

Thermal behaviour and the prospect spread of an invasive benthic top predator onto the Euro-Arctic shelves

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ABSTRACT

Aim A focal task for invasion biology is to identify the environmental variables and biological traits that set and underpin realised and potential habitats of invasive species. Ecophysiology provides powerful empirical knowledge that connects theory with natural phenomena and may improve the accuracy of species distribution modelling. We used the introduced Kamchatka red king crab *Paralithodes camtschaticus* of the Barents Sea as a prime case to show how thermal behaviour may drive the spreading of a marine invader in context of ocean warming. Finally, we discuss the conceivable consequences for a poleward spread of invasive top predators on native marine biota, conservation and management policies.

Location Barents Sea, Euro-Arctic shelves, Northeast Atlantic.

Methods We used novel and non-manipulative tests which allowed adult red king crab to freely select and monitor ambient temperature *in situ* across a < 1–14 °C gradient by means of a temperature data storage tag attached to the carapace.

Results Adult red king crab, irrespective of body size, maturation stage and nutritional state, (1) displays clear behavioural thermoregulation in a heterothermal environment and, (2) conclusively selects temperatures in the coldest end of a gradient and avoids temperatures > 4 °C. The final thermal preferendum matches completely present day Arctic shelf temperatures north and east in the Barents Sea.

Main conclusions This is the first published study on the thermal behaviour of a marine invasive top predator. Our tests and the concurrent realised habitat north-east of Kola Peninsula suggest that the introduced red king crab is capable of invading the Euro-Arctic shelves in less than three decades. We argue that current management practices of the introduced red king crab compromise Arctic biodiversity and conservation and, to counteract further spreading, we recommend free fisheries on this species across its entire distributional area in the Northeast Atlantic.

Keywords

Arctic shelves, invasive species, Kamchatka red king crab, *Paralithodes camtschaticus*, prospect spread, realised and potential habitats, thermal behaviour.

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INTRODUCTION

Biological invasions are generally considered a major threat to native organisms and, in the light of climate change and increased human activity, native biota of the Arctic seas and

shelves is particularly at risk of being confronted by invasive species (CAFF, 2013; Fernandez *et al.*, 2014). Climate change and ocean warming presently shift range boundaries of fishes and other marine organisms northward (Hollowed *et al.*, 2013; Poloczanska *et al.*, 2013; Christiansen *et al.*,

2014), and direct human activity mediates the spreading of non-native species (Havel *et al.*, 2015) either by infrastructure such as water channels (Leppäkoski *et al.*, 2002; Keller *et al.*, 2011), accidental leakages from aquaculture and shipping enterprises (Miller & Ruiz, 2014; Ware *et al.*, 2014) or by managed translocations (deliberate introductions). Therefore, knowledge of environmental preferences and thresholds for invasive species in novel environments is fundamental to assess their potential spreading and impact on native biota and to initiate proper counter measures for conservation (Ricciardi *et al.*, 2000; Somero, 2005; Cooke *et al.*, 2014).

Big pictures and concepts in conservation biogeography and invasion biology are rooted in case studies that connect theory with natural phenomena. The Kamchatka red king crab (hereafter red king crab), *Paralithodes camtschaticus* (Tilesius, 1815), Lithodidae, is a prime case to gain important insights to how marine invasive species may disperse and impact native biodiversity and conservation *sensu lato* because its history, from the first and failed attempts of translocation in the 1930s (Yu. I. Galkin cited in Timofeev, [1999]) into the full-grown invasive species of today, is meticulously documented. The red king crab, a native and valuable fisheries resource to the Bering Sea and the North Pacific, is the most prominent and infamous example of a marine invasive species intentionally introduced to the Northeast Atlantic (Sundet, 2014). In the period 1961–1969, scientists from the former Soviet Union successfully transferred the animal from the Far East (Peter the Great Bay and Sea of Okhotsk, Fig. 1) into the Barents Sea to support commercial fisheries in the Kola region (Orlov & Ivanov, 1978). Since then, the red king crab has become firmly established in the Barents Sea biota, and the population has increased from a mere ~ 2600 introduced adults during the 1960s to an estimated peak abundance of > 20 million adult specimens in 2003 (Orlov & Ivanov, 1978; Matishov *et al.*, 2012). The animal is currently spreading westward along the Norwegian coast of Finnmark and to the north-east in Russian offshore waters (Sundet, 2014) (Fig. 1). Speculations about the spreading of red king crab now and again spark eye-catching headlines in the international press such as: "... a red army of monster crustaceans – marshaled by Soviet-era leaders – is threatening to invade Western Europe ... as far south as Spain and Portugal ..." (National Geographic, 2004).

