2013–2023 (Fig. 3A). The relative abundance of spawners significantly shifted to red king crab from blue king crab over the time series. A similar shift occurred in age-0 catch ratios between 1983–1984 and 2017–2019 (Fig. 3B).

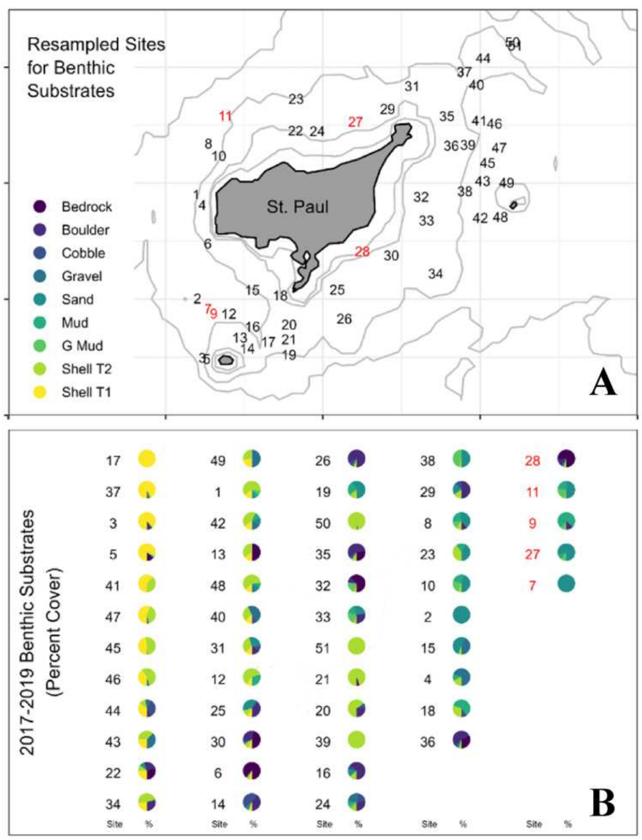
Fig. 3. Relative change in female spawner crab abundances from 1976 to 2023 compared to age-0 settlement-stage crab abundances from 1983–1984 and 2017–2019 studies for blue king crab (BKC, *Paralithodes platypus*) and red king crab (RKC, *Paralithodes camtschaticus*) in the Pribilof Islands. (A) Estimated abundances of mature-sized female spawners (millions of crab) from the annual National Oceanic and Atmospheric Administration Eastern Bering Sea bottom trawl survey (Szuwalski 2022; Stockhausen 2023; Zacher et al. 2023). (B) Log-transformed ratio of blue king crab to red king crab spawner abundances from the trawl survey timeseries (black circles) with similar catch ratios plotted for newly-settled age-0 crab estimated from the 1983–1984 (large blue circle) and 2017–2019 (large red circle) studies.



3.2. Sea floor substrate assessment relative to juvenile crab settlement

Quantitative percent cover estimates of sea floor substrates were achieved at a total of 103 sites from 2016 to 2019, with 51 of these sites overlapping with historically sampled stations (Fig. 4A). A total of 46 sites (90%) had at least one common substrate type recorded in both 1983–1984 and 2017–2019. The remaining five sites (10%) had no common substrates. Most sites had multiple substrates present. Twelve

Fig. 4. Relative comparison of benthic substrates at 51 stations sampled near Saint Paul Island in both modern (2017–2019) and historical (1983–1984) periods at locations formerly occupied by Pribilof Islands juvenile blue king crab (*Paralithodes platypus*). Historical, qualitative observations were based on beam trawl and rock dredge observations. Modern quantitative observations were based on video and still image analyses. (A) Approximately 90% of resampled station locations surrounding Saint Paul Island showed no discernable change in benthic habitat substrate over time, whereas five stations (∼10% total, red font) did not share any common substrates and were deemed to have qualitatively changed over time. (B) Quantitative visualization of physical substrate composition and habitat type (percent cover) at each resampled station. Pie slices (colors) represent substrate types identified in Panel A. Pies are ordered left-to-right by column based on decreasing percent cover of intact shellhash Type 1 substrate. Shell T1 locations are generally concentrated east and south of Saint Paul Island.



sites had greater than 20% cover of intact shellhash Type 1 (Fig. 4B, left-most column).

By incorporating previously published data on benthic habitat at a larger number of sites ($n = 436$), the modeled cover and distribution of rocks, grains, intact Shell T1, and crushed Shell T2 (Figs. 5A–5D) provides a comprehensive depiction of Saint Paul Island nearshore habitats similar to the historical period (Fig. A2). Coastlines and intertidal zones in windward (south and west) facing areas are typically rough, rocky cliffs while leeward (north and east) coastlines are low-lying sandy beaches and dunes separated by rocky promontories (Fig. 5A). Adjacent, submerged rocky reefs give way to grain-based habitats at ∼20–30 m depth (Fig. 5B). Intact Shell T1 material occurs almost exclusively in leeward areas to the east of Saint Paul Island along the 40–50 m isobath (Fig. 5C). Crushed Shell T2 material was typically found with intact shells but had much wider and mixed distribution (Fig. 5D).

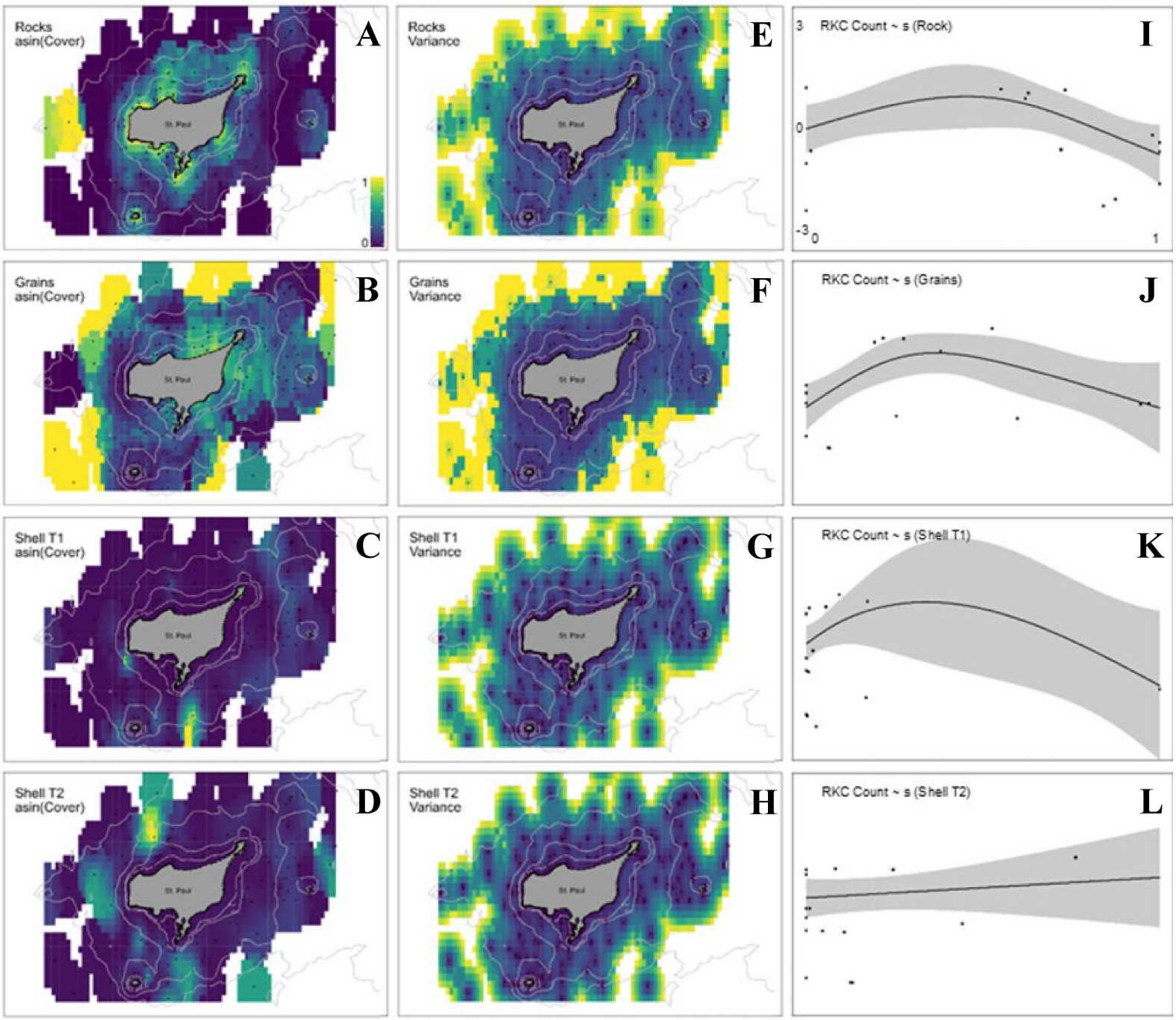
GAM models for red king crab catch associations with nearby substrate types was analyzed at 17 sites (Table 3). Settlement of red king crab appears to be higher in complex, multiple substrate seafloor habitats while lower catches are associated with single-substrate habitats (Figs. 5I–5L). The number of age-0 red king crab per site increased significantly in habitats composed of larger grain sizes (arcsine transformed percent cover) to intermediate values and in habitats composed of small grain sizes ($p = 0.009$, Dev. Exp. = 51%, Fig. 5J). Red king crab catches were also significantly higher ($p = 0.054$) at intermediate values of rocky habitat, explaining nearly 37% of model deviation (Fig. 5I). No significant relationships between red king crab catches and intact Shell T1 or crushed Shell T2 were observed, although the model performed better for Type 1 (Dev. Exp. = 27%, Fig. 2.5K) than Type 2 (Dev. Exp. = 3%, Fig. 5L).

