

Review

# Ecology and Distribution of Red King Crab Larvae in the Barents Sea: A Review

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**Abstract:** The red king crab (RKC) is a large invasive species inhabiting bottom communities in the Barents Sea. Larval stages of RKC play an important role in determining the spread and recruitment of the population in the coastal waters. We present a review of studies concerned with the ecology of RKC larvae in the Barents Sea focusing on their dynamics and role in the trophic food webs as well as on the role of environmental factors in driving RKC zoeae. Zoeal stages are larger, and their development time is shorter in the Barents Sea compared to the North Pacific. RKC larvae appear in late January–February and can be found in the coastal plankton until mid-July. Mass hatching of RKC larvae in the Barents Sea starts in late March–early April. The highest densities of RKC larvae are located in small semi-enclosed bays and inlets with weak water exchange or local eddies as well as in inner parts of fjords. Size structures of the zoeal populations are similar in the inshore waters to the west of Kola Bay but slightly differ from those in more eastern regions. RKC larvae perform daily vertical migrations and move to deeper depths during bright daylight hours and tend to rise during night hours. RKC larvae are plankton feeders that ingest both phyto- and zooplankton. A set of environmental variables including food conditions, water temperature, and advective influence are the most important factors driving the spatial distribution, phenology, survival rates, development, growth, and interannual fluctuations of RKC larvae. Recent climatic changes in the Arctic may have both negative and positive consequences for RKC larvae.

**Keywords:** *Paralithodes camtchaticus*; invasive species; meroplankton; zoeae; coastal ecology; phenology; environmental impact; Arctic



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## 1. Introduction

The Barents Sea is one of the largest shelf areas representing a transition zone connecting the Atlantic and Arctic Oceans [1–3]. The Arctic Ocean and adjacent seas demonstrate clear natural climate variability ranging from seasonal to multi-decadal time scales. Recent studies have documented a dramatic reduction in the Arctic sea-ice coverage during the summer period [4–6]. The sea-ice retreat has resulted in large areas of the Arctic Ocean becoming more accessible that led to increased human activities [5–8]. Other reported climatic changes include the freshening of surface waters and their warming associated with enhanced river discharge and ice melting [9,10]. These processes may be responsible for shifts in water stratification, light regime, acidification, nutrient availability, biogeochemical cycles, and carbon fluxes in the marine ecosystems of the Arctic Ocean and adjacent shelf regions [11,12] leading to borealization of flora and fauna [13–15]. Human activity may reinforce the effects of the environmental perturbations leading to altering of the Arctic marine ecosystems [16,17].

The Barents Sea can be divided into two regions with different climate regimes. The northern part is characterized by a cold Arctic climate, lower productivity, and an ice-associated ecosystem [1,2,18]. The southern regions represent warmer areas with highly productive ecosystems and advanced fisheries [19,20]. There is a Polar Front area in the Barents Sea representing a zone where the Arctic and Atlantic waters mix and interact [11,21].

Differences between the northern and southern regions are associated with the influence of warm and saline Atlantic Water entering from the southwest on colder and fresher Arctic waters dominating in the north. Recent observations have revealed an increased Atlantic Water inflow that causes a rise in water temperature, reductions in the sea-ice extent, and shifting of the Polar Front north-eastward [5,6,9,10,22].

Fisheries in the Barents Sea play an important role in the economics of countries exploring marine living resources in the region (especially Russia and Norway) [2]. Several species of fish and shellfish have been exploited over the past centuries [16,23]. The most important fish species include Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), capelin (*Mallotus villosus*), beaked redfish (*Sebastes mentella*), golden redfish (*Sebastes norvegicus*), and Greenland halibut (*Reinhardtius hippoglossoides*). Economically important crustaceans include northern shrimp (*Pandalus borealis*), red king crab (*Paralithodes camtschaticus*), and snow crab (*Chionoecetes opilio*) [1,2,11,23–25].

The red king crab, *Paralithodes camtschaticus* (Tilesius, 1815) (RKC) is one of the world's largest crustaceans (adult males reach 12 kg in weight and 27 cm in carapace length) [26,27]. The species is native to the North Pacific and occurs from British Columbia north through the Bering Sea, and southwest to Korea [26]. RKC was introduced into the Barents Sea from the Sea of Japan and the West Kamchatka waters by Russian scientists during the 1960s [28,29]. The goal of the introduction was to improve the fishery potential of the area. The introduction was declared to be successful, and the crab had formed a sustainable population by the mid-1990s [23,27,29]. In Russia, this new valuable fishing resource has been commercially exploited since 2004 [24,25,30,31]. In the past decade, the abundance of RKC has fluctuated significantly depending on environmental factors and fishing pressure [30,31], and annual landings have increased considerably accounting for 9836 t in 2019, 10,820 t in 2020, and 11,629 t in 2021 [32,33]. Recently, a small-scale recreation fishery was renewed with an annual quota of 100 t [34]. The meat of RKC is a high-quality product containing large amounts of valuable substances [35]. By-products of the crab are also rich in desirable components including chitin, chitosan, proteolytic enzymes, and fatty acids [36–38].

Non-indigenous species are recognized as agents that may have the largest impact on native benthic communities [39–42]. The benthic fauna represents an important component of the Arctic marine food webs and bottom secondary production was found to contribute a significant part to the diet of commercial demersal fish [43]. As RKC is a top predator it may compete with benthivorous fish and benthic organisms for food [44]. Some authors reported reduced benthic diversity and biomass at some coastal sites after the RKC introduction [40,44]. Furthermore, this species has become a host for a variety of epibiotic and symbiotic species [32,33,40,45] promoting their range expansion and possible cascading impacts on the ecosystem [33].

Many aspects of the RKC biology, ecology, fisheries, aquaculture, and management have been intensively studied and reviewed [23–25,27,29–35,41,42,44–63]. The larvae of RKC exist during the spring period and they occur in the plankton during 8–10 weeks and then settle to the bottom [29]. Larval stages are considered a crucial phase in determining the survival and stock recruitment of crabs and other crustaceans worldwide [64]. However, mechanisms affecting the development of larvae and successful recruitment of the RKC population in the Barents Sea remain less studied. Taking into account the invasive status of RKC and its potential for further range expansion through larval dispersion, this topic is of high significance for modeling both RKC invasion scenarios and their recruitment patterns in the Barents Sea.

This paper aims to summarize data regarding the ecology and distribution of RKC larvae in the Barents Sea. We focused on the morphology, seasonal dynamics, size structure, phenology, and the possible role of RKC larvae in the meroplankton and coastal trophic food webs as well as environmental impacts on zoeal stages of RKC. We also compared published results with data obtained for the native regions.

## 2. Occurrence and General Biology of RKC in the Barents Sea

RKC was found to occur in the coastal waters of the southern Barents Sea, along the Norwegian coast, and northeast of the Kola Peninsula from the original area of introduction (Kola Bay, Russia) (Figure 1).

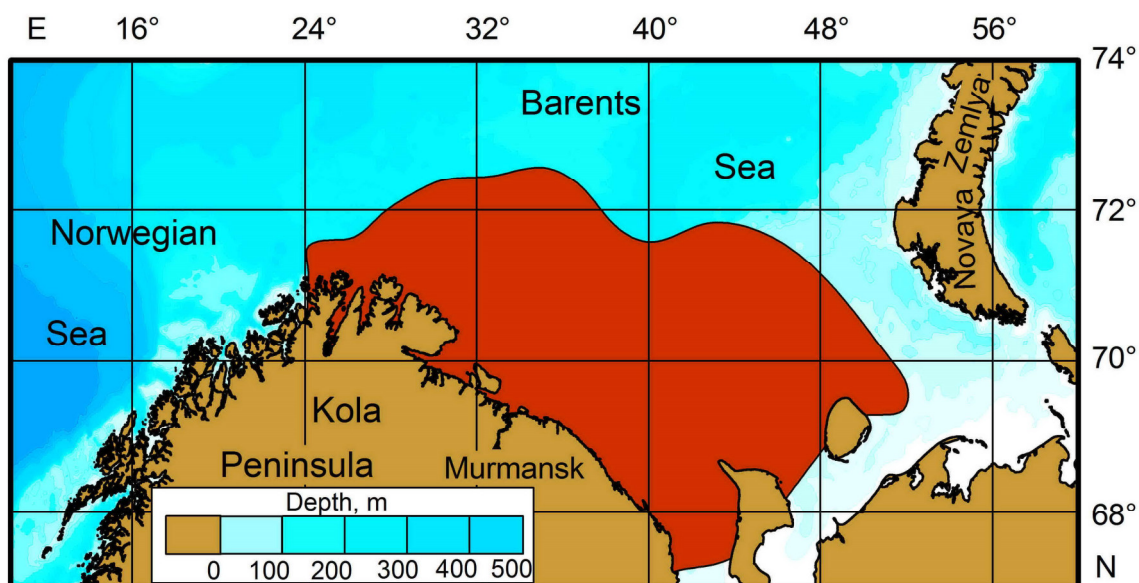


Figure 1. Distribution of red king crabs in the Barents Sea (adapted from [24]).

Recently, the first records of RKC have been documented in the White Sea suggesting continued range expansion [24,25,27]. In Russian waters of the Barents Sea, RKC inhabit shallow (3 m) to deep waters (335 m), at  $-0.8$  °C to  $+8.5$  °C [27]. They form mating aggregations at coastal sites during spring. In autumn, RKC individuals segregate by sex, and males and females form aggregations in deep and shallow waters, respectively [24,25,27]. RKC is a high-level predator feeding on abundant bottom animals including mollusks, polychaetes, and echinoderms [44]. They can also feed on fish offal in the regions where multispecies fishing occurs [44,65]. The main predators of RKC are cod, wolffish, and skates [24,25,27,29].

Mating takes place in spring (April–May) and eggs are fertilized externally. The vast majority of RKC females in Russian waters release their eggs at relatively shallow-water sites (80–90 m) [29]. The females hatch their old eggs and start the process of molting and spawning new eggs in March–April. In coastal waters, the size at which 50% of females become mature ranges from 104.0 to 110.2 mm in carapace length (CL) [55].