The study of invasive species intersects multiple disciplines spanning from biology to social sciences and management (Richardson & Whittaker, 2010). A key topic in invasion biology is to identify the environmental variables and biological traits that define and underpin realised (confirmed presence) and potential (threshold) habitats of introduced species in both donor and recipient areas (Jiménez-Valverde *et al.*, 2008). Empirical knowledge of environmental preferences and physiological tolerances is deemed particularly valuable to pinpoint potential habitats and invasion routes – core issues for spread models, integrating statistical and

mechanistic approaches, and in forecasts of realistic dispersal scenarios for invasive species (Somero, 2005; Kearney & Porter, 2009; Franklin, 2013).

In view of ocean warming, ambient temperature has become the most pervasive abiotic variable that governs the spatial distribution and the geographic spreading of ectothermic animals. Crustaceans have body temperatures similar to that of the surrounding water but, in hetero-thermal environments, freely moving animals may readily regulate body temperature by actively seeking temperature zones that optimise physiological processes such as food conversion and growth, that is display behavioural thermoregulation (Lagerspetz & Vainio, 2006).

The terms acclimation and acclimatisation denote phenotypic adjustments to abiotic stimuli in the laboratory and in nature, respectively (Cossins & Bowler, 1987). When subjected to a thermal gradient in the laboratory, ectotherms eventually gravitate towards a stable and narrow thermal zone, the final thermal preferendum (FTP), which is considered to be a species-specific trait unaffected by thermal history, for example acclimation temperature (Fry, 1947; Jobling, 1981). In fishes, the FTP is usually obtained after 24–48 h in a gradient. In nature, on the other hand, the realised thermal acclimatisation zone is defined by a multitude of non-thermal variables such as life cycle stage, prey–predator relationships, growth trajectories, infections and hypoxia that should be considered in studies of thermal preferenda in ectotherms (Christiansen *et al.*, 1997; Lagerspetz & Vainio, 2006; Somero, 2010; Golovanov, 2013; Killen, 2014).

Species-specific responses to cold and heat preclude uncritical extrapolations across ectothermic taxa and biomes and necessitate tailored tests for focal species in question. In its native Pacific waters, red king crab occurs across ambient temperatures -1.8–18 °C (Matishov *et al.*, 2008; Stevens & Lovrich, 2014). In the Barents Sea, the thermal habitat of red king crab is less studied, but finds span ambient temperatures -0.8–8.5 °C, with males predominantly at 4–6 °C and females at 5–7 °C (Pinchukov & Sundet, 2011). A shortage of empirical data on the thermal behaviour and environmental thresholds for larvae and adults clearly hamper substantiated distribution modelling and spread scenarios of red king crab in the Northeast Atlantic.

Through a series of novel and non-manipulative laboratory experiments, we tested temperature selection and FTP by adult red king crab and provide the first strong indices for a potential spread of this introduced species northward. An invasion of red king crab onto the Euro-Arctic shelves will inevitably have wide consequences for ecology, conservation and socio-economy albeit the magnitude of impact is as yet speculative. Our results are discussed in context of realised and potential habitats, ocean warming and Arctic marine wildlife. We argue that current (mis)management practices of introduced red king crab may compromise Arctic biodiversity and conservation as outlined in the recent Arctic Biodiversity Assessment Report commissioned by the Arctic Council (CAFF, 2013).