3.3. Seasonal development of age-0 king crab relative to temperature

In 2017–2019, zooplankton net deployments ($n = 14$) caught two blue king crab and 20 red king crab. In 1983–84, zooplankton net deployments ($n = 155$) caught 2595 blue king crab and 766 red king crab. Earliest zooplankton sampling in April 1984 showed low abundance but proportionally high occurrence (>75%) of stage 1 zoeae, signaling the recent start of egg hatch. Peak crab larval abundance in the water column occurred in May 1983, consisting primarily of the first two zoeal stages (66%–98%), with a few zoeae 3 (Fig. 6A, Table A2). Larval catch in late May (2017 and 2018) progressed from zoeal stage 4 to post-larval glaucothoe by late June. No larvae or glaucothoe king crab were caught in July and August in any year. Rock dredges and settlement collectors were utilized to examine benthic settlement of blue king crab and red king crab (age-0, C1–C5) from late July through early September. Juvenile instar stages C1, C2, and C3 were caught with increasing age over that late summer period: C1 primarily in late July and early August (48%–71%), C2 throughout August and in highest abundances, and C3 primarily occurring late August through early September (65%–72%). A few C4–C5 stages appeared in late August and September.

Summer seawater temperatures increased in all years from ∼4–6 °C in early summer to 9–10 °C by late summer (Fig. 6B) and were 1–2 °C warmer throughout the season in 2019 compared to 2017 and 2018. In comparison, historical seawater temperatures in September were close to those in 2017 and 2018 (8–9 °C). May 1983 and April 1984 spring seawater temperatures were very cold (−1 °C) with observed sea ice cover in the Pribilof Islands. Spring sea ice was absent in 2017–2019. Similar heating trends exist between seawater and air temperatures (Fig. 6C); however, air temperatures were

Fig. 5. Krige interpolations of benthic substrate cover and generalized additive model (GAM) results testing associations between substrate type and cover with total age-0 red king crab (RKC, *Paralithodes camtschaticus*) settler abundance in crab collectors from 17 stations sampled between 2017 and 2019 in nearshore nursery habitats of Saint Paul Island, Alaska. A–D) Percent substrate cover (arcsine-transformed percent cover) for each substrate type was interpolated separately using all available habitat data. Maximum distance of interpolation was set at 0.045 decimal degrees (~2.7 km). High percent cover of substrates are in light colors (blue ~25%–50%, green ~50%–75%, and yellow ~75%–100%) while low cover substrates are the darkest color (purple ~0%–25%). E–H) Estimated krige model variance for each substrate. I–L) GAM-predicted RKC abundance (log-scale) partial residuals with 95% confidence bands (*y*-axis scale, 3 to −3) predicting RKC collector counts per station as a function of substrate cover (*x*-axis scale, 0–1).



typically 1–2 °C warmer than water temperatures and reached upwards of 12 °C in 2016 and 2019.

4. Discussion

We observed a very low abundance of larval and settler blue king crab in both pelagic and benthic habitats and infer that low larval supply is likely causing the sustained low level of abundance of the Pribilof Islands blue king crab stock. Benthic nursery habitats were relatively unchanged, and we suggest that the availability of complex habitats are not likely limiting. We caught only ten total blue king crab over three years: one larva, one post-larval glaucothoe, and eight benthic age-0 crabs. Seven of the newly settled blue king crab were caught with collectors at resampled historical sites (Fig. 2A/2C). This study is the first to use these settlement collectors to capture juvenile blue king crab and it is possible that the collectors are ineffective for sampling blue king crab. However, the prevalence of red king crab in the settlement collectors suggests otherwise. Additional evidence of a very

Table 3. Modeled substrate habitat cover and substrate association to juvenile red king crab (RKC, *Paralithodes camtschaticus*) catch in sausage-shaped artificial collectors (SAC) for assessment of settlement potential in nursery habitats near Saint Paul Island for 2017–2019.

KRIG interpolation Substrate cover	*N*	N grids	Range (dec.deg.)		Bias (ME) [a]		Error (MSNE ∼ 1) [a]
Arcsine (Rocks) ∼ 1	436	2695	0.0162		−0.030		0.74
Arcsine (Grains) ∼ 1	436	2695	0.0093		0.016		0.86
Arcsine (Shell T1) ∼ 1	436	2695	0.0474		0.002		2.88
Arcsine (Shell T2) ∼ 1	436	2695	0.1544		0.007		4.63
GAM: Negative binomial [b]			Predictor ∼ substrate cover ($k = 4$)				
Response: RKC SAC count	***N***	**edf**	**Chi.sq**	**R-sq. (adj.)**	***p*-value**	**AIC**	**Dev. Exp. (%)**
Count ∼ s(Rocks)	17	2.03	7.03	0.30	0.054	108.3	36.6
Count ∼ s(Grains)	17	2.44	13.99	0.33	0.009	105.1	51.3
Count ∼ s(Shell T1)	17	1.87	4.83	0.12	0.107	110.1	27.3
Count ∼ s(Shell T2)	17	1.00	0.51	−0.04	0.474	112.9	3.0

Note: Kriging (KRIG) model interpolation equation and validation statistics including number of data points (N), number of grids interpolated (N Grids), range limit of spatial correlation among pairs of data points measured in decimal degrees, model bias/mean error (ME), and mean square normalized error (MSNE). Generalized additive model (GAM) results using a negative binomial process to estimate substrates relationship with observed RKC catch (Predictor). GAM summary statistics including number of stations (data points, N), effective degrees of freedom (edf), chi-square, *R*-square, and *p* test statistics, Akaike Information Criterion score (AIC), and the percent of residual deviance explained by the model (Dev. Exp.). Final GAMs were refit with restricted maximum likelihood (REML).
[a] KRIG performance metrics: Bias (ME) best near ∼0 and Error (MSNE) best near ∼1.
[b] Negative binomial models selected outperformed Poisson models by maximum likelihood (ML) comparison.

low supply of juvenile blue king crab was the complete absence of age-1 juveniles in diver and camera surveys.

Settled red king crab are similarly in low supply in the Saint Paul Island region, yet settler abundances were higher in 2017–2019 relative to 1983–1984 (Fig. 2B–2D). Previously (1983/1984) rare red king crab juveniles are now common and appear to be more widely dispersed throughout nearshore nursery habitats. Annual age-0 mean CPUE of red king crab settlers ranged from 0.20 to 0.82 ind. per collector, which is lower than previous studies using similar collector bags near Kodiak, Alaska (∼2–8 ind. per collector) (Donaldson et al. 1992; Blau and Byersdorfer 1994; Murphy and Blau 2002) and Juneau, Alaska (∼2–5 ind. per collector) (Loher and Armstrong 2000; Pirtle and Stoner 2010). We observed a lower catch in 2018 settlement collectors relative to 2017 and 2019. We suspect that poor weather (increased storms and weather damage to gear) reduced gear performance in 2018. Red king crab settlement within collectors, larval capture in plankton tows, and age-1 crab observations by divers suggests a consistently low supply of juvenile red king crab to the benthos in the study area.

We successfully used settlement collectors to assess juvenile king crab supply in the Saint Paul Island area. Population assessments conducted with trawls are not able to effectively sample age-0 or age-1 juvenile king crab due to large gear mesh size and inability to sample in rocky habitats (Szuwalski 2022; Stockhausen 2023). Similar artificial collectors have been used to create reliable larval recruitment indices for other important shellfish stocks including USA West Coast Dungeness crab (Rasmuson et al. 2022), East Coast lobsters and blue crab (Hovel and Lipcius 2001; Wahle et al. 2012; White et al. 2024), and Australian scallops and lobsters (Phillips and McWilliam 1986; Sause et al. 1987).