Individual fecundity ranges between 70,000 and 700,000 eggs, averaging 250,000 eggs per female [66], indicating a high reproductive potential of RKC and a high ability to sustain rapid population growth in new areas. Planktonic larvae pass through four zoeal stages, and glaucothoe, which is able to settle and metamorphose into the first benthic instar [67]. Mass appearance of RKC larvae in plankton is detected in March–April at depths of 50–240 m [68]. After a series of molting events, RKC larvae settle on the bottom and develop into juvenile crabs with a carapace width (CW) of 2 mm [29]. Juvenile crabs molt several times per year depending on size [31,51]. Adult RKC females molt annually before mating [29,69]. Males with CW < 100 mm molt at least annually, and those > 110 mm CW less often. Larger males (CW > 150 mm) molt once every 3 and 4 years, respectively [24,70]. The sizes of juvenile crabs at age 0–5 years were estimated to be 1.2, 9.9, 30.0, 53.3, 71.8, and 83.8 mm CL, respectively [25,54]. Males reach a commercial size of 150 mm CW (or 137 mm CL) after 10 years of growth [25]. The most common epibionts of RKC are copepods, amphipods, and hydrozoans [33,49,50,52,71].

### 3. Larval Morphology of RKC in the Barents Sea

Four zoeal stages (zoeae I–IV) are reported for RKC [67,72]. Growth and development characteristics of each zoeal instar reared in the laboratory have been investigated by Epelbaum et al. [73] and are presented in Table 1.

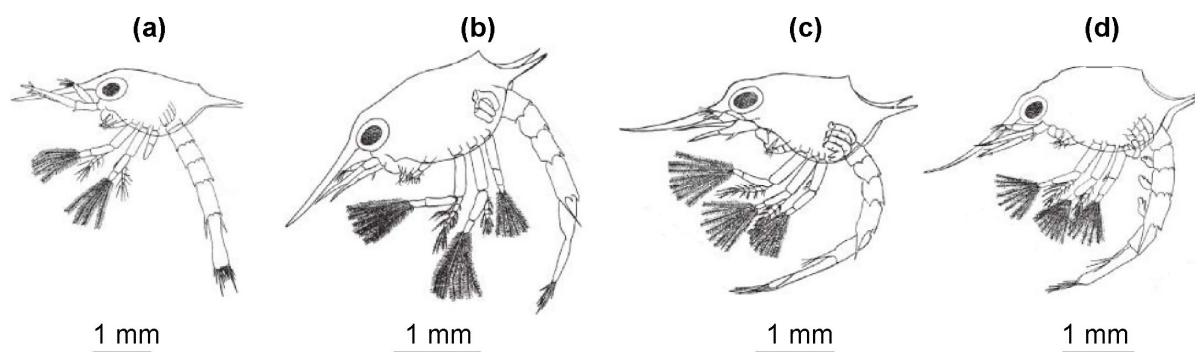
**Table 1.** Morphology, growth, development, and mass of zoeal stages of red king crab from the Barents Sea and North Pacific [73–76].

Stage	Duration, Days	Carapace Length, mm	Rostrum Length, mm	Abdomen Length, mm	Wet Mass, mg	Dry Mass, mg
T = 7–8 °C		Barents Sea				
Zoea I	10	1.39	1.29	nd	0.86	0.110
Zoea II	10	1.63	1.52	nd	1.41	0.165
Zoea III	9	1.83	1.53	nd	2.00	0.250
Zoea IV	10	2.07	1.63	nd	2.67	0.300
T = 8 °C		North Pacific				
Zoea I	12	1.18	1.45	2.63	nd	0.045
Zoea II	15	1.38	1.5	2.83	nd	0.084
Zoea III	26	1.45	1.6	3.25	nd	0.109
Zoea IV	33	1.53	1.3	3.63	nd	0.191

Note(s): nd—no data.

RKC ovigerous females hatched the larvae to be tested originated from Ura Bay (69°21'29" N, 32°56'02" E, southern Barents Sea). To compare the data for the Barents Sea we also present morphological and developmental characteristics for RKC larvae from the native regions (North Pacific) [74–76]. Comparisons show that the zoeal stages are larger and their development is shorter in the Barents Sea than in the North Pacific (Table 1).

Zoea I has a carapace without spinules or setae on the surface (Figure 2a).



**Figure 2.** Common larval stages of red king crab: (a) zoea I, (b) zoea II, (c) zoea III, (d) zoea IV. Adapted from [72,75].

Rostrum elongated, slightly shorter than carapace length. There are two posterior spines. Carapace morphology is similar for all zoeal stages remaining essentially the same throughout larval development (zoeae I–IV). Antennules have a single segment and bear six olfactory setae. Antennae have a peduncle and a longer exopodite with five setae [67]. The diagnostic formula of setae on the maxillipeds is (4, 4, 0) [75]. Thoracic appendages (pereiopods) are rudimentary buds hidden beneath the carapace. The abdomen has five segments, with the last four having lateral spines (the last of which are the longest) and four small spines on the dorsal edge. The telson is fan-shaped with two symmetrical lobes separated by a medial notch, each bearing six setae and an outer spine [67,77]. There are two–three pairs of large yellow or green chromatophores on the carapace; arrangement of red/orange chromatophores varies [72,73].



Zoea II (Figure 2b) has a carapace, antennae, mandibles, pereopods, abdomen, and telson proportionally higher than those of Zoea I, but otherwise unchanged [73]. The eyes are located on stalks and are movable. The Mxp setal formula is (7, 7, 6) [74]. The telson is more elongated [67].

Zoea III (Figure 2c) has a carapace, antenna, mandibles, maxillule, and telson proportionally higher than those of Zoea II, but otherwise unchanged [73]. All maxillipeds have eight setae, thus the setal formula is (8, 8, 8) [75]. The elongated telson is divided, demonstrating the rise to the sixth abdominal segment. Pairs of pleopod buds appear on abdominal segments 2 through 5, and a pair of uropod buds appears on segment 6 [67].

Zoea IV (Figure 2d) has a carapace, antenna, mandibles, maxillule, and telson proportionally higher than those of Zoea III, but otherwise unchanged [73]. The Mxp setal formula is (8, 8, 8) [75]. Thoracic appendages are visible below the carapace, and the first has a definite cheliped [67,72].

#### 4. Abundance, Phenology, and Distribution of RKC Larvae in the Barents Sea

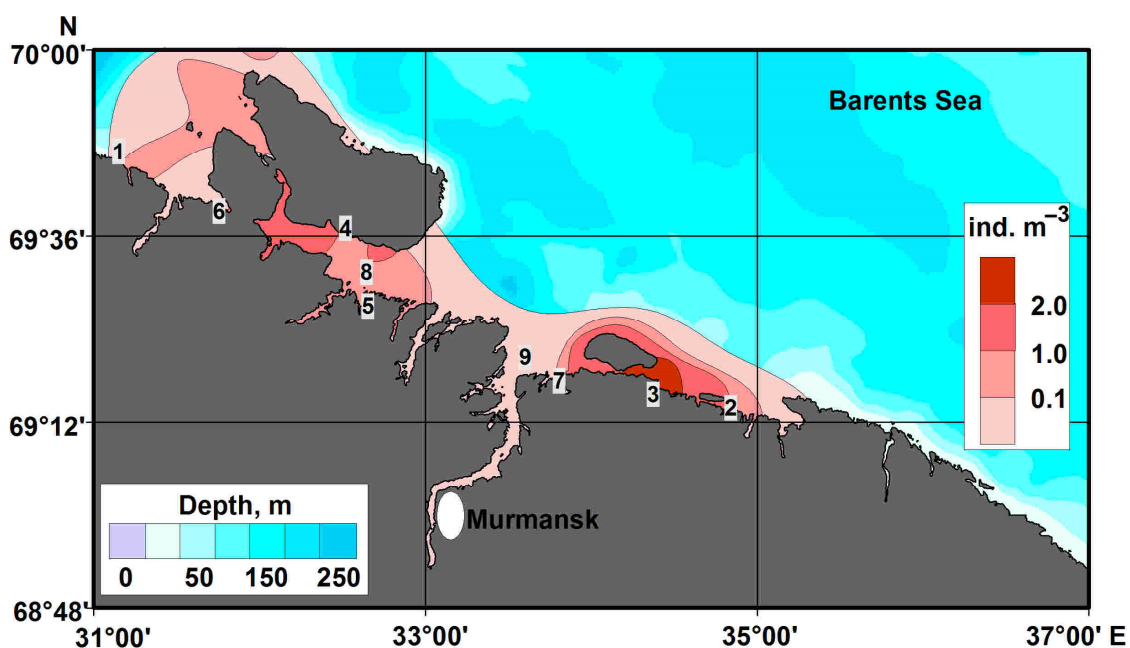
##### 4.1. Horizontal Pattern

The most comprehensive data on the abundance of RKC larvae in Russian waters of the Barents Sea come from the works conducted in the coastal area including bays and inshore areas [68,78–84].