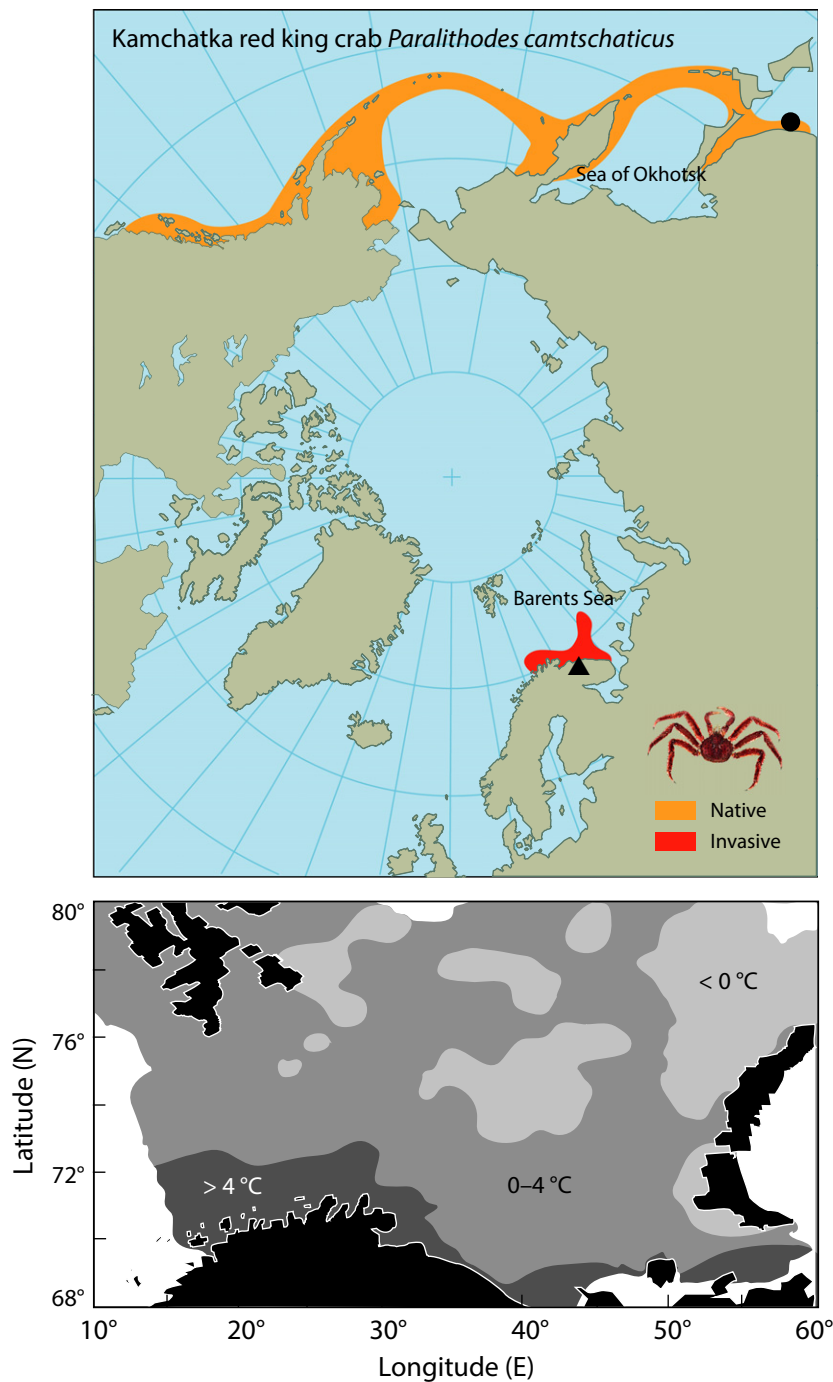


Figure 1 Upper panel – geographic distribution of native and invasive (introduced) Kamchatka red king crab *Paralithodes camtschaticus* (modified from R. Pravettoni, <http://www.grida.no/>). The filled circle denotes the main site of sampling (Peter the Great Bay near Vladivostok), and the filled triangle denotes the main site of introduction (Kola Bay near Murmansk). Lower panel – near bottom temperatures of the Barents Sea in August–September 2009 (modified from Boitsov *et al.*, 2012): > 4 °C (dark grey), 0–4 °C (grey) and < 0 °C (light grey). The 0–4 °C area demarcates the potential thermal habitat for introduced animals (cf. Fig. 3).