Juvenile blue king crab settlers have a dorsal-ventral flattened carapace, reduced carapace spines, white carapace coloration, and candy cane striped leg coloration (red/white alternating bands); all traits that benefit juvenile crab occupation, movement, and crypsis within complex shellhash structures (Tapella et al. 2009). Field observations and modeled Shell T1 distribution shows a distinct habitat band at 170°W along the 40 m depth contour. Our few settlement collectors near this habitat band did not outperform collectors located elsewhere relative to blue king crab catch. Future and increased density of sampling in this habitat band is recommended to confirm juvenile blue king crab occupation.

In contrast, juvenile red king crab are now more widespread across the study region and inhabit a variety of complex substrates (Stevens and Kittaka 1998; Loher and Armstrong 2000; Pirtle and Stoner 2010). Red king crab morphology and behaviors likely allow for more general habitat associations, as larger carapace spines, more variable coloration, and increased aggression aids both crypsis and survival (Dew 1990; Long et al. 2012). The apparent expansion of juvenile red king crab near Saint Paul Island in this study is likely driven by a stable supply of larvae, plasticity in settlement habitat selection, reduced competition with blue king crab, and continued benthic habitat protections and enforcement of no-trawl zones.

The near complete lack of settlement in Pribilof Islands blue king crab after two decades without directed fisheries appears to be driven by limited larval supply from low spawning stock abundance and contributing environmental changes. Bottom-up controls (Hairston et al. 1960) such as habitat availability and temperature changes may provide local indicators relative to the status of the EBS

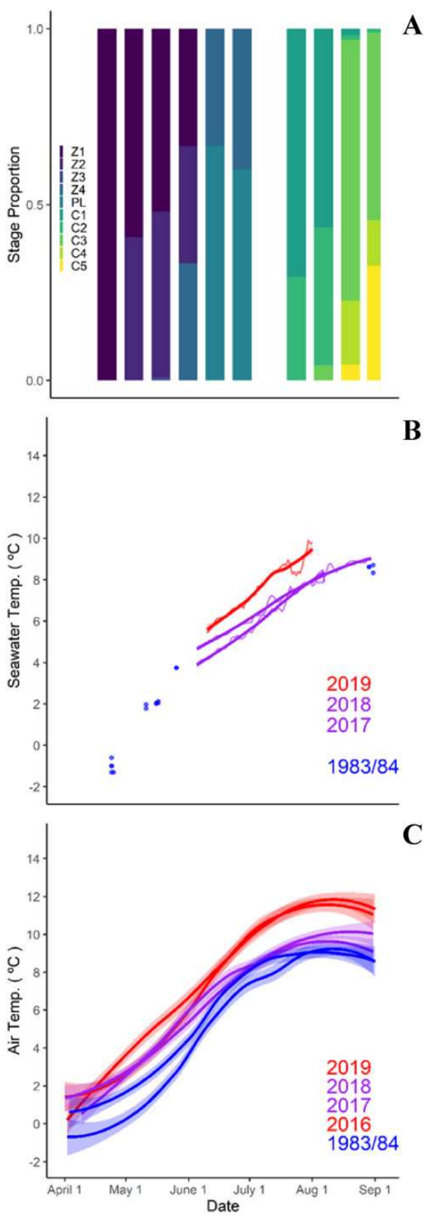


Fig. 6. Seasonal larval and post-larval development time of combined blue king crab (*Paralithodes platypus*) and red king crab (*Paralithodes camtschaticus*) catches in nearshore Saint Paul Island, Alaska pelagic and benthic habitats relative to seawater and air temperature trends in study years 1983–1984 and 2016–2019. (A) Proportional stage composition of early larval zoeal (Z1–Z4), post-larval glaucothoe (PL), and benthic crabs (C1–C5) by sampling period (14 days). Mean proportions were estimated for biweekly periods from April to early September (minimum ordinal date 90, maximum ordinal date 254). (B) Mean daily bottom (35 m depth) seawater temperatures by ordinal day east of Otter Island at our Otter, Northeast Station for 2017–2019 (thin lines) with LOESS smoother (heavy lines). Nearest historical (1983–1984) bottom temperature data (blue circles) were located within a few kilometers of the 2017–2019 station. (C) US National Weather Service, Saint Paul Airport Station mean daily air temperatures by ordinal day covering the larval period and settlement windows across all years of historical and recent study observation.

ecosystem (Samhouri et al. 2014; Siddon 2023). Top-down controls (Fretwell 1987) such as fish predation do not appear to be a limiting factor at present for juvenile king crab in low densities. For example, in our companion study no predation events occurred at a near-coastal (i.e., natural) site during juvenile red king crab tethering experiments and no larval or juvenile king crab were observed in fish diet analyses (Weems 2024).

Blue and red king crab settlement is influenced by the development of planktotrophic larvae prior to transition to the benthos. Our assessment of early life king crab development in nearshore habitats shows peak larval hatch, pelagic development, and settlement occurs between early spring and middle summer. Historically, winter sea ice has surrounded the Pribilof Islands from January to March creating supercooled seawaters (−1.7 to 0 °C) that linger into early summer (Kowalik and Stabeno 1999; Hunt et al. 2008). Reduced sea ice cover and warmer conditions are more prevalent today which may change larval developmental rates and pelagic duration, delivery mechanisms to complex habitats, or access to lipid-rich food resources (e.g., diatoms *Thalassiosira* spp.) (Copeman et al. 2012, 2014; Stevens 2014).

Successful larval dispersal and settlement are impacted by local oceanographic conditions, which appears to vary with the regional climate. Possible evidence for this comes from individual-based models (IBM) linked to regional ocean modeling systems (ROMS), which have been the primary tool for predicting larval transport relative to environmental conditions. A developing Pribilof Islands blue king crab ROMS–IBM suggests circular water flow and surface transport towards the islands in the Pribilof Islands domain may be strengthened in the mid-summer period during warm years (C. Parada and R. Foy, University of Concepción Chile and NOAA Juneau, personal communications, 2023). In a warming climate this may create a potential missmatch in larval delivery to nursery habitats, where larvae may be released outside of the oceanographic front delineating the Pribilof domain and settlers may be dispersed away from complex nearshore habitats. Blue king crab distributions (including spawners) from the summer trawl survey are centered east and north of Saint Paul and Saint George Islands near the edge of the EBS cold pool (Zacher et al. 2023). If blue king crab spawners prefer cool waters (Somerton 1985; Somerton and Macintosh 1985), reduction of the cold pool and increasing nearshore temperatures under climate change may draw spawners to deeper waters outside of the Pribilof oceanographic domain. Furthermore, the nearest blue king crab stock at Saint Matthew Island is downstream and not connected to the Pribilof Islands stock in larval transport simulations, which is supported by some observable genetic divergence between the stocks (Stoutamore 2014). Very few blue king crab have ever been observed upstream along the Alaska Peninsula or in Bristol Bay (McMurray et al. 1984; Zacher et al. 2023).

Pribilof Islands red king crab settlers may originate from local spawners as well as the remote Bristol Bay stock. We presume local Pribilof Islands spawners are the primary source of larvae given our observed settler supply and distribution, a wide footprint of adults in recent trawl years (Zacher et al. 2023), and ROMS–IBM simulations suggesting nearshore retention of larvae and post-larvae (Daly et al. 2020). Daly et al. (2020) also suggest that under certain environmental conditions red king crab larvae produced along the southwest Alaska Peninsula may have a greater opportunity for offshore and northwesterly advection toward the Pribilof Islands. Weakening of southwesterly winds along the Alaska Peninsula in the spring under warm climate conditions may cause a relaxation of nearshore currents and reduced larval advection toward inner Bristol Bay. It is possible that a pulse of larval cohorts from the Peninsula to the Pribilofs may have contributed to the increases in Pribilof Islands red king crab in the late 1980s. Today, the southwest portion of the Bristol Bay red king crab stock has largely disappeared (Armstrong et al. 1993; Dew and McConnaughey 2005; Zacher et al. 2023). Therefore, the quantity of larvae supplied to the Pribilofs from Bristol Bay as described may be limited. Homogenous genealogy among southeast Bering Sea red king crab stocks spread across Bristol Bay, Pribilof, and Northern Districts supports some level of mixing (Grant and Cheng 2012; Vulstek et al. 2013), although new genomic methods may provide more stock delineation (C. St. John, Cornell University Ithaca, personal communications, 2023).