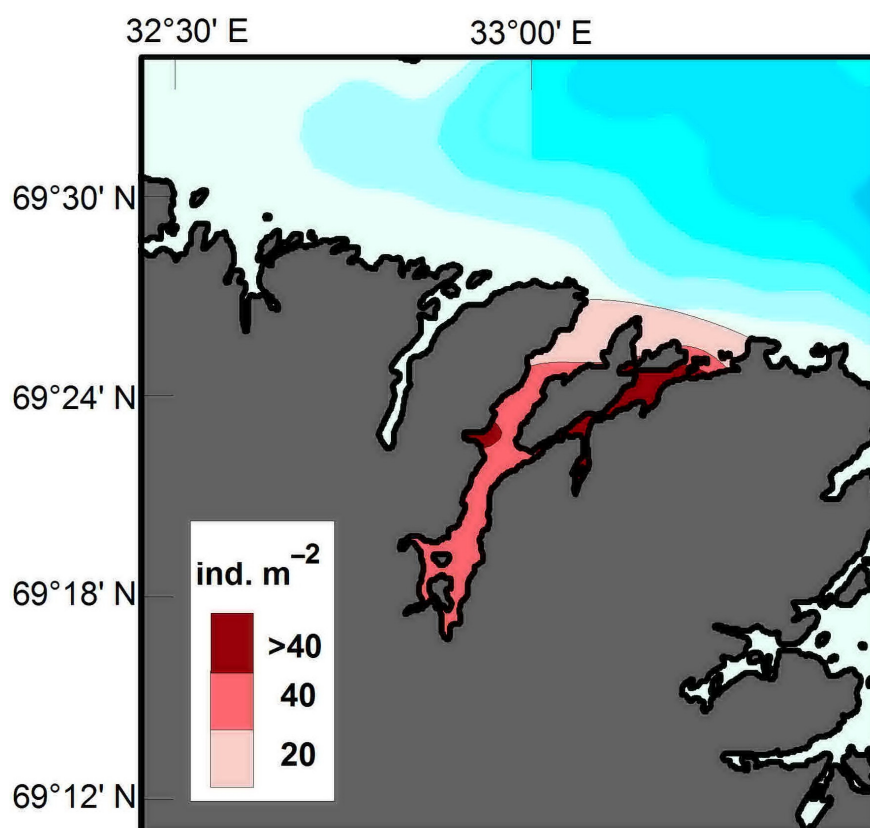
From 1996 to 1999, studies covered the area from Varanger-fjord to Cape Svyatoy Nos. The larvae were caught with Juday nets (0.11 m<sup>2</sup>, 168 µm), IKS nets (0.5 m<sup>2</sup>, 330 µm), and trawl nets (330 µm) in the spring period (March–mid-May). The total size of the larvae was determined as the distance from the beginning of the rostrum to the posterior margin of the carapace [68]. The abundance of RKC larvae was expressed as individuals per 1 m<sup>3</sup> or 1 m<sup>2</sup> (ind. m<sup>-3</sup> and ind. m<sup>-2</sup>, respectively). Mass hatching of RKC larvae in the Barents Sea was found to begin in late March–early April. Females carrying developed eggs occurred in the coastal zone (40–240 m) from Varanger-fjord in the west to Maly Oleniy Island in the east (Figure 3). High densities of ovigerous females (25–100 ind. km<sup>-2</sup>) were recorded in the shallow waters of Medvezhya Bay, Eina Bay, Vichany Bay, Bolshaya Volokovaya Bay, Dolgaya Bay, Motovsky Bay, and Kola Bay (Figure 3). The water temperature at the bottom layer in those areas varied from 0.5 to 1.9 °C [68]. Zoeae I appeared in early April [68]. The maximum density of the larvae was noted in Medvezhya Bay (52 ind. m<sup>-3</sup>) and the inner part of Motovsky Bay (18 ind. m<sup>-3</sup>) (Figure 3).

First zoeae II were recorded in April but a bulk of larvae comprised zoeae I [68]. In May, zoeae II were found along the entire coastal waters with a maximum density (44 ind. m<sup>-3</sup>) occurring in the inner parts of the bays. The larvae were reported to prefer shallow-water sites (85–156 m) and colder waters (−0.19 °C in April and 2.15 °C in May). Zoeae III began to occur in mid-May [68]. The larvae occurred in the shallow coastal waters at 59–133 m depths from Varanger-fjord to the Seven Islands archipelago (68°50' N, 37°12' E) [68]. The occurrence of zoeae III in more eastern areas was probably associated with the dispersal of the larvae with the Murmansk coastal current eastward. The average abundance of zoeae III did not exceed 0.1–0.4 ind. m<sup>-3</sup>, reaching maximum values in bays (1.8 ind. m<sup>-3</sup>), where the larvae existed in the plankton until the settlement due to local circulation [68]. Zoeae IV occurred occasionally suggesting that their appearance would be in the late May–early June [68]. Therefore, the presence of RKC larvae in the coastal Barents Sea was proposed to be from March to mid or late June. The size of RKC larvae ranged from 2.4 to 5.8 mm, averaging 3.39 ± 0.02 mm for zoea I, 3.80 ± 0.10 mm for zoea II and 4.27 ± 0.04 mm for zoea III [68].

In Ura Bay, RKC larvae were found mainly along the eastern coast and in the inner part during the period 1996–1999 (Figure 4).



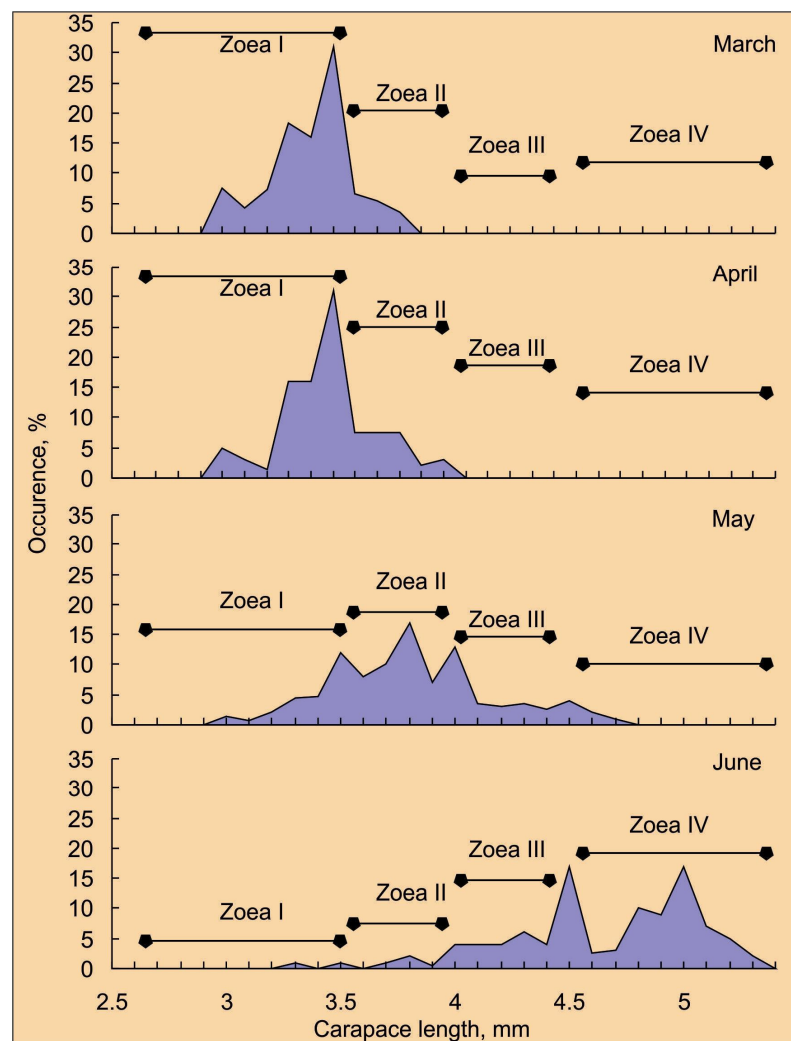
**Figure 3.** Distribution and abundance (individuals  $m^{-3}$ ) of red king crab larvae (zoea I) in Russian waters of the Barents Sea (spring 1996–1997) (modified from [68]). 1—Varanger-fjord, 2—Maly Oleniy Island, 3—Medvezhaya Bay, 4—Eina Bay, 5—Vichany Bay, 6—Bolshaya Volokovaya Bay, 7—Dolgaya Bay, 8—Motovsky Bay, 9—Kola Bay.



**Figure 4.** Distribution and abundance (individuals  $m^{-2}$ ) of red king crab larvae in Russian waters of the Barents Sea (spring 1996–1999, Ura Bay) (modified from [79]).

The maximum density of the larvae was 198 ind. m<sup>-2</sup>. In the central part of the bay, the larval density tended to be lower than 40 ind. m<sup>-2</sup> and the same values were recorded in the outer part. The inshore waters adjacent to Ura Bay had a low abundance of RKC zoeae (<20 ind. m<sup>-2</sup>) [79]. The average density of RKC larvae was 40.4 ind. m<sup>-2</sup> in 1996 and a 4-fold decrease was registered in 1998 (10.2 ind. m<sup>-2</sup>) and 1999 (12.4 ind. m<sup>-2</sup>) [79]. The authors concluded that aggregations of RKC larvae in Ura Bay were present at sites with low water exchange [79]. Similar patterns have been documented for other small bays and inlets of the Kola Peninsula with local eddies preventing the dispersal of RKC larvae to offshore waters [68,79].