METHODS

Test animals

Intact adult male and female red king crab were collected in crab pots in Varangerfjorden and Tanafjorden, North Norway, and transported live to the Aquaculture Research Station in Tromsø, Norway. Animals were ID-tagged and distributed in 700 l holding tanks supplied with stable running seawater (~ 6.5 °C, salinity ~ 32) and held at the natural photoperiod (~ 70 °N, midnight sun: 17 May–20 July).

During the acclimation period (primo February–mid June 2007), animals were fed in excess manufactured pellets for cod culture (Dana Feed A/S) and fish carcasses.

Tests of thermal behaviour

Altogether 26 adult animals pertaining to three maturation groups were tested in a temperature gradient (Table 1): sexually mature males (SMM, $n = 12$), immature females (IFM, $n = 7$) and ovigerous females (OFM, $n = 7$). Temperature tests were conducted in two flow-through PVC channels

Table 1 Temperature means (\pm SEM) and ranges selected by introduced Kamchatka red king crab *Paralithodes camtschaticus* in a thermal gradient ($< 1\text{--}14$ °C) during a 24-h test period

| Group | Animals (<i>n</i>) | CL (mm) | Tests (<i>n</i>) | Temperature logs (<i>n</i>) | Selected temperature (°C) | |
|-------|----------------------|---------|--------------------|-------------------------------|---------------------------|-----------------------|
| | | | | | Fed | Unfed |
| SMM | 12 | 108–121 | 24 | 11,520 | 2.7 (0.2) 0.9–13.5 | 3.0 (0.2) 1.3–13.5 |
| IFM | 7 | 100–115 | 14* | 6,240 | 2.5 (0.3) 1.0–13.7 | 2.7 (0.3) 1.8–13.5 |
| OFM | 7 | 112–148 | 14* | 6,240 | 2.9 (0.2) 2.0–13.5 | 3.5 (0.4) 0.6–13.5 |

There were no statistically significant differences in temperature selection neither within nor across groups.

CL, carapace length; SMM, sexually mature males; IFM, immature females; OFM, ovigerous females.

*One test on fed animals excluded from statistical analysis (cf. Fig. 3c, e).

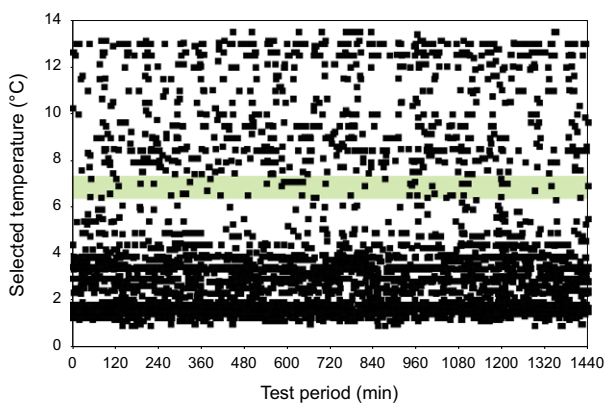


Figure 2 Temperatures selected and recorded by introduced Kamchatka red king crab *Paralithodes camtschaticus* exemplified by 12 fed males (SMM, *n* temperature logs = 5760) tested individually for 24 h in a thermal gradient ($< 1\text{--}14$ °C). Filled symbols depict the thermal footprints of the 12 animals combined, and the horizontal shaded bar indicates the stable acclimation temperature (~ 6.5 °C) of the holding tanks. See text and Table 1 for further information.

(water volume: $2.6 \times 0.9 \times 0.3$ m). A stable horizontal thermal gradient, range: $< 1\text{--}14$ °C, was obtained by mixing cooled and warmed water at four length ward sites with separate inlets and outflows. Valves ensured that the gradient could be reversed or turned off and on within minutes. Temperatures were checked daily, and water flow was adjusted accordingly to secure gradient stability. At the start of a test, a single animal was removed from the holding tank, and a temperature data storage tag (DST, iBKrill-AlphaMach, Inc., QC, Sainte-Julie, Canada) was attached dorsally to the carapace. The DST was programmed to log ambient temperature every 3 min, that is a 24-h test period would render 480 temperature recordings per animal. In effect, an animal was left undisturbed during tests while it freely monitored the selected temperature across the $< 1\text{--}14$ °C gradient (Fig. 2). Prior to the main tests, a series of pilot studies were successfully run by reversing the gradient to ensure that animals

actually responded to temperature *per se* and not to the channel or surroundings. Direct observations also revealed that animals were not unduly affected by the DST.