The Pribilof Island blue king crab stock is unlikely to rebuild given the very low rate of larval supply observed in this study and is clearly recruitment limited. Two rebuilding plans have failed to produce spawner recovery, though they have provided beneficial habitat protections and fishing exclusion zones (Salveson 2004; Foy et al. 2014). In 2024, the EBS survey failed to catch any Pribilof Island blue king crab—a time-series first (M. Litzow, NOAA Kodiak, personal communications, 2024). Low abundances of blue king crab may be sustained through an Allee effect (Allee 1927; Myers et al. 1995), particularly reduced mating success. The ratio of blue king crab settlers to red king crab settlers mirrors the spawner ratios in historical and modern periods and suggests that larval survival and delivery rates are similar between the species. Differential larval survival, such as increased predation during settlement or early juvenile stages, does not appear to be a likely explanation for depensation in blue king crab (Weems 2024). In contrast, low abundances of Pribilof Islands red king crab are considered healthy (status > two times B_{msy}) and model-estimated recruitment appears to be sufficient to maintain this population (Szuwalski 2022). This further suggests that were the blue king crab spawning stock at a higher level of abundance, recruitment through the early benthic phase would likewise increase commensurately. The very low abundance of spawners combined with almost no recruitment to the benthos suggests that alternative approaches for rebuilding should be considered, such as stock rehabilitation through aquaculture and stock enhancement (Stevens 2006*b*; Daly and Swingle 2013; Reum et al. 2020). However, such an effort should be preceded by studies examining survival and growth of early benthic phase blue king crabs to determine if other processes, including changed spawning location, errant larval dispersal, or competition with similarly-aged red king crab, are further precluding blue king crab recovery in the system.

Acknowledgements

This work was completed with the support of the Saint Paul Island community and the authors acknowledge the Unangax̂ peoples as rightful stewards of the land and sea in the Pribilof Islands. We would like to thank the North Pacific Research Board, Bering Sea Fisheries Research Foundation, Central Bering Sea Fisherman's Association, City Government of Saint Paul, Alaska King Crab Research, Rehabilitation and Biology Program, Alaska Department of Fish and Game, and UAF Graduate School for additional support. Undergraduate technicians A. Filardo, D. Lowrey, K.L. Reece, J. Renee, and RV *Lunax̂* Captain R. Warner were invaluable to our field work. We additionally thank F. Mueter, D. Kimmel, B. Daly, C. Siddon, D. Armstrong, and our anonymous reviewer for their valuable comments on this manuscript.

Article information

History dates

Received: 5 August 2024
Accepted: 17 October 2024
Accepted manuscript online: 27 January 2025
Version of record online: 3 March 2025

Data availability

A project final report, datasets, code, and videos are permanently archived by NPRB and available online by searching NPRB Core Project 1608 (https://nprb.org/project-search/#metadata/0df136dc-2c01-4c2b-8305-cdec02eb3bd3/project/files) and through DataONE (https://doi.org/10.24431/rw1k6br).

Author information

Author ORCIDs

Jared D. Weems https://orcid.org/0000-0001-5784-5707
W. Christopher Long https://orcid.org/0000-0002-7095-1245
Lauren M. Divine https://orcid.org/0000-0002-0695-0176
Ginny L. Eckert https://orcid.org/0000-0002-7538-7081

Author notes

Present address for Jared D. Weems is Alaska Department of Fish and Game, Commercial Fisheries Division, Kodiak, Alaska 99615, USA.

Author contributions

Conceptualization: JDW, WCL, LMD, GLE
Data curation: JDW
Formal analysis: JDW
Funding acquisition: JDW, WCL, GLE
Investigation: JDW, WCL, LMD, GLE

Methodology: JDW, WCL, GLE
Project administration: JDW, GLE
Resources: JDW, WCL, LMD
Software: JDW
Supervision: GLE
Validation: JDW, WCL, GLE
Visualization: JDW
Writing – original draft: JDW
Writing – review & editing: JDW, WCL, LMD, GLE

Competing interests

The authors declare there are no competing interests.

Funding information

This research was supported by the North Pacific Research Board (NPRB #1608).

References

Allee, W.C. 1927. Animal Aggregations. Q. Rev. Biol. **2**(3): 367–398. doi:10.1086/394281.

Armstrong, D., Long, W.C., Armstrong, J.J., McDonald, P.S., Kvistad, J., Doty, A., et al. 2015. Blue king crab, habitat, and the ecosystem: Data rescue from the 1980s. North Pacific Research Board Report Final Report **1321**: 1–27.

Armstrong, D.A., Armstrong, J.L., Jenson, G., Palacios, R., and Williams, G. 1987. Distribution, abundance, and biology of blue king and Korean hair crabs around the Pribilof Islands. U.S. Department of Commerce, NOAA, Outer Continental Shelf Environmental Assessment Program Final Report. **67**: 1–278.

Armstrong, D.A., Armstrong, J.L., Palacios, R., Williams, G., Jensen, G.C., and Pearson, W. 1985. Early life history of juvenile blue king crab, *Paralithodes platypus*, around the Pribilof Islands. *In* Proceedings of the International King Crab Symposium. *Edited by* S.K. Davis, F. Gaffney, J. McCrary, A.J. Paul and R.S. Otto. Alaska Sea Grant Program, University of Alaska Fairbanks. AK-SG-85-12: 211–229.

Armstrong, D.A., Wainwright, T.C., Jensen, G.C., Dinnel, P.A., and Andersen, H.B. 1993. Taking refuge from bycatch issues: red king crab (*Paralithodes camtschaticus*) and trawl fisheries in the Eastern Bering Sea. Can. J. Fish. Aquat. Sci. **50**(9): 1993–2000. NRC Research Press. doi:10.1139/f93-223.

Blau, S.F., and Byersdorfer, S.C. 1994. Sausage-shaped artificial collector developed in Alaska to study young-of-year red king crabs. Bull. Mar. Sci. **55**(2–3): 878–886.

Burgos, J., Ernst, B., Armstrong, D., and Orensanz, J. 2013. Fluctuations in range and abundance of snow crab (*Chionoecetes opilio*) from the Eastern Bering Sea: what role for Pacific cod (*Gadus macrocephalus*) predation? Bull. Mar. Sci. **89**(1): 57–81. doi:10.5343/bms.2011.1137.

Copeman, L., Daly, B., Eckert, G.L., and Swingle, J. 2014. Storage and utilization of lipid classes and fatty acids during the early ontogeny of blue king crab, *Paralithodes platypus*. Aquaculture, **424-425**: 86–94. doi:10.1016/j.aquaculture.2013.12.025.

Copeman, L.A., Stoner, A.W., Ottmar, M.L., Daly, B., Parrish, C.C., and Eckert, G.L. 2012. Total lipids, lipid classes, and fatty acids of newly settled red king crab (*Paralithodes camtschaticus*): comparison of hatchery-cultured and wild crabs. J. Shellfish Res. **31**(1): 153–165. doi:10.2983/035.031.0119.

Daly, B., and Long, W.C. 2014. Intra-guild predation among early benthic phase red and blue king crabs: evidence for a habitat-mediated competitive advantage. J. Exp. Mar. Biol. Ecol. **451**: 98–104. doi:10.1016/j.jembe.2013.11.011.

Daly, B., Parada, C., Loher, T., Hinckley, S., Hermann, A.J., and Armstrong, D. 2020. Red king crab larval advection in Bristol Bay: implications for recruitment variability. Fish. Oceanogr. **29**(6): 505–525. doi:10.1111/fog.12492.

Daly, B., and Swingle, J.S. 2013. High-density nursery culture of recently-settled blue king crabs (*Paralithodes platypus*): comparisons to red king crabs (*Paralithodes camtschaticus*). Aquaculture, **416-417**: 196–200. doi:10.1016/j.aquaculture.2013.09.024.

Dew, C.B. 1990. Behavioral ecology of podding red king crab, *Paralithodes camtschatica*. Can. J. Fish. Aquat. Sci. **47**(10): 1944–1958. doi:10.1139/f90-219.

Dew, C.B., and McConnaughey, R.A. 2005. Did trawling on the brood stock contribute to the collapse of Alaska's king crab? Ecol. Appl. **15**(3): 919–941. doi:10.1890/03-5231.

Donaldson, W.E., Byersdorfer, S., Pengilly, D., and Blau, S.F. 1992. Growth of red king crab, *Paralithodes camtschaticus* (Tilesius, 1815) in artificial habitat collectors at Kodiak, Alaska. J. Shellfish Res. **11**: 85–89.