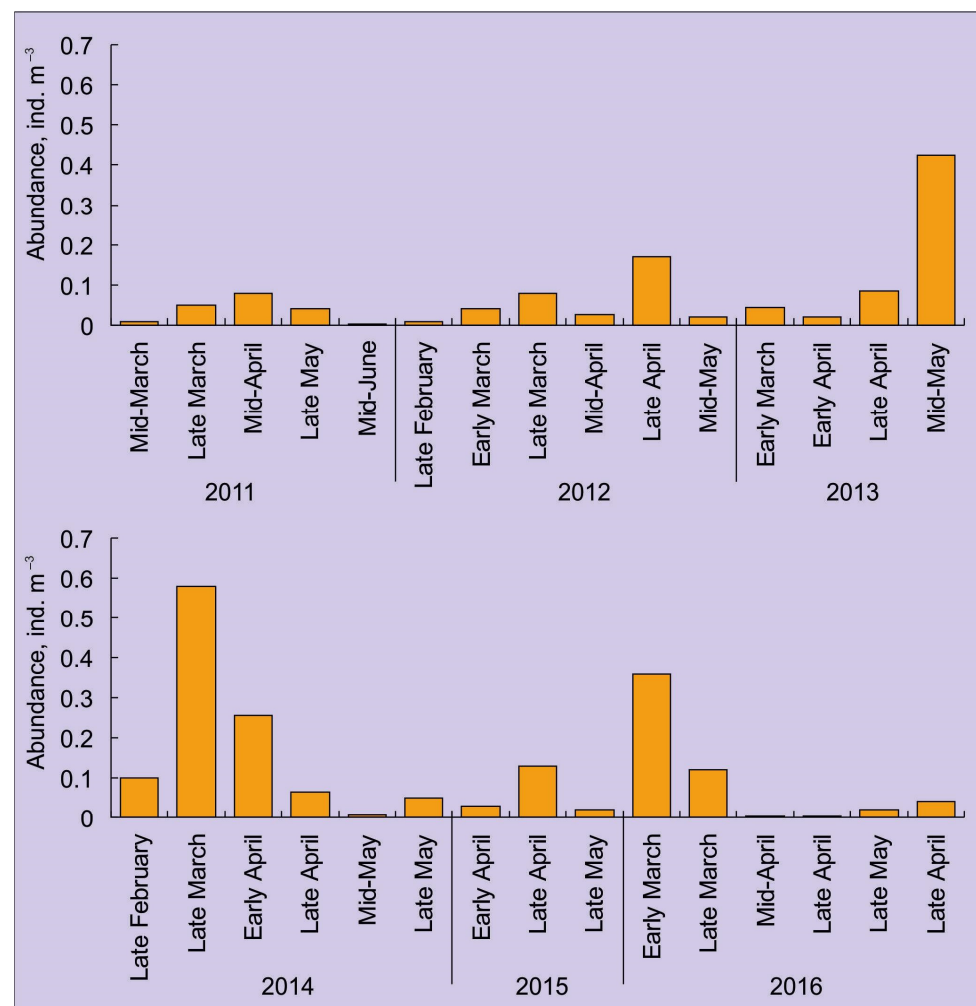
The first RKC larvae appeared in the plankton of Ura Bay in early March [79] as zoea I, while zoeae II appeared in late March. Zoeae III began to occur in April. The highest density of RKC larvae was reported in late April–early May, i.e., during the period of seasonal zooplankton maximum (Table S1). The maximum density of zoeae I–IV ranged from 50 to 198 ind. m<sup>-2</sup> with zoeae II–III being the most numerous (Table S2). The total larval density decreased to 10–40 ind m<sup>-2</sup> by late May. In June, zoeae accounted for 4–28 ind. m<sup>-2</sup> and the bulk of larvae were present as zoea IV (95%). Subsequent development of zoea IV into glaucotoe, a postlarval stage, and settlement were reported in late June [79]. The dynamics of zoeal size in Ura Bay is shown in Figure 5. There was a clear increase in the total body size from earlier to late stages (Figure 5) [79].



**Figure 5.** Occurrence of red king crab larvae and their size structure in Russian waters of the Barents Sea (spring 1996–1999, Ura Bay) (modified from [79]).

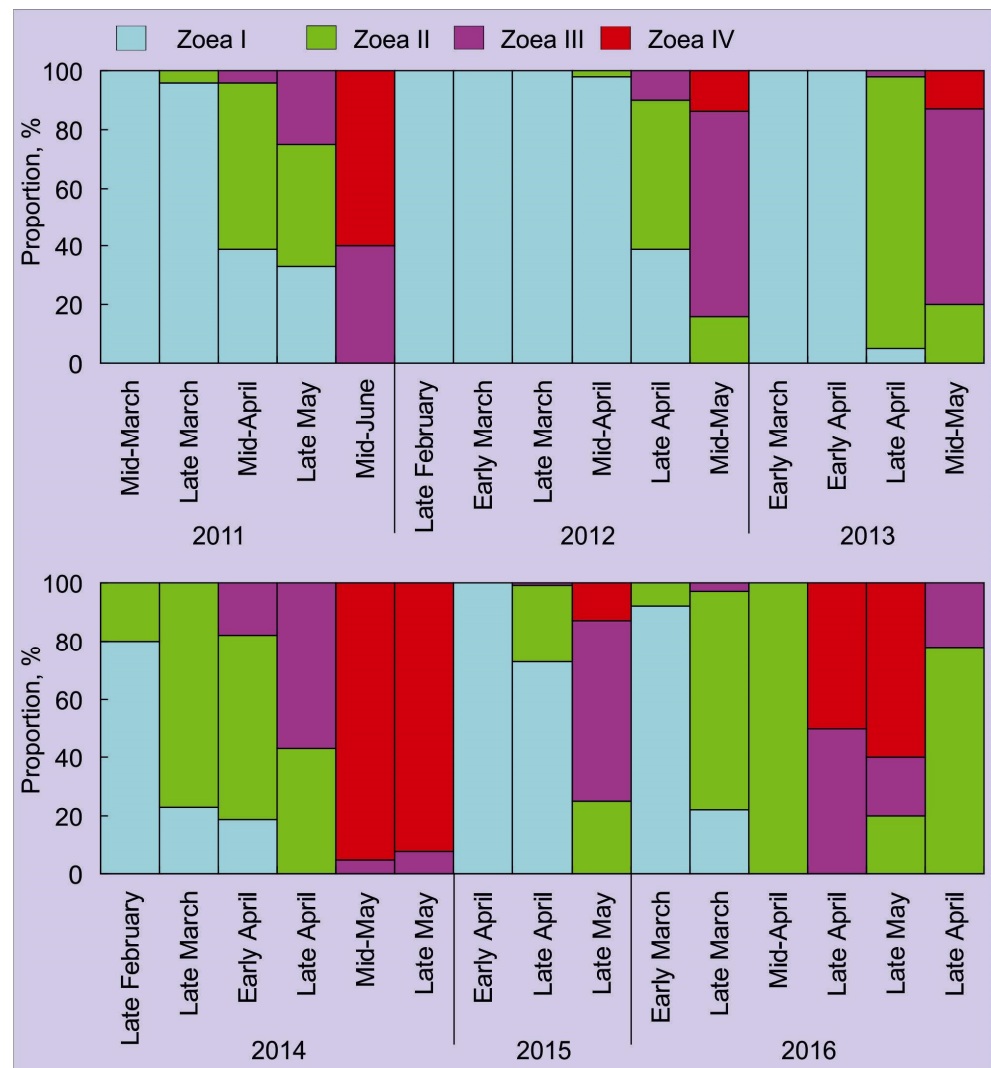
In May 2007, RKC larvae were caught in the coastal plankton using a Juday net (0.11 m<sup>2</sup> sampling area, 168 µm mesh size) and they were present mainly as zoea III [80]. The total number of zoeae varied from 7.4 to 23.9 ind. m<sup>-3</sup> [80,83]. The lowest abundance was found for zoea I which occupied the coastal waters adjacent to Kola Bay. The highest abundance of zoeae II–III was registered to the west of Kola Bay [80,83]. The average abundance of RKC larvae was estimated to be 12.1 ind. m<sup>-3</sup>. The average sizes of the zoeae were smaller (zoea I: 2.8–3.4, 3.26 ± 0.33 mm, zoea II: 3.5–4, 3.72 ± 0.26 mm, zoea III: 4.1–4.4, 4.19 ± 0.22 mm) relative to the values reported in the western regions (Ura Bay and Medvezhya Bay), but higher than in Kola Bay and Motovsky Bay. This allowed the authors to propose that the eastern sub-populations of RKC might be somewhat isolated from the western sub-population [80,83].

During the period 2010–2016, pelagic larvae were sampled using IKS nets (0.5 m<sup>2</sup> sampling area, 330 µm). RKC larvae occurred in the plankton of Ura Bay from February to June. There was a strong interannual variability in the average number of the larvae [82] (Figures 6 and 7). The most abundant aggregations of larvae were caught in the middle part of the bay. The number of RKC larvae tended to decrease in offshore waters. Zoeae prefer to inhabit the subsurface layer (25 m) where their density was higher than in the surface layer [81,84].



**Figure 6.** Seasonal abundance (individuals m<sup>-3</sup>) of red king crab larvae in Russian waters of the Barents Sea (2011–2016, Ura Bay) (modified from [81,84]).





**Figure 7.** Stage structure of red king crab larvae in Russian waters of the Barents Sea (2011–2016, Ura Bay) (modified from [81,84]).

Analysis of the stage structure of RKC larvae suggests the existence of zoeae I until mid-April–late May (Figure 7). Zoeae II were the dominating stage in late April–May (Figure 7). Zoeae III–IV usually prevailed among all stages in May–June (Figure 7). Peaks of RKC larvae were observed in March (in 2014 and 2016), April (in 2011, 2012, and 2015) in May (in 2013) (Figure 6) [81,84].

The integrated abundance of RKC larvae differed between years in Ura Bay over the period of 2011–2016 (Table 2) and it was proposed to be controlled by variations in water temperature [81].

In 2017, there was a very low zoeal density ( $0.002 \text{ ind. m}^{-3}$ ) in the plankton in late April. Zoeae III–IV were dominating stages. The total abundance of RKC larvae had clearly increased to  $0.02 \text{ ind. m}^{-3}$  by late May and zoea IV became the most common (60%). In 2018, a survey was conducted only in late April. The average zoeal density was  $0.04 \text{ ind. m}^{-3}$ . Only zoeae II–III were caught and zoeae II were the most numerous (78%) [84].

An analysis of the long-term dataset (2011–2018) obtained in Ura Bay allowed the authors to make general conclusions on the phenology of RKC larvae. The larval period of RKC lasts from February to June. Zoeae I are commonly found from February to late April although they may be present in the plankton until May in some years (e.g., in 2011). The survival rate of RKC larvae may vary between years. The maximum densities of RKC larvae are frequently found in the middle basin and tend to decrease in the outer waters.

The earliest appearance of zoeae in the plankton was noted in 2014 and 2016 when total larval densities demonstrated the highest levels [81,84].