From 20 March to 16 June, single animals were tested twice in the gradient, that is both fed and unfed. Unfed animals were food deprived for about 2 weeks prior to the test. The animals were left in the gradient for 48 h without access to food. During the first 24 h, animals were allowed to habituate to the gradient. Only data logged during the last 24 h were used in the subsequent analyses. Temperature data were downloaded to a PC, and tested animals were returned to the holding tank.

Data analyses

Selected temperatures within and across maturation groups (*n* = 480 logs per animal per test) were analysed using ANOVA with data compared to a normal distribution using Kolmogorov–Smirnov Lilliefors. Homogeneity was checked using Levene's test (SYSTAT v. 12-Systat Software, Inc., San Jose, CA, USA). Data are presented as mean \pm standard error (SEM), and statistical significance was assumed when $P < 0.05$. Individual test data are available upon request to the senior author (J.S.C.).

RESULTS

The temperatures selected by individual red king crab are disclosed in Fig. 3a–f. Animals explored the entire temperature range of the gradient $< 1\text{--}14$ °C (Table 1; Fig. 2) but 68–78% of the temperature recordings gravitated within the $< 1\text{--}4$ °C zone (Fig. 3). The selected mean temperature (ST) was completely decoupled from body size (carapace length, CL: $100\text{--}148$ mm) irrespective of maturation group and nutritional state ($ST = 0.009 CL + 2.97$, $r^2 = 0.019$, $P = ns$, $n = 50$) and ranged from 2.5 °C ± 0.3 in fed IFM to 3.5 °C ± 0.4 in unfed OFM (Table 1). However, there were no statistical differences in selected temperature neither within nor across maturation groups ($F_{2,50} = 1.43$, $P = 0.249$) (Table 1). The overall selected mean temperatures

in the gradient, on the other hand, were significantly below (3.0–4.0 $\Delta^{\circ}\text{C}$) the acclimation temperature of the holding tanks ($\sim 6.5^{\circ}\text{C}$) (Fig. 3).

To sum up, our study shows that adult red king crab, irrespective of body size, maturation stage and nutritional state, (1) displays clear behavioural thermoregulation in a heterothermal environment and, (2) conclusively selects temperatures in the coldest end of a gradient (2.5–3.5 $^{\circ}\text{C}$) and avoids temperatures $> 4^{\circ}\text{C}$ (Fig. 3).

DISCUSSION

Looming invasion of introduced red king crab onto the Euro-Arctic shelves

Native Pacific and introduced Atlantic populations of red king crab show similar genetic diversity which suggests that alleged founder effects are insignificant and that the disjunct populations share the same physiological capacity for spreading into new areas (Jørstad *et al.*, 2007; Grant *et al.*, 2014). Experimental studies with live animals have pros and cons. Laboratory animals collected in the field are inevitably artificially selected and do not necessarily reflect natural populations. On the other hand, our tests were simple and the red king crabs were able to freely and undisturbed explore the entire temperature gradient, regulate body temperature by behavioural means and log ambient temperatures *in situ* (Fig. 2). A high level of precision (reproducibility) was obtained for all the tested animals (Fig. 3), and the accuracy (true value) is deemed credible as the selected mean temperatures were well within those observed in the field (Pinchukov & Sundet, 2011). Moreover, the selected mean temperatures in the gradient were consistently lower than the imposed acclimation temperature of the holding tanks (Fig. 3). This suggests that the animals actually gravitated towards their FTP within 48 h in the gradient.