Epelbaum, A.B., Borisov, R.R., and Kovatcheva, N.P. 2006. Early development of the red king crab *Paralithodes camtschaticus* from the Barents Sea reared under laboratory conditions: morphology and behavior. J. Mar. Biol. Assoc. U.K. **86**: 317–333. doi:10.1017/S0025315406013178.

Foy, R.J., Miller, S., Stram, D., Fey, M., Lewis, S., Gasper, J.R., and Harrington, G.A. 2014. Final environmental assessment for proposed Amendment 43 to the Fishery Management Plan for Bering Sea /Aleutian Islands King and Tanner Crabs and proposed amendment 103 to the Fishery Management Plan for groundfish of the Bering Sea and Aleutian Islands to prevent overfishing and rebuild Pribilof Islands blue king crab. North Pacific Fisheries Management Council Report. Anchorage, Alaska. pp. 1–202. Available from https://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.698.8777&rep=rep1&type=pdf [accessed 9 August 2022].

Fretwell, S.D. 1987. Food chain dynamics: the central theory of ecology? Oikos, **50**(3): 291. doi:10.2307/3565489.

Gräler, B., Pebesma, E., and Heuvelink, G. 2016. Spatio-temporal interpolation using gstat. R J. **8**(1): 204–218. doi:10.32614/RJ-2016-014.

Grant, W.S., and Cheng, W. 2012. Incorporating deep and shallow components of genetic structure into the management of Alaskan red king crab. Evol. Appl. **5**(8): 820–837. doi:10.1111/J.1752-4571.2012.00260.X.

Gundlach, E.R., Kendziorek, M., Thomson, E., Whitney, J., and Sowles, A. 1999. Sensitivity mapping of the Pribil of Islands, Alaska, an area of extreme environmental sensitivity. *In* International Oil Spill Conference: Beyond 2000 Balancing Perspectives. Seattle, Washington. pp. 981–984. Available from http://meridian.allenpress.com/iosc/article-pdf/1999/1/981/1752753/2169-3358-1999-1-981.pdf.

Hairston, N.G., Smith, F.E., and Slobodkin, L.B. 1960. Community structure, population control, and competition. Am. Nat. **94**(879): 421–425. Science Press. doi:10.1086/282146.

Hartnoll, R.G. 2001. Growth in crustacea—Twenty years on. Hydrobiologia, **449**: 111–122. Springer, Dordrecht. doi:10.1007/978-94-017-0645-2_11.

Haynes, E. 1973. Descriptions of prezoeae and stage I zoeae of *Chionoecetes bairdi* and *C. opilio* (Oxyrhyncha, Oregoniinae). Fish. Bull. U.S. **71**(3): 769–775.

Haynes, E. 1984. Early zoeal stages of *placetron wosnessenskii* and *rhinolithodes wosnessenskii* (Decapoda, Anomura, Lithodidae) and review of lithodid larvae of the northern North Pacific Ocean. Fish Bull. U.S. **82**(2): 315–324.

Hoffman, E.G. 1968. Description of laboratory-reared larvae of *Paralithodes platypus* (Decapoda, Anomura, Lithodidae). J. Fish. Res. Board Can. **25**(3): 439–455. NRC Research Press. doi:10.1139/f68-039.

Hovel, K.A., and Lipcius, R.N. 2001. Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. Ecology, **82**(7): 1814–1829. doi:10.1890/0012-9658.

Hunt, G.L., Coyle, K.O., Eisner, L.B., Farley, E. V., Heintz, R.A., Mueter, F., et al. 2011. Climate impacts on Eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the oscillating Control hypothesis. ICES J. Mar. Sci. **68**(6): 1230–1243. doi:10.1093/icesjms/fsr036.

Hunt, G.L., Stabeno, P.J., Strom, S., and Napp, J.M. 2008. Patterns of spatial and temporal variation in the marine ecosystem of the southeastern Bering Sea, with special reference to the Pribilof Domain. Deep Sea Res. Part II, **55**(16–17): 1919–1944. doi:10.1016/j.dsr2.2008.04.032.

Jensen, G.C., Andersen, H.B., and Armstrong, D.A. 1992. Differentiating *paralithodes* larvae using telson spines: a tail of two species. Fish. Bull. U.S. **90**(4): 778–783.

Kittaka, J., Stevens, B.G., Teshima, S., and Ishikawa, M. 2002. Larval culture of king crabs *Paralithodes camtschaticus* and *P. brevipes*. *In* Crabs in cold water regions: biology, management, and economics. *Edited by* A.J. Paul, E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie and T.C. Shirley. Alaska Sea Grant College Program, University of Alaska Fairbanks. pp. 189–209. Available from. doi:10.4027/ccwrbme.2002.15.

Konishi, K., and Shikatani, N. 1999. Identification manual for larvae of commercially important crab in Japan. II. Anomuran crabs. Bull. Natl. Res. Inst. Aquacult. **28**: 5–13.

Kowalik, Z., and Stabeno, P. 1999. Trapped motion around the Pribilof Islands in the Bering Sea. J. Geophys. Res. Oceans, **104**(C11): 25667–25684. Blackwell Publishing Ltd. doi:10.1029/1999jc900209.

Kurata, H. 1963. Larva of Decapod Crustacea of Hokkaido: 1. Atelecyclidae (Atelecyclinae), 2. Majidae (Pisinae), 5. Paguridae (Anomura), 6. Lithodidae (Anomura), 7. Porcellanidae (Anomura). Bull. Hokkaido Reg. Fish. Res. Lab. **27**: 13–70.

Livingston, P.A. 1989. Interannual trends in Pacific cod, *Gadus macrocephalus*, predation on three commercially important crab species in the Eastern Bering Sea. Fish. Bull. U.S. **87**(4): 807–827.

Loher, T., and Armstrong, D.A. 2000. Effects of habitat complexity and relative larval supply on the establishment of early benthic phase red king crab (*Paralithodes camtschaticus* Tilesius, 1815) populations in Auke Bay, Alaska. J. Exp. Mar. Biol. Ecol. **245**(1): 83–109. doi:10.1016/s0022-0981(99)00157-4.

Long, W.C., and Daly, B. 2017. Upper thermal tolerance in red and blue king crab: sublethal and lethal effects. Mar. Biol. **164**: 162. doi:10.1007/S00227-017-3190-1.

Long, W.C., Popp, J., Swiney, K.M., and Van Sant, S.B. 2012. Cannibalism in red king crab, *Paralithodes camtschaticus* (Tilesius, 1815): effects of habitat type and predator density on predator functional response. J. Exp. Mar. Biol. Ecol. **422-423**: 101–106. doi:10.1016/J.JEMBE.2012.04.019.

Long, W.C., Van Sant, S.B., and Haaga, J.A. 2015. Habitat, predation, growth, and coexistence: could interactions between juvenile red and blue king crabs limit blue king crab productivity? J. Exp. Mar. Biol. Ecol. **464**: 58–67. doi:10.1016/j.jembe.2014.12.011.

Long, W.C., Van Sant, S.B., Swiney, K.M., and Foy, R.J. 2017. Survival, growth, and morphology of blue king crabs: effect of ocean acidification decreases with exposure time. ICES J. Mar. Sci. **74**(4): 1033–1041. doi:10.1093/icesjms/fsw197.

Lyons, C., Eckert, G., and Stoner, A.W. 2016. Influence of temperature and congener presence on habitat preference and fish predation in blue (*Paralithodes platypus* Brandt, 1850) and red (*P. camtschaticus* Tilesius, 1815) king crabs (Anomura: Lithodidae). J. Crustac. Biol. **36**(1): 12–22. doi:10.1163/1937240X-00002391.

Makarov, R.R. 1967. Larvae of the shrimps and crabs of the West Kamchatkan shelf and their distribution (Translation of Russian Book by B. Haiga and A.L. Rice). National Lending Library for Science and Technology. pp. 199.

McMurray, G., Vogel, A.H., Fishman, P.A., Armstrong, D.A., and Jewett, S.C. 1984. Distribution of larval and juvenile red king crabs (Paralithodes camtschatica) in Bristol Bay. U.S. Department of Interior, Minerals Management Service, Alaska OCS Region. Anchorage, Alaska.267–477 [accessed 8 March 2022].

Morado, J., Shavey, C., Ryazanova, T., and White, V. 2014. Diseases of king crabs and other anomalies. *In* King Crabs of the World. CRC Press. pp. 139–210. doi:10.1201/b16664-7.

Murphy, M.C., and Blau, S.F. 2002. Post-larval red king crab density dependence in artificial collectors, Kodiak, Alaska. *In* High Latitude Crabs: Biology, Management, and Economics. University of Alaska Fairbanks, Anchorage, Alaska. pp. 545–547. Available from https://seagrant.uaf.edu/bookstore/pubs/AK-SG-96-02.html [accessed 22 April 2021].