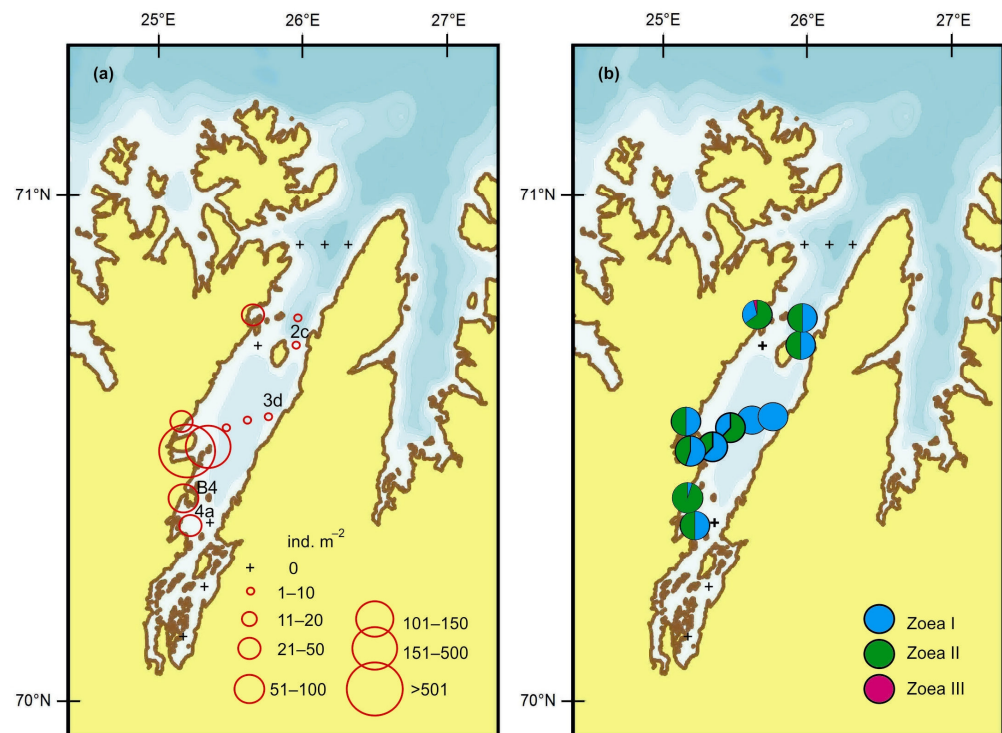
The most extensive research on the phenology of RKC larvae in the Norwegian waters is that of Michelsen et al. [85–87] conducted in 2013–2014 using a WP2 plankton net (0.255 m<sup>2</sup> sampling area, 180 μm mesh size). The study area, Porsangerfjord (70.0–71.0° N, 25–26.5° E), represents one of the largest fjords in Norway. The outer and middle basins are classified as semi-enclosed sites affected by a strong influx of waters from the Norwegian Coastal Current and Atlantic Ocean. The water exchange rate between the inner and middle basins is low, and the inner basin is affected by freshwater runoff during spring and summer [85–87].

Zoea I was the most common larval stage in 2013, being present from February to April (Figures 8 and 9).

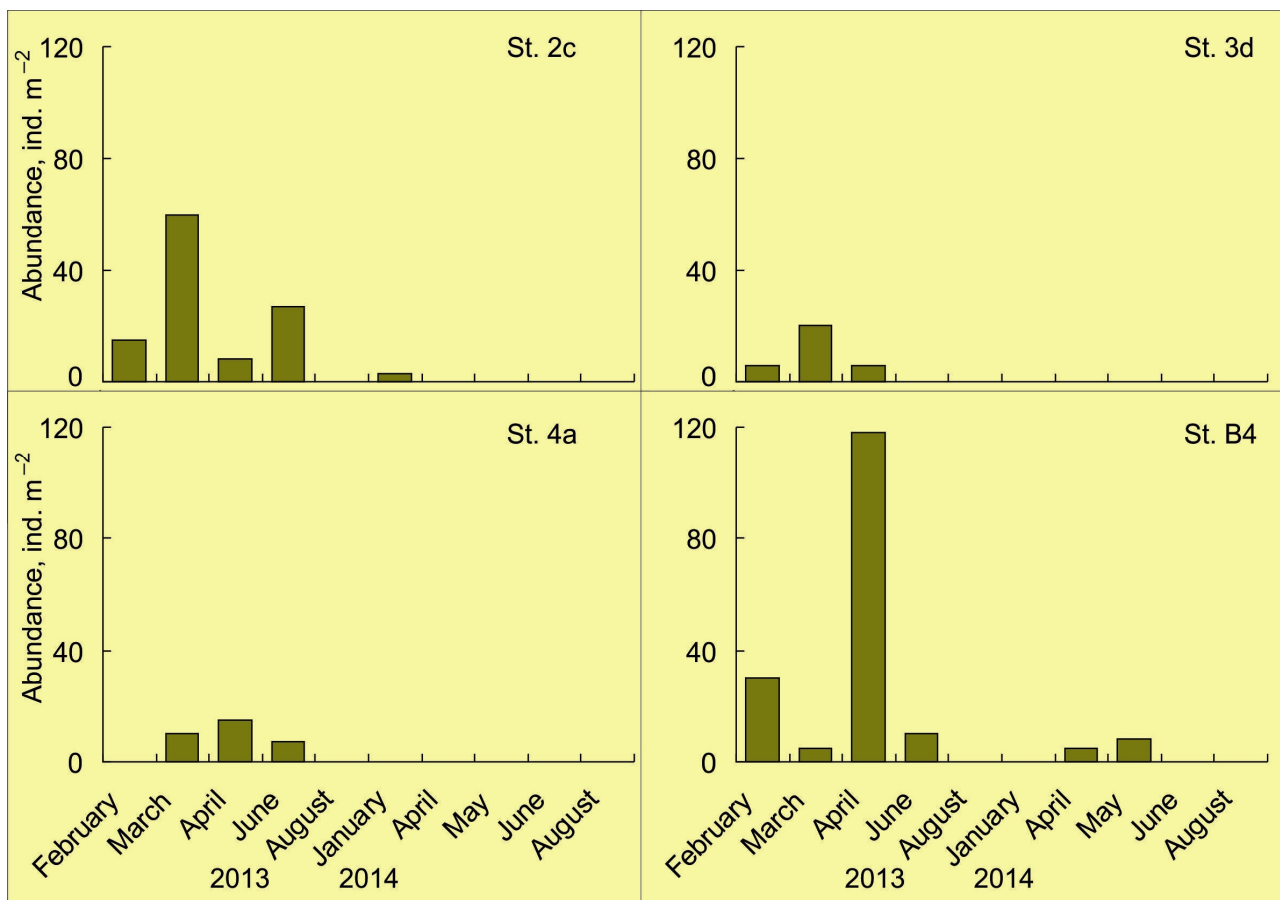
**Table 2.** Total abundance (individuals m<sup>-2</sup>) of red king crab larvae in the plankton in Ura Bay in 2011–2016 (adapted from [81]).

Year	Late February	Early-March	Late March	Early April	Late April	Late May
2011	-	1.0	1.0	-	7.0	4.0
2012	2.0	4.0	6.5	24.0	20.0	2.0
2013	-	4.0	-	2.0	3.5	16.0
2014	3.3	-	33.1	13.0	1.8	1.5
2015	-	-	-	1.5	6.5	1.0
2016	-	25.0	6.0	0.0	-	0.0

Note(s): ‘-’—not found.



**Figure 8.** Distribution of red king crab larvae in Norwegian waters of the Barents Sea (April 2013, Porsangerfjord) (modified from [87]): (a) abundance (individuals m<sup>-2</sup>), (b) stage structure. 2c, 3d, B4, and 4a represent codes for sampling stations.



**Figure 9.** Seasonal abundance (individuals  $m^{-2}$ ) of red king crab larvae at different stations (see Figure 8) in Norwegian waters of the Barents Sea (Porsangerfjord) (modified from [87]).

The first appearance of this stage was observed in January. In 2014, the density of zoeae I reached a maximum in March (up to  $57 \text{ ind. m}^{-2}$ ) and in April ( $111 \text{ ind. m}^{-2}$ ) (Figure 9) [87]. Zoeae II were found to occur in April. In 2014, no zoeae II were sampled due to a lack of sampling in January–May. Only single zoeae III were detected in the plankton in April 2014. Zoeae IV were found in May 2014 and June 2013 [87]. The highest densities of RKC larvae were recorded in the middle basin (Figure 8). In April 2013, the highest density of RKC larvae was revealed in the middle basin and bays ( $23\text{--}883 \text{ ind. m}^{-2}$ ) (Figures 8 and 9) [85–87]. Zoeae I–II of RKC were registered throughout the fjord, with stage Zoa I being the most abundant. Zoeae III were found in the outer part of the fjord (Figure 8) [87]. Considering the low number of stage IV zoeae and glaucothoe in June and their absence in August of both years, the authors concluded that the RKC larvae settled in late June or July [85–87]. The early and prolonged occurrence of zoea I (January–April) in the plankton was suggested to be associated with earlier spawning of ovigerous females in shallow Norwegian waters [85–87] and a prolonged hatching period of individual RKC females ( $>1$  month) [88]. The protracted presence of zoea I might reflect unfavorable food conditions for survival and growth from January to March [85–87].

Table 3 summarizes data regarding the occurrence of RKC larvae in the plankton of the North Pacific region and in the Barents Sea.