Myers, R.A., Barrowman, N.J., Hutchings, J.A., and Rosenberg, A.A. 1995. Population dynamics of exploited fish stocks at low population levels. Science, **269**(5227): 1106–1108. Am Assoc Adv Sci. doi:10.1126/SCIENCE.269.5227.1106. PMID: 17755535.

National Research Council. 2011. Guide for the Care and Use of Laboratory Animals(8th ed.). National Academies Press. doi:10.17226/12910NOAA.

Office of Coast Survey. 2020. NOS Bathymetric Maps: Chart 16382, Edition 12.

Oliver, M.A., and Webster, R. 2014. A tutorial guide to geostatistics: Computing and modelling variograms and kriging. Elsevier. doi:10.1016/j.catena.2013.09.006.

Orensanz, J., Ernst, B., Armstrong, D.A., Stabeno, P., and Livingston, P. 2004. Contraction of the geographic range of distribution of snow crab (*Chionoecetes opilio*) in the Eastern Bering Sea: an environmental ratchet? Calif. Coop. Ocean. Fish. Investig. Rep. **45**: 65–79.

Palacios, R., Armstrong, D.A., Armstrong, J.L., and Williams, G. 1985. Community analysis applied to characterization of blue king crab habitat around the Pribilof Islands. *In* Proceedings of the International King Crab Symposium. *Edited by* S.K. Davis, F. Gaffney, J. McCrary, A.J. Paul and R.S. Otto. Alaska Sea Grant Program, University of Alaska Fairbanks. AK-SG-85-12: 193–209.

Pante, E., Simon-Bouhet, B., and Irisson, J. 2023. Marmap: import, plot and analyze bathymetric and topographic data. R package version 1.0.1. Available from https://CRAN.R-project.org/package=marmap.

Phillips, B.F., and McWilliam, P.S. 1986. The pelagic phase of spiny lobster development. Can. J. Fish. Aquat. Sci. **43**(11): 2153–2163. NRC Research Press Ottawa, Canada. doi:10.1139/F86-264.

Pirtle, J.L., Eckert, G.L., and Stoner, A.W. 2012. Habitat structure influences the survival and predator-prey interactions of early juvenile red king crab *Paralithodes camtschaticus*. Mar. Ecol. Prog. Ser. **465**: 169–184. doi:10.3354/meps09883.

Pirtle, J.L., and Stoner, A.W. 2010. Red king crab (*Paralithodes camtschaticus*) early post-settlement habitat choice: structure, food, and ontogeny. J. Exp. Mar. Biol. Ecol. **393**(1–2): 130–137. doi:10.1016/j.jembe.2010.07.012.

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Rasmuson, L.K., Jackson, T., Edwards, C.A., O'Malley, K.G., and Shanks, A. 2022. A decade of modeled dispersal of Dungeness crab *cancer magister* larvae in the California Current. Mar. Ecol. Prog. Series, **686**: 127–140. doi:10.3354/MEPS13993.

Renner, H.M., Mueter, F., Drummond, B.A., Warzybok, J.A., and Sinclair, E.H. 2012. Patterns of change in diets of two piscivorous seabird species during 35 years in the Pribilof Islands. Deep-Sea Res. II Top Stud. Oceanogr. **65–70**: 273–291. doi:10.1016/j.dsr2.2012.02.014.

Reum, J.C.P., McDonald, P.S., Long, W.C., Holsman, K.K., Divine, L., Armstrong, D., and Armstrong, J. 2020. Rapid assessment of management options for promoting stock rebuilding in data-poor species under climate change. Conserv. Biol. **34**(3): 611–621. doi:10.1111/COBI.13427. PMID: 31663172.

Richar, J.I., Kruse, G.H., Curchitser, E., and Hermann, A.J. 2015. Patterns in connectivity and retention of simulated Tanner crab (*Chionoecetes bairdi*) larvae in the Eastern Bering Sea. Prog. Oceanogr. **138**: 475–485. doi:10.1016/j.pocean.2014.08.001.

Rosenkranz, G., Tyler, A., Kruse, G., and Niebauer, H. 2001. Effects of water temperature and wind on year-class success of Tanner crabs in Bristol Bay, Fish. Oceanogr. **10**(1): 1–12. doi:10.1046/j.1365-2419.2001.00153.x.

Ryazanova, T. V., Fedotov, P.A., and Kharlamenko, V.I. 2016. The bitter crab syndrome in commercial crabs in the western part of the Bering and Chukchi Seas. Russ. J. Mar. Biol. **42**(5): 409–413. doi:10.1134/s1063074016050096.

Salveson, S. 2004. Environmental assessment for Amendment 17 to the fishery management plan for the king and tanner crab fisheries in the Bering Sea/Aleutian Islands: a rebuilding plan for the Pribilof Islands blue king crab stock. North Pacific Fishery Management Council, Anchorage, Alaska. pp. 1–87. Available from https://repository.library.noaa.gov/view/noaa/18139 [accessed 3 December 2023].

Samhouri, J.F., Haupt, A.J., Levin, P.S., Link, J.S., and Shuford, R. 2014. Lessons learned from developing integrated ecosystem assessments to inform marine ecosystem-based management in the USA. ICES J. Mar. Sci. **71**(5): 1205–1215. Oxford Academic. doi:10.1093/ICESJMS/FST141.

Sato, S., and Tanaka, S. 1949. Study on larval stage of *paralithodes camtschatica* (Tilesius), 1. Morphological research report (Translation by L.M. Nakatsu, US Fish & Wildlife Service, 1968). Hokkaido Fish. Exp. Station, **1**: 7–24. Fish and Wildlife Service, Hokkaido, Japan.

Sause, B.L., Gwyther, D., and Burgess, D. 1987. Larval settlement, juvenile growth, and the potential use of spatfall indices to predict recruitment of the scallop *Pecten alba tate* in Port Phillip Bay, Victoria, Australia. Fish. Res. **6**(1): 81–92. doi:10.1016/0165-7836(87)90008-7.

Schmidt, V.E., and Rzhanov, Y. 2012. Measurement of micro-bathymetry with a GoPro underwater stereo camera pair. *In* Oceans conference. *Edited by* U.S. of N. Hampshire. Center for Coastal and Ocean Mapping, Durham, NH. pp. 1–6. doi:10.1109/OCEANS.2012.6404786.

Schnute, J.T., Boers, N., and Haigh, R. 2022. PBSmapping: mapping fisheries data and spatial analysis tools. R package version 2.73.2. Available from https://CRAN.Rproject.org/package=PBSmapping.

Short, J.W., Geiger, H.J., Fritz, L.W., and Warrenchuk, J.J. 2021. First-year survival of northern fur seals (*Callorhinus ursinus*) can be explained by pollock (*Gadus chalcogrammus*) catches in the Eastern Bering Sea. J. Mar. Sci. Eng. **9**(9): 975. doi:10.3390/JMSE9090975.

Siddon, E. 2023. Ecosystem status report 2023: Eastern Bering Sea stock assessment and fishery evaluation report. North Pacific Fishery Management Council, Anchorage, Alaska. pp. 1–241.

Somerton, D.A. 1985. The disjunct distribution of blue king crab, paralithodes platypus, in Alaska: some hypotheses. *In* Proceedings of the International King Crab Symposium. *Edited by* B. Melteff and N. Mollett. Alaska Sea Grant Program, Anchorage, Alaska. pp. 13–21. Available from https://repository.library.noaa.gov/view/noaa/40678 [accessed 28 February 2024].

Somerton, D.A., and Macintosh, R.A. 1985. Reproductive biology of the female blue king crab *paralithodes platypus* near the Pribilof Islands, Alaska. J. Crustac. Biol. **5**(3): 365–376. doi:10.2307/1547908.

Stabeno, P.J., and Bell, S.W. 2019. Extreme conditions in the Bering Sea (2017–2018): record-breaking low sea-ice extent. Geophys. Res. Lett. **46**(15): 8952–8959. doi:10.1029/2019GL083816.

Stabeno, P.J., Bond, N.A., and Salo, S.A. 2007. On the recent warming of the southeastern Bering Sea shelf. Deep-Sea Res II: Top Stud Oceanogr **54**(23–26): 2599–2618. Available from http://www.sciencedirect.com/science/article/B6VGC-4R5H1KG-1/2/41274b6c0fd26e285f97d9b038b02c77.

Stevens, B. 2014. Development and biology of king crab larvae. *In* King Crabs of the World. CRC Press. pp. 233–260. doi:10.1201/b16664-9.

Stevens, B.G. 2006a. Timing and duration of larval hatching for blue king crab *paralithodes platypus* brandt, 1850 held in the laboratory. J. Crustac. Biol. **26**(4): 495–502. doi:10.1651/s-2677.1.

Stevens, B.G. 2006b. Is it possible to enhance king crab populations in Alaska? *In* Alaska Crab Stock: Enhancement and Rehabilitation Workshop Proceedings. pp. 79–89.

Stevens, B.G., and Kittaka, J. 1998. Post-larval settling behavior, substrate preference, and time to metamorphosis for red king crab *Paralithodes camtschaticus*. Mar. Ecol. Prog. Series, **167**: 197–206. doi:10.3354/meps167197.

Stockhausen, W.T. 2023. 2023 Stock assessment and fishery evaluation report for the Pribilof Islands blue king crab fisheries of the Bering Sea and Aleutian Islands regions. *In* 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, Anchorage, AK. pp. 1–112.

Stoner, A.W., Copeman, L.A., and Ottmar, M.L. 2013. Molting, growth, and energetics of newly settled blue king crab: effects of temperature and comparisons with red king crab. J. Exp. Mar. Biol. Ecol. **442**: 10–21. doi:10.1016/j.jembe.2013.02.002.

Stoner, A.W., Ottmar, M.L., and Copeman, L.A. 2010. Temperature effects on the molting, growth, and lipid composition of newly settled red king crab. J. Exp. Mar. Biol. Ecol. **393**(1–2): 138–147. doi:10.1016/J.JEMBE.2010.07.011.

Stoutamore, J.L. 2014. Population genetics and mating structure of blue king crab (*Paralithodes platypus*). Master of Science, University of Alaska Fairbanks, Fairbanks, AK.

Swingle, J.S., Daly, B., Eckert, G., and Hetrick, J. 2013a. Blue king crab hatchery manual. Alutiiq Pride Shellfish Hatchery /AKCRRAB Program: 1–62.

Swingle, J.S., Daly, B., Eckert, G., and Hetrick, J. 2013b. Red king crab hatchery manual. Alutiiq Pride Shellfish Hatchery /AKCRRAB Program: 1–79.

Szuwalski, C. 2022. 2022 assessment for Pribilof Islands red king crab. *In* 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, Anchorage, Alaska. pp. 1–47.

Tapella, F., Romero, M.C., Stevens, B.G., and Buck, C.L. 2009. Substrate preferences and redistribution of blue king crab *paralithodes platypus* glaucothoe and first crab on natural substrates in the laboratory. J. Exp. Mar. Biol. Ecol. **372**(1–2): 31–35. doi:10.1016/j.jembe.2009.02.003.

Use of Fishes in Research Committee. 2014. Guidelines for the use of fishes in research. *Edited by* American Fisheries Society, American Institute of Fishery Research Biologists, & American Society of Ichthyologists and Herpetologists. American Fisheries Society. Available from https://fisheries.org/docs/wp/Guidelines-for-Use-of-Fishes.pdf.

Vulstek, S.C., Linderoth, T.P., Guyon, J.R., and Tallmon, D.A. 2013. Spatiotemporal population genetic structure and mating system of red king crab (*Paralithodes camtschaticus*) in Alaska. J. Crustac. Biol. **33**(5): 691–701. doi:10.1163/1937240X-00002173.

Wahle, R.A., Bergeron, C., Tremblay, J., Wilson, C., Burdett-Coutts, V., Comeau, M., et al. 2012. The geography and bathymetry of American lobster benthic recruitment as measured by diver-based suction sampling and passive collectors. Mar. Biol. Res. **9**(1): 42–58. doi:10.1080/17451000.2012.727428.

Wainwright, T.C., Armstrong, D.A., Andersen, H.B., Dinnel, P.A., Herren, D.W., Jensen, G.C., et al. 1992. Coastal fisheries oceanography of the southern Bering Sea and north Aleutian basin: Port Moller king crab studies. U.S. Department of Interior. MMS, Alaska OCS Region Final Report **92–0040**: 167.

Weems, J. 2024. Early Life Biology and Ecology of King and Tanner Crabs in the Bering and Chukchi Seas. Dissertation, University of Alaska Fairbanks. Available from http://uaf.idm.oclc.org/login?url=https://www.proquest.com/dissertations-theses/early-life-biology-ecology-king-tanner-crabs/docview/3051992613/se-2?accountid=14470.

Westphal, M.J., Tamone, S.L., and Eckert, G.L. 2014. Comparison of first year growth among field, hatchery- and laboratory-raised juvenile red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), in Alaska. J Crustac. Biol. **34**(3): 319–325. doi:10.1163/1937240X-00002228.

White, L.M., Sainte-Marie, B., Lawton, P., and Rochette, R. 2024. Using benthic recruitment densities to forecast fisheries recruitment of American lobster in Atlantic Canada. Can. J. Fish. Aquat. Sci. **81**(10): 1369–1384. doi:10.1139/CJFAS-2023-0277.

Wood, S.N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. J. Am. Statist. Assoc. **99**: 673–686. doi:10.1198/016214504000000980.

Wood, S.N. 2017. Generalized additive models: an introduction with R. *In* Generalized additive models: an introduction with R. 2nd ed. CRC Press. doi:10.1201/9781315370279/GENERALIZED-ADDITIVE-MODELS-SIMON-WOOD.

Zacher, L.S., Richar, J.I., Fedewa, E.J., Ryznar, E.R., and Litzow, M.A. 2023. The 2022 eastern and northern Bering Sea continental shelf trawl surveys: results for commercial crab species. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-462: 253. doi:10.25923/r6px-9707.

Appendix A

Table A1. Pribilof Islands blue king crab (*Paralithodes platypus*) and red king crab (*Paralithodes camtschaticus*) abundance indices for larvae and early juvenile stages near Saint Paul Island for the historical study in 1983–1984 (Armstrong et al. 1985, 1987, 2015; Palacios et al. 1985).

				1983–1984 Historical study—Saint Paul Island area [a]												
				Carapace	Zooplankton tow abundance						Beam trawl catch			Rock dredge catch		
	Stage/Molt	Approx.	Occupied	Length	1983 May		1983 Aug.		1984 Apr.		1983 May	1983 Aug.	1984 Apr.	1983 May	1983 Aug.	1984 Apr.
Species	Number	Age Class	Habitat(s)	mm	ind./m^3	SE	ind./m^3	SE	ind./m^3	SE						
Blue king crab *Paralithodes platypus*	Zoea 1	age-0	Pelagic	–	0.584	0.084	0	–	0.007	0.003						
	Zoea 2	age-0	Pelagic	–	0.226	0.033	0	–	0	–						
	Zoea 3	age-0	Pelagic	–	0.003	0.002	0	–	0	–						
	Zoea 4	age-0	Pelagic	–	0	–	0	–	0	–						
	Glaucothoe	age-0	Pel. / Ben.	–	0	–	0	–	0	–						
											count	count	count	count	count	count
	Instar C1	age-0	Benthic	2							0	0	0	0	1	0
	Instar C2	age-0	Benthic	3							0	4	0	0	160	0
	Instar C3	age-0	Benthic	4							0	3	4	0	40	28
	Instar C4	age-0	Benthic	5							1	0	23	0	10	33
	Instar C5	age-0	Benthic	6							0	4	29	0	21	16
											count	count	count	count	count	count
	Instar C6	age-1	Benthic	7							0	4	29	0	30	3
	Instar C7	age-1	Benthic	8							1	10	7	0	72	3
	Instar C8	age-1	Benthic	9–10							5	5	3	0	90	10
	Instar C9	age-1	Benthic	11–12							4	3	5	0	23	4
	Instar C10	age-1	Benthic	13–15							3	14	13	0	12	2
	Instar C11+	age-1+	Benthic	16–20							0	28	36	0	14	3

Can. J. Fish. Aquat. Sci. **82:** 1–21 (2025) | dx.doi.org/10.1139/cjfas-2024-0227

Can. J. Fish. Aquat. Sci. **82**: 1–21 (2025) | dx.doi.org/10.1139/cjfas-2024-0227

Table A1. (*concluded*).