**Table 3.** Occurrence of red king crab larvae in the plankton of the Barents Sea and the North Pacific region.

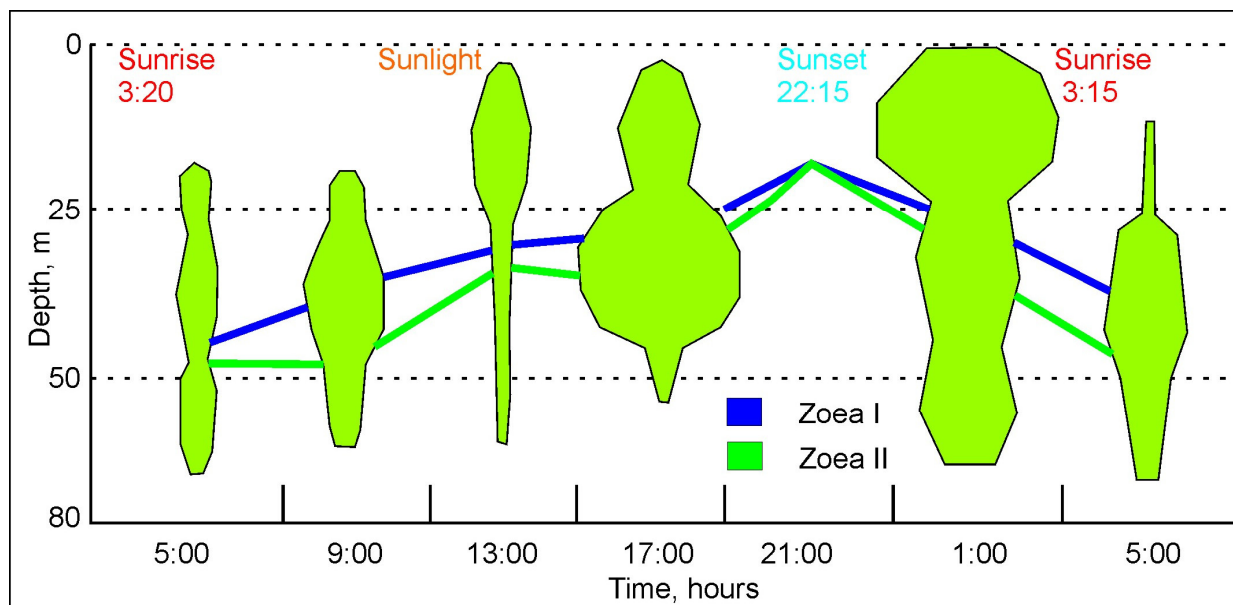
Stage	Region	Period	Reference
Barents Sea			
Zoea I	Ura Bay	Early March–May	[78,79,89]
	Ura Bay	February–May	[81,82,84]
	Coastal waters	Mid–April–May	[68]
	Coastal waters	May	[80,83]
	Porsangerfjord	January–April	[87]
Zoea II	Ura Bay	March–May	[78,79,89]
	Ura Bay	February–May	[81,82,84]
	Coastal waters	Mid–April–May	[68]
	Coastal waters	May	[80,83]
Zoea III	Porsangerfjord	April	[87]
	Ura Bay	March–June	[78,79,89]
	Ura Bay	April–June	[81,82,84]
	Coastal waters	May	[68]
	Coastal waters	May	[80,83]
Zoea IV	Porsangerfjord	April	[87]
	Ura Bay	April–June	[78,79,89]
	Ura Bay	May–June	[81,82,84]
	Coastal waters	May	[80,83]
	Open waters	May	[90]
Porsangerfjord	May–June	[87]	
North Pacific			
Zoea I	Bristol Bay	March–July	[91]
	Western Sakhalin waters	March–April	[92]
	Western Sakhalin waters	May–June	[75]
	Western Kamchatka waters	March–April	[75]
	Kamchatka waters	April–July	[92]
	Gulf of Alaska	Early April–late May	[93,94]
	South–eastern Bering Sea	Mid–April–late June	[92]
	Aniva Bay, Sea of Japan	April	[95]
	The Peter Great Bay, Sea of Japan	Late April–late May	[75]
	Sea of Japan	Late April–late May	[75]
Zoea II	Gulf of Alaska	April–June	[94]
	Kamchatka waters	May–July	[92]
Zoea III	Gulf of Alaska	Mid–April–July	[94]
	Kamchatka waters	June–early July	[92]
Zoea IV	Gulf of Alaska	Mid–April–July	[93,94]
	Tartar Strait	Early May	[95]
	Kamchatka waters	June–early July	[92]

The time of hatching and occurrence of zoeae are similar in the Barents Sea and native areas. The appearance of larvae in the plankton was noted in populations at higher latitudes (Barents Sea and Gulf of Alaska) and in more southern Pacific regions (Sea of Japan and western coastal waters of South Sakhalin). However, there are clear differences in water temperature between the regions (<1 °C in the Barents Sea vs. 4.5–6.0 °C in the Gulf of Alaska) [93]. The period of occurrence in the plankton is also similar, while in the Pacific region, RKC larvae may be present until July in different habitats. Therefore, one can suggest that RKC larvae have a fairly wide ecological plasticity and water temperature is not a limiting factor.

#### 4.2. Vertical Pattern

The vertical distribution of RKC larvae was studied in Medvezhya Bay (69°17' N, 34°24' E) in May 1999 [68]. Sampling was performed at three water strata (0–25 m, 25–50 m, and 50 m–bottom) using a Juday net every 4 h. A total of 1059 RKC zoeae were caught

with zoea I being the most abundant (56%). Zoea II accounted ca. 44% and only two zoeae III (<0.002%) were present in the plankton [68]. Zoeae I–II occurred at all water horizons during the day and formed aggregations in the surface and intermediate layers (Figure 10).



**Figure 10.** Vertical distribution of red king crab larvae in Russian waters of the Barents Sea (Medvezhya Bay, 3–4 May 1999) (modified from [68]). The areas of the polygons are proportional to the number of RKC larvae at different depths.

Most RKC larvae occupied the intermediate layer in the morning and afternoon hours (Figure 10). The zoeae were found to move into the near-surface layer during the hours of darkness reaching the highest density at 01:00 a.m. (Figure 10). Further, there was a sinking of the larvae and they formed aggregations below 25 m by sunrise. The author did not find significant differences in the daily dynamics of zoea I and II although zoea I demonstrated a smoother pattern indicating their lower mobility (Figure 10) [68]. The highest density of RKC larvae (up to 74.0 ind. m<sup>-3</sup>) was noted in the inner part at a depth of 57 m [68]. The total abundance of the zoeae ranged between 1 and 87 ind. m<sup>-3</sup> averaging 17.5 ind. m<sup>-3</sup> in the middle part. There was a clear decrease in the total zoeal density (14.1 ind. m<sup>-3</sup>) in the outer part whereas the open water adjacent to the bay had the lowest density [68].

Similar to the Barents Sea, a study conducted in the Bering Sea has documented that RKC larvae migrated to deeper waters during bright daylight hours [96]. RKC zoeae tended to move up in the water column to feed during the day, rather than at night similar to most planktonic organisms in Auke Bay, Alaska [97]. The authors showed that the proportion of larvae with food in their guts always exceeded 80%, but reached a minimum at 24:00 h and was maximal at 04:00 to 08:00 a.m. [97] suggesting a more intensive feeding rate of the larvae in shallow waters during the daytime and less intensive in deep waters and at night. Active feeding was revealed at 04:00–08:00, while at 16:00 it tended to be greater for zoeae III–IV than for zoeae I–II [97]. The larval presence and feeding behavior were associated with the highest chlorophyll *a* concentrations at 8 m depth and a peak of copepod nauplii at 5 m depth [97]. Reduced feeding by RKC larvae in deep waters during night hours might be explained by lowered food availability or by reduced temperatures which can decrease the larval metabolic rates [97]. Data from the native regions of RKC larvae indicate that vertical migratory patterns may differ between zoeal stages [96,97].



## 5. Role of RKC Larvae in Plankton Communities in the Barents Sea

Experimental studies provided evidence that decapod larvae are omnivorous, feeding on phytoplankton and co-occurring mesozooplankton including copepod nauplii, other benthic invertebrate larvae, and conspecific and unrelated zoeae [98]. RKC larvae were also found to be plankton feeders consuming both phytoplankton and zooplankton [99]. As they pass through various stages of their development, during which they molt four times, they feed on phyto- and zooplankton in the pelagic layer for two months [67].

The feeding rates in the RKC larvae have been studied intensively under laboratory conditions [72,100–102]. One study revealed that RKC zoeae fed on diatoms [72]. Other studies have emphasized the importance of other sources for promoting the development and growth of RKC larvae including various zooplankton animals (larvae of bottom animals, nauplii, etc.) [100,101]. RKC zoeae fed on *Artemia* nauplii demonstrated highly variable feeding rates between individuals, days and stages, but these increased steadily through the development of RKC larvae. The total number of nauplii ingested by zoea I–IV was found to be 89.2, 162.6, 229.6, and 296.2 ind., respectively, and the total number consumed through all four stages averaged 760 ind. [101]. Other authors revealed that the consumption rates of *Artemia* nauplii by zoeae I–IV were 11, 22, 33, and 42 ind.<sup>-1</sup>, respectively, at 8 °C and total consumption through all larval stages averaged 1054 nauplii per zoea. [102]. Another study has shown that RKC zoeae are able to capture and ingest a relatively wide range of particle sizes, from 2 µm to 100 µm but they do not show true hunting behavior and rely on an encounter feeding mechanism [103].

Experimental research revealed that zoea I of RKC ingested copepods (size range 0.8 mm) at an average rate of 4 ind. d<sup>-1</sup> if fed within 60 h of hatching [104], this emphasizes the importance for RKC larvae to feed within 60 h of hatching. Microalgae *Thalassiosira*, *Chaetoceros*, *Skeletonema*, and small zooplankton larvae (Copepoda nauplii, barnacle nauplii, polychaete trochophores, and copepodites) were found to be the main food items for zoeal plankton under experimental conditions with natural seawater from Auke Bay, Alaska [94]. Cell concentrations of phytoplankton required to provide maintenance, growth, and development of RKC larvae over 5 days at 5.5 °C were about 1800–13200 cells mL<sup>-1</sup> [94]. Earlier larvae were able to ingest copepod nauplii at densities > 200 ind. L<sup>-1</sup> [94]. Phytoplankton (*Thalassiosira* spp. and *Skeletonema*) were the most preferable food for zoeal plankton while densities of *Chaetoceros* and copepod nauplii were too low to support the growth and survival of first-feeding larvae [94]. The total abundances of phyto- and zooplankton demonstrate pronounced spatio-temporal fluctuations during the spring period at high latitudes [12,105–112]. Such fluctuations can affect the survival and growth rates in RKC larvae in the Bering Sea and other native regions. The zoeae that occur earlier encounter better feeding conditions, with maximal abundances of *Thalassiosira* spp. and minimal densities of potential zooplankton competitors that promote a faster growth rate, higher survival rate, and successful development. The larvae that hatch later encounter phytoplankton dominated by less nutritious species and more competitors. Later stages of RKC larvae survive better on diets that contain some zooplankton in addition to phytoplankton. RKC zoeae I reared in natural seawater with low phytoplankton concentrations (Resurrection Bay) showed no growth or just barely maintained their body weight [113]. Moreover, the phytoplankton community in Resurrection Bay was composed mainly of pennate cells that are not considered to be good food sources, rather than the large centric diatoms similar to *Thalassiosira* that are preferred by RKC larvae [113].

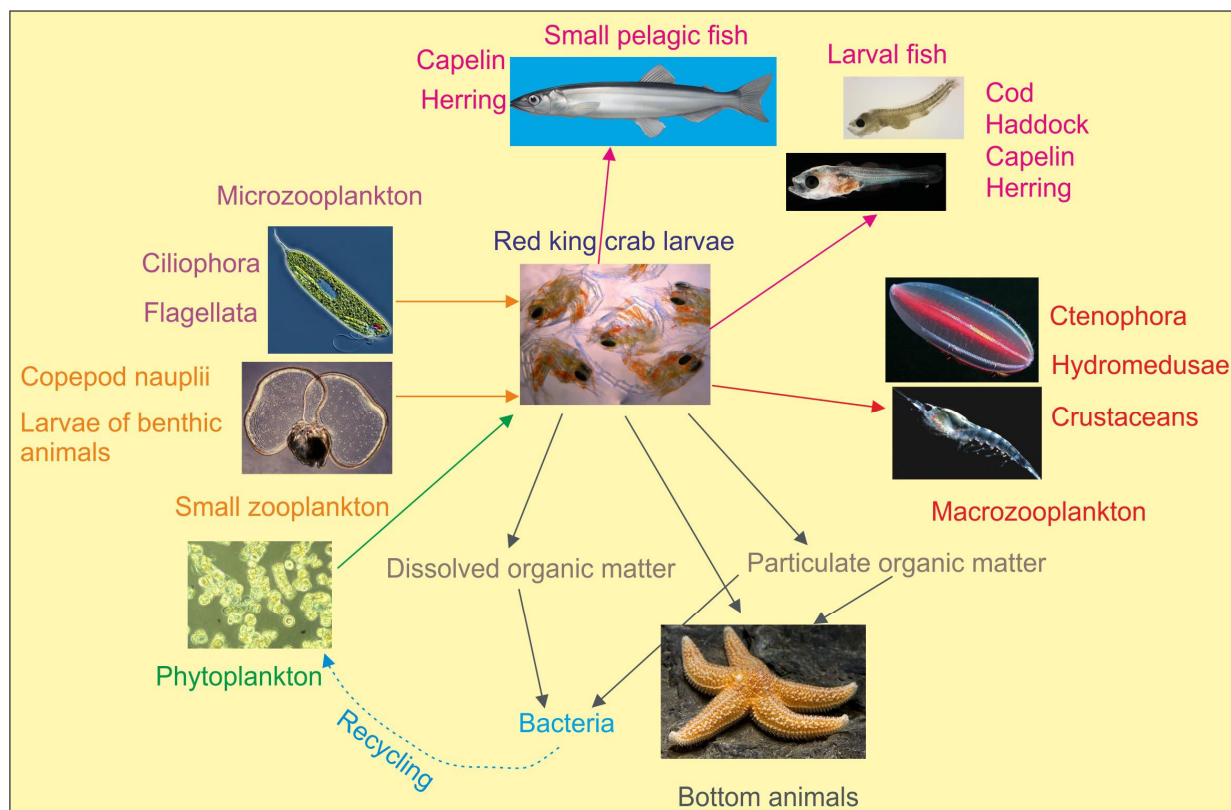
In spring, zoeal plankton represent a major part of meroplankton and, therefore, strongly affect the functioning of pelagic ecosystems in the Barents Sea. Between 1996 and 1999, the average occurrence of RKC larvae along the Murmansk coast was 34.22% of the total number of Decapoda larvae at depths above 150 m and 16.7% at depths less than 150 m. It was found that RKC larvae reached the maximum relative abundance in the coastal waters adjacent to Kola Bay (54.5%), in Motovsky Bay (36.6%) and in Varanger-fjord (30.1%) [68]. In the areas located to the west of Kola Bay, the contribution of RKC zoeae was much lower and did not exceed 3.0% while in the eastern regions they were absent. Therefore,

RKC larvae are considered a dominant component among decapod crustaceans existing in the plankton during the spring period. Moreover, they may amount to a considerable proportion of the total mesozooplankton in the western coastal waters. For instance, the relative density of RKC larvae can reach 70% of the total mesozooplankton biomass during the hatching period [68,83]. Their average proportion in the total mesozooplankton biomass in the coastal areas of Varanger-fjord, Motovsky Bay, and near Kola Bay varied from 1.2 to 46.4%, with maximum values being present in the shallow bays or in the inner parts of inlets [68,80,83]. There is a clear decline in the contribution of RKC zoea to the total zooplankton density towards the open sea. In spring 2016, RKC larvae accounted for 0.1 ind.  $m^{-3}$  (<0.01% in the total mesozooplankton abundance) and 0.03 mg dry mass  $m^{-3}$  (0.02% in the total mesozooplankton biomass) in the southern Barents Sea [90]. In Norwegian waters, the mean proportions of RKC zoea varied from 0.02 to 0.2% of the total meroplankton in April 2013 [85–87].

From 1996 to 1999, zoea I was found to be the most numerous stage that contributed significantly to the total mesozooplankton biomass during the early spring period. Later, when zoeae II–III were dominating, their proportions in the total mesozooplankton biomass decreased considerably [68]. Phytoplankton density reaches a peak in March–April in the southern Barents Sea including small bays and inlets [105]. Phytoplankton abundance can vary from some thousands to two million cells per liter with *Thalassiosira*, *Chaetoceros*, *Navicula*, and *Nitzschia* being the most numerous taxa [12,105,106]. Copepoda nauplii and larvae of bottom animals become the dominant coastal zooplankton assemblages in April when their densities can be as high as >7000–10,000 ind  $m^{-3}$  while in the early spring (March) they amount <1000 ind.  $m^{-3}$  [83,107,109]. Therefore, we may suppose that the microalgae are the main food resource for zoeae of RKC in March and that copepod nauplii and other meroplanktonic animals start to play a significant role in the feeding of RKC larvae in April–May. The predation pressure of other herbivorous zooplankton reducing the availability of food can also affect the abundance of king crab larvae in April–May [89].

Juvenile sockeye salmon and RKC co-occur along the Alaska Peninsula and there is some evidence that juvenile salmon may consume RKC zoeae in the Bering Sea. The major prey items for salmon were euphausiids, copepods, cladocerans, and sand lance; however, decapod larvae were also found to occur in the diet [114]. Juvenile salmon in Georgia Strait, British Columbia, Canada was found to consume significant numbers of crab zoeae and megalops [115]. An experimental study has demonstrated that RKC zoeae constituted 1% of the diet of juvenile sockeye salmon and that fish predation induced clear mortality of RKC larvae leading to variation in recruitment [116]. There are a few papers dealing with the consumption of RKC larvae by other marine organisms in the Barents Sea. Some studies have reported RKC larvae as potential food prey for juvenile demersal fish (cod, haddock) and for plankton-feeding fish (capelin and herring) [68,89]. Being a common member of meroplankton, RKC zoeae may also be ingested by macrozooplankton (e.g., medusae and ctenophores) during the spring period (Figure 11).

However, additional investigations focused on the role of RKC larvae in the diets of other plankton animals are needed to obtain a comprehensive pattern.



**Figure 11.** Trophic position of the red king crab larvae in the pelagic food web of the Barents Sea.

## 6. Environmental Impact on RKC Larvae in the Barents Sea

The larval period of any bottom animal is considered the most vulnerable stage of its life cycle, and some factors have a crucial significance, especially food availability (see above), temperature, salinity, water circulation/currents and acidification [67,92,117,118].

### 6.1. Temperature and Salinity

Survival rates of RKC larvae at various temperatures have been mainly studied under laboratory conditions. The survival of RKC zoea I was highest between 5 °C and 10 °C [119]. Another study reported the greatest survival rate (60%) at 8 °C while only a few larvae molted to zoea II at 0 °C [76]. RKC larvae generally occur in a true marine environment with oceanic salinity (ca. 35 psu). Some experimental studies have found a decline in the survival of RKC larvae below 15 psu at temperatures of 7–10 °C [119]. Nakanishi [76] revealed that the optimal salinity at which 100% survival occurred after 24 h of acclimation was wide (from 20 to 67 psu) at lower temperatures (−1.8 °C to 8 °C) and narrow (about 27 to 33 psu) at 13 °C and above for zoeae I–II. The survival rate for zoeae III–IV was as high as 100% at salinity 13.4–40 psu and at 8 °C. The highest index of activity for the zoeae after 48 h was registered at temperatures from 3 °C to 18 °C for all larval stages, at salinities of 25–30 psu for zoeae I–II, and at 33.5 psu for zoeae III–IV [76]. Another experimental study has documented high survival rates (>85%) of RKC zoea I at temperatures from 0 °C to 27 °C and salinities from 10 to 30 psu [120]. However, the survival rate was lower (<50%) at salinities <15 psu, and no larvae survived at temperatures > 18 °C; zoea II had similar salinity tolerance but survived best at temperatures below 9 °C [120]. A temperature range of 12–18 °C and a salinity range of 20–30 psu were favorable for molting from zoea I to zoea II while 3–18 °C and 15–30 psu were preferable for molting from zoea II to zoea III [120]. Swingle et al. [121] reported that higher temperatures can accelerate the growth rate in RKC larvae so that the stoking periods from the newly hatched first stage zoea to the glaucothoe and to the first juvenile crab stage were 21 and 35 days, respectively, at 11 °C and 30 and 50 days at 8 °C. In general, RKC larvae have a fairly wide range of tolerance

for both temperature and salinity while zoea II has a more restricted range, with greatly reduced survival above 6 °C or below 25 psu. This ontogenetic change in tolerance with age is also confirmed by an increase in salinity preference from zoea I to zoea II [76,120].