				1983–1984 Historical study—Saint Paul Island area [a]												
				Carapace	Zooplankton tow abundance						Beam trawl catch			Rock dredge catch		
	Stage/Molt	Approx.	Occupied	Length	1983 May		1983 Aug.		1984 Apr.		1983 May	1983 Aug.	1984 Apr.	1983 May	1983 Aug.	1984 Apr.
Species	Number	Age Class	Habitat(s)	mm	ind./m^3	SE	ind./m^3	SE	ind./m^3	SE						
Red king crab *Paralithodes camtschaticus*	Zoea 1	age-0	Pelagic	–	0.204	0.030	0	–	0.005	0.002						
	Zoea 2	age-0	Pelagic	–	0.026	0.005	0	–	0	–						
	Zoea 3	age-0	Pelagic	–	0.001	0.001	0	–	0	–						
	Zoea 4	age-0	Pelagic	–	0	–	0	–	0	–						
	Glaucothoe	age-0	Pel. / Ben.	–	0	–	0	–	0	–						
											count	count	count	count	count	count
	Instar C1	age-0	Benthic	2							0	0	0	0	1	0
	Instar C2	age-0	Benthic	3							0	0	0	0	1	0
	Instar C3	age-0	Benthic	4							0	0	3	0	0	5
	Instar C4	age-0	Benthic	5							0	0	0	0	0	2
	Instar C5	age-0	Benthic	6							0	0	1	0	2	1
											count	count	count	count	count	count
	Instar C6	age-1	Benthic	7							0	0	0	0	1	0
	Instar C7	age-1	Benthic	8							0	0	0	0	0	1
	Instar C8	age-1	Benthic	9–10							0	0	0	0	0	0
	Instar C9	age-1	Benthic	11–12							0	0	0	0	0	0
	Instar C10	age-1	Benthic	13–15							0	0	1	0	0	0
	Instar C11+	age-1+	Benthic	16–20							0	2	0	0	0	0

Note: Abundance indices with standard error (SE) for larvae (individuals/m3), age-0 instar and age-1 juveniles (total number observed) in beam trawl and rock dredge catches were calculated for assigned stage classes with standard error (SE) based on binned carapace lengths.
[a] US Minerals Management Service, Outer Continental Shelf Environmental Assessment Program Saint Paul Island research area between 57–57.5 degrees North and 169.5–171 degrees West (Quadrants 1–4).

Canadian Science Publishing

Table A2. Combined blue king crab (*Paralithodes platypus*) and red king crab (*Paralithodes camtschaticus*) pelagic larval zoeae (Z1-Z4), post-larval glaucothoe (PL), and early benthic juveniles (C1–C5) mean proportional contribution across historical (1983–1983) and current (2017–2019) study catches used to estimate development and settlement time of king crab larvae in the Saint Paul Island, Alaska region.

Date			Crab Proportional Contribution by Stage [b]									
Month	Day [a]	Day Range	Z1	Z2	Z3	Z4	PL	C1	C2	C3	C4	C5
April	1	(90, 104]										
	15	(104, 118]	1.00	0	0	0	0	0	0	0	0	0
	28	(118, 132]	0.78	0.23	0	0	0	0	0	0	0	0
May	12	(132, 146]	0.50	0.48	0.02	0	0	0	0	0	0	0
	26	(146, 160]	0.33	0.33	0	0.33	0	0	0	0	0	0
June	9	(160, 174]	0	0	0	0.25	0.75	0	0	0	0	0
	23	(174, 188]	0	0	0	0.33	0.67	0	0	0	0	0
July	7	(188, 202]										
	21	(202, 216]	0	0	0	0	0	0.71	0.29	0	0	0
August	4	(216, 230]	0	0	0	0	0	0.48	0.50	0.02	0	0
	18	(230, 244]	0	0	0	0	0	0.02	0.10	0.72	0.13	0.04
September	1	(244, 254]	0	0	0	0	0	0	0.08	0.65	0.09	0.18

Note: Stage contribution was identified for each gear type based on daily presence and then averaged to produce one set of proportional values across all stages for each 14 day period. This data corresponds to Fig. 6.
[a] Day of month is approximate as calendar days do not always match (e.g., leap years).
[b] Data sets: Zooplankton (May 1983, April 1984, June–August 2017–2018), SACs (July–September 2017–2019), and Rock Dredge (August–September 1983).

Fig. A1. Focal species photographs of (A) age-0 settler blue king crab (*Paralithodes platypus*, BKC, ~2–5 mm carapace length), (B) age-1 juvenile BKC (~6–13 mm CL), (C) age-0 settler red king crab (*Paralithodes camtschaticus*, ~2–5 mm CL length), and (D) age-1 juvenile RKC (~6–13 mm CL). Age-0 king crab are the recently-settled benthic stages after completion of the pelagic larval phase and are the targeted age-class we used to examine settlement dynamics near Saint Paul Island, Alaska. Images by J. Weems (A/C, D) and S. Goodman (B, Bering Sea Fisheries Research Foundation, Seattle).

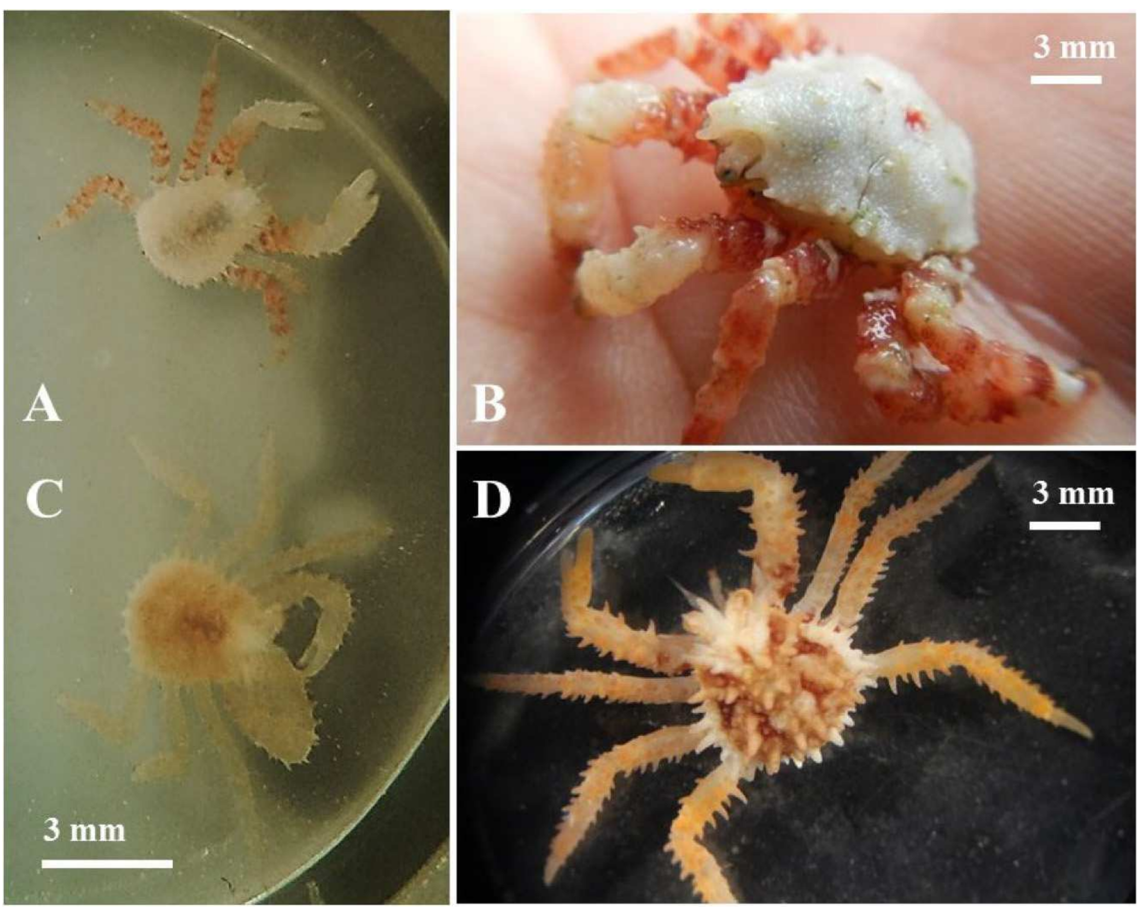


Fig. A2. Historical-study physical substrate maps from Armstrong et al. (1985, 1987) and Palacios et al. (1985) of (A) rock, gravel, cobble, and sand; as well as (B) large-intact empty shells and live mollusks (I, shellhash Type 1) and crushed or pulverized shell material (II, shellhash Type 2) summarized from beam trawl, rock dredge, and side-scan sonar data collected for seafloor habitat assessments in nearshore Saint Paul Island, Alaska areas. Three oceanographic and fisheries sampling surveys were supported by the US Minerals Management Service, Outer Continental Shelf Environmental Assessment Program (MMS-OCSEAP) targeting juvenile blue king crab (*Paralithodes platypus*), juvenile hair crab (*Erimacrus isenbeckii*), and benthic habitat assessments relative to potential oil and gas resource exploration and environmental mitigation requirements.