Experimental investigations with RKC larvae from the Barents Sea have revealed that their tolerance towards high water temperatures increased significantly both with the larval stage and the acclimation temperature [122]. Zoeae IV were found to be the most temperature resistant (100% absolute mortality at 23.2 °C) compared to the zoea I stage which was killed at 21.5 °C. The authors also found that absolute mortality was not observed for each larval stage at subzero temperatures close to the freezing point of seawater (−1.7 °C). This might indicate a potential for a successful dispersal of RKC larvae to the north in the Barents Sea and into the more eastern regions [122]. Laboratory studies have shown that RKC larvae demonstrated the highest survival rate at temperatures of 6 °C when compared to 1–3 °C [123]. These estimations explain why RKC have become a successful invader in the Barents Sea.

In the wild, RKC larvae encounter temperatures from −1.8 °C to 14 °C and salinities from 15 to 30 psu although they may experience reduced salinities in nearshore surface waters during vertical migrations as has been shown for the coastal zone of Alaska [120]. In Auke Bay, Alaska, RKC larvae occurred at depths from 10 to 30 m and preferred salinity > 27 psu [120]. Survival rates of RKC larvae were negatively affected by low-salinity waters, but probably not by temperatures within normal environmental ranges [120]. Under natural conditions, low temperatures would cause slower movements and prolonged intermolt periods, increasing vulnerability to predation [120]. The timing of the presence of RKC larvae usually corresponds to seawater temperature, and lowered temperatures may result in slower development and longer occurrence in the plankton [92]. Delays in the appearance of RKC larvae in the plankton are noted in years with low water temperatures [91]. The earlier appearance of crab larvae in the plankton is usually associated with the participation of young RKC females in reproduction [78,79,88].

In Ura Bay (coastal Barents Sea) in 2011–2016, a peak of RKC larval abundance occurred in April after the spring increase in water temperature. However, there was an earlier occurrence of zoeae (2014 and 2016) and this pattern was due to the strong warming [81,84]. Interestingly, the thermal conditions of previous years (2013 and 2015) had a great influence on the hatching time and appearance of RKC larvae [81,84]. An analysis of available data showed that the earlier appearance and the largest number of RKC larvae were typical for the “anomalously warm” years of 2014 and 2016 [81]. There was also a delay in the appearance of zoeae in the years following the “cold” year. Similar patterns were noted in the North Pacific region. Hatching and the first appearance of RKC larvae were detected earlier off the Western Kamchatka in “warm” years [124]. Differences in the timing of RKC larvae hatching in “cold” and “warm” years were also reported in Peter the Great Bay (Sea of Japan) where warm springs and very hot summers were unfavorable for settling of RKC larvae [125]. It is more likely that positive water temperature anomalies would not be so critical for developing RKC larvae in the Barents Sea because embryo development occurs in the bottom layer where water temperature is rather stable. In contrast, warming would affect strongly the total density of RKC larvae in the coastal waters that is confirmed by close associations between temperature fluctuations and stock dynamics of juvenile RKC in the coastal zone of the Barents Sea [31].

## 6.2. Currents

The settling ability of marine bottom invertebrates is strongly associated with dispersal processes, local circulation patterns, and transport of meroplanktonic stages with currents [126]. Several authors have documented the importance of currents for dispersing zoal plankton from inshore waters to the open ocean where mass mortality of the larvae can occur [127,128]. Transport of larvae from their hatch locations to settlement areas involves diffusion, i.e., the spread of numerous individuals away from an initial central location and advection, i.e., the process when an individual or a population is transported



away from their starting locations and arriving at a defined endpoint [129]. Advection–diffusion processes can have large ramifications for species with pelagic larvae, influencing population stability and productivity. Advection may deliver larvae to unsuitable habitats, causing them to die at settlement [129].

In the case of RKC, a significant role of circulation patterns has been demonstrated by Daly et al. [130]. The authors applied a biophysical and oceanographic circulation model to investigate larval connectivity of more recent female spatial distributions and evaluate the importance of climate variability on larval advection trajectories. They found that predicted settlement success was associated with larval pelagic duration and oceanographic circulation patterns as follows: shorter advective distance was driven by warmer conditions, leading to higher rates of local retention in comparison to cold conditions. Furthermore, most RKC larvae hatched in southwest Bristol Bay were advected offshore away from good habitats, whereas larvae hatched in central and nearshore Bristol Bay were retained in or transported to good habitats along the Alaska Peninsula [130].

A study based on modeling the RKC larvae dispersal process has shown that the bulk of zoeae released in sheltered bays and small inlets would be retained within the fjords in the Barents Sea and adjacent Norwegian waters [131]. The adult RKC females residing and spawning within fjords could potentially increase the probability of RLC larvae to occupy shallow, sheltered and complex benthic habitats representing important sites for juvenile survival [131]. The authors have also established that the coastal regions in the Barents Sea seemed to be the main settling areas for RKC and have also shown the impact of wind regimes and the Ekman drift on the larval trajectories. The model has proposed the general eastward direction of dispersal and advection of RKC larvae in the westbound direction along the coast [131].

### 6.3. Acidification

Experimental studies have reported that the development of RKC embryos differed morphologically between control and acidified treatments after only a month of exposure with embryos being larger and yolks being smaller in acidified water [118]. Low-pH water was found to decrease the embryonic developmental rate and can reduce the embryonic activity of various benthic species [132–136]. However, the developmental rates of RKC larvae were faster in acidified water. The larger embryos and smaller yolks of RKC suggested that the embryos might use a greater amount of their energetic reserves to grow. Another possible explanation of this phenomenon is that smaller yolks reflect increased energetic costs in acidified water [137]. Greater hatching duration under low-PH conditions could be owing to an increase in environmental variability. Lithodid crabs probably show a bet-hedging strategy in which they spread larval release over a long period to increase the ability that some larvae will be released at a time with high food availability that may maximize the survival rate of RKC larvae [138]. Therefore, pH may impact hatching duration in RLC by increasing perceived environment variability or unpredictability and thus food availability [67,117].

Acidification was found to be responsible for morphological differences between the larval stage, with RLC larvae hatched from embryos held in low-pH water being larger and longer than those held in control water [118]. This result contradicted some previous studies that reported marine larvae reared in acidified water are frequently smaller or malformed relative to those reared in control water [139,140]. This increase in size could affect the fitness of RKC in the wild. There were no differences in dry mass, carbon, and nitrogen content in newly hatched larvae between acidified and control waters [118]. This suggests that increased size was primarily driven by higher water content or that acidified larvae were smaller in width and thus had a similar volume. Calcium content was higher in both female exoskeletons in acidified waters and in larvae held in low-pH water [118].



#### 6.4. Overall Environmental Changes

Population fluctuations of most crab species are associated with recruitment variability [141,142]. Total crab abundances tend to increase through recruitment and decrease due to catch and natural mortality [24,25,30,31]. RKC recruitment was found to be periodic in Alaskan waters [143] and population density increases quickly during a period of strong recruitment and reaches peaks right after the poor recruitment period begins. RKC recruitment can vary greatly over time. Recruitment fluctuations may be connected with changes in spawning biomass, environmental factors, competition, and predation [24,25,30,31]. Environmental factors including water temperature, wind, and barometric pressure may strongly influence food availability and larval transport, growth, and survival of RKC in native regions [67]. Predation on eggs and larvae will also impact recruitment processes [144]. In the Barents Sea, warming may cause significant changes in pelagic food webs [5,6,16,83] and this may lead to variability in RKC stocks [24,25,30,31]. We may propose that enhanced water temperature will affect the survival rate, growth, and developmental time of RKC larvae in the coastal Barents Sea. Increased water temperature may be unfavorable for RKC larvae. At the same time, warming may cause earlier phytoplankton peaks and higher food availability for zoeal plankton, which would be beneficial for RKC larvae. Anyway, the potential response of meroplanktonic stages of RKC to environmental changes remains unclear and needs to be further studied.

#### 7. Conclusions

*Paralithodes camtschaticus* has become a successful invader in the Barents Sea and supports profitable fisheries in Russia and Norway. Larvae of RKC represent a major part of meroplankton assemblages in coastal waters during the spring period and have a measurable impact on the phyto- and zooplankton as consumers of microalgae and small pelagic animals. Mass hatching of RKC larvae occurs in April while the first zoeae can be detected in late January–February. Zoeal plankton could be detected until mid-July. Development from stage zoea I to zoea IV lasts two months. Spatial patterns of RKC larvae are mainly controlled by currents, water exchange, and advection. There is pronounced patchiness in the distribution of RKC larvae with dense aggregations being present in small bays, inlets, and inner parts of fjords. Lower abundances of RKC larvae are typical for the offshore zone. Peak density generally coincides with spring bloom. During the hatching period, the total biomass of RKC larvae can reach 70% of the total mesozooplankton biomass. Food quality and availability and environmental conditions (hydrology, circulation patterns, climatic forcing) are the main drivers determining inter-annual variability in abundance, growth, and survival rates of RKC larvae in the Barents Sea. Considering strong climatic changes in the Arctic during the past decades, we may propose that there would be further spreading of RKC in the eastern and northern regions of the Barents Sea as well as south along the Norwegian coast.

**Supplementary Materials:** The following are available online at <https://www.mdpi.com/article/10.3390/w14152328/s1>, Table S1: Mean abundance (individuals m<sup>-2</sup>) of red king crab larvae in the plankton in Ura Bay in 1996–1999. Table S2: Total abundance (individuals m<sup>-2</sup>) of different zoea stages (ZI–ZIV) of in the plankton in Ura Bay in 1996–1999.

**Author Contributions:** Conceptualization, V.G.D. and A.G.D.; methodology, V.G.D.; software, V.G.D.; validation, A.G.D.; formal analysis, V.G.D. and A.G.D.; investigation, V.G.D.; resources, V.G.D.; data curation, A.G.D.; writing—original draft preparation, V.G.D. and A.G.D.; writing—review and editing, V.G.D. and A.G.D.; visualization, V.G.D. and A.G.D.; supervision, A.G.D.; project administration, A.G.D. All authors have read and agreed to the published version of the manuscript.

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