Freely moving crustaceans avoid extreme temperatures by behavioural thermoregulation (Lagerspetz & Vainio, 2006). Although red king crab entered gradient extremes 0.6 and 13.7 $^{\circ}\text{C}$ (Table 1), the bulk of recordings ($\sim 72\%$) was obtained within the $< 1\text{--}4^{\circ}\text{C}$ temperature zone (Fig. 3). Fishes generally seek higher temperatures during the spawning season compared with other life stages (Christiansen *et al.*, 1997). A relatively high mean temperature was selected by OFM (3.5 $^{\circ}\text{C}$), but it was not statistically different from those of the other groups (2.5–3.0 $^{\circ}\text{C}$). Nutritional state (i.e. fed vs. unfed) also affects temperature selection in fishes but results are inconclusive (Christiansen *et al.*, 1997). Fed and unfed red king crab, on the other hand, selected similar temperatures. Interestingly, a growth study of introduced red king crab showed that adult males fed at and subjected to constant temperatures 4, 8 and 12 $^{\circ}\text{C}$ had the better food conversion efficiency at the lowest temperature (Siikavuopio & James, 2015). The selected mean temperature (2.7 $^{\circ}\text{C}$) by fed males (Table 1; Figs 2 & 3a), thus, suggests that food conversion is even more efficient at ambient temperatures

$< 4^{\circ}\text{C}$. For technical reasons, red king crabs were tested one by one and an experimental shortfall may lie in the fact that the species is gregarious by nature (Sundet, 2014). Social interactions may affect temperature selection in fishes (Christiansen *et al.*, 1997), but this has yet to be tested for crustaceans.

The FTP depicts the temperature zone within which biochemical and physiological processes become fine-tuned (Hochachka, 1991). The FTP is readily measured under the stringent settings of a laboratory. In nature, on the other hand, the complex, subtle and often impenetrable interplay linking biology, environment and climate sets the realised thermal habitat of a species, and inevitably weakens the accuracy and predictive power of species distribution modelling drawn solely from field and statistical metrics (Christiansen *et al.*, 1997; Somero, 2005; Bellard *et al.*, 2013; Franklin, 2013). For example, polar cod *Boreogadus saida* (Lepechin, 1774) is an abundant gadoid in the subzero waters of the Arctic seas (Christiansen & Fevolden, 2000) but, in the laboratory, the species selects considerably higher temperatures (3–5 $^{\circ}\text{C}$) and shows pronounced hardiness to $\sim 14^{\circ}\text{C}$ (Schurmann & Christiansen, 1994; Christiansen *et al.*, 1997). In effect, the polar cod is both a cold stenotherm in its realised habitat and a eurytherm in physiological capacity – a eurythermy that might be elicited once environmental conditions change. In other words, the manifestation of realised and potential habitats differs in temporal scale: the realised habitat results from short-term changes in environment and biotic interactions while the potential habitat reflects adaptations carved on an evolutionary time-scale.

To identify the underlying environmental, ecological, behavioural, physiological and genetic mechanisms of realised and potential habitats is a focal task for conservation biogeography and invasion biology (Somero, 2005, 2010; Franklin, 2013; Fordham *et al.*, 2014). Following the above considerations, the FTP is an empirical metric that gives powerful and accurate insights to dispersal potentials inferred from ambient temperatures that are selected and, in particular, avoided by ectotherms in nature.

Near seafloor temperatures $> 0^{\circ}\text{C}$ cover $\sim 70\text{--}95\%$ (years 2000–2010) the area of the Barents Sea (Boitsov *et al.*, 2012), and the FTP of the introduced red king crab (Table 1) matches completely present day shelf temperatures west and north of Svalbard Archipelago at latitudes $\sim 74\text{--}80^{\circ}\text{N}$, large parts of the northern and central Barents Sea and to the north-east of Kola Peninsula (Boitsov *et al.*, 2012; Fig. 1). Notably, the latter area was recently invaded by red king crab. Our tests and the concurrent realised habitat off Kola indicate that the introduced red king crab may indeed invade the Euro-Arctic shelves $< 4^{\circ}\text{C}$ and, thus, abate speculations about a southward spreading.

Data on dispersal rates for the introduced red king crab are scarce. Occasional observations of single animals along the Norwegian coast south to Bergen ($\sim 60^{\circ}\text{N}$) and one extraordinary find in the Mediterranean Sea are all ascribed transplants from fishing vessels or ballast water (Faccia *et al.*, 2009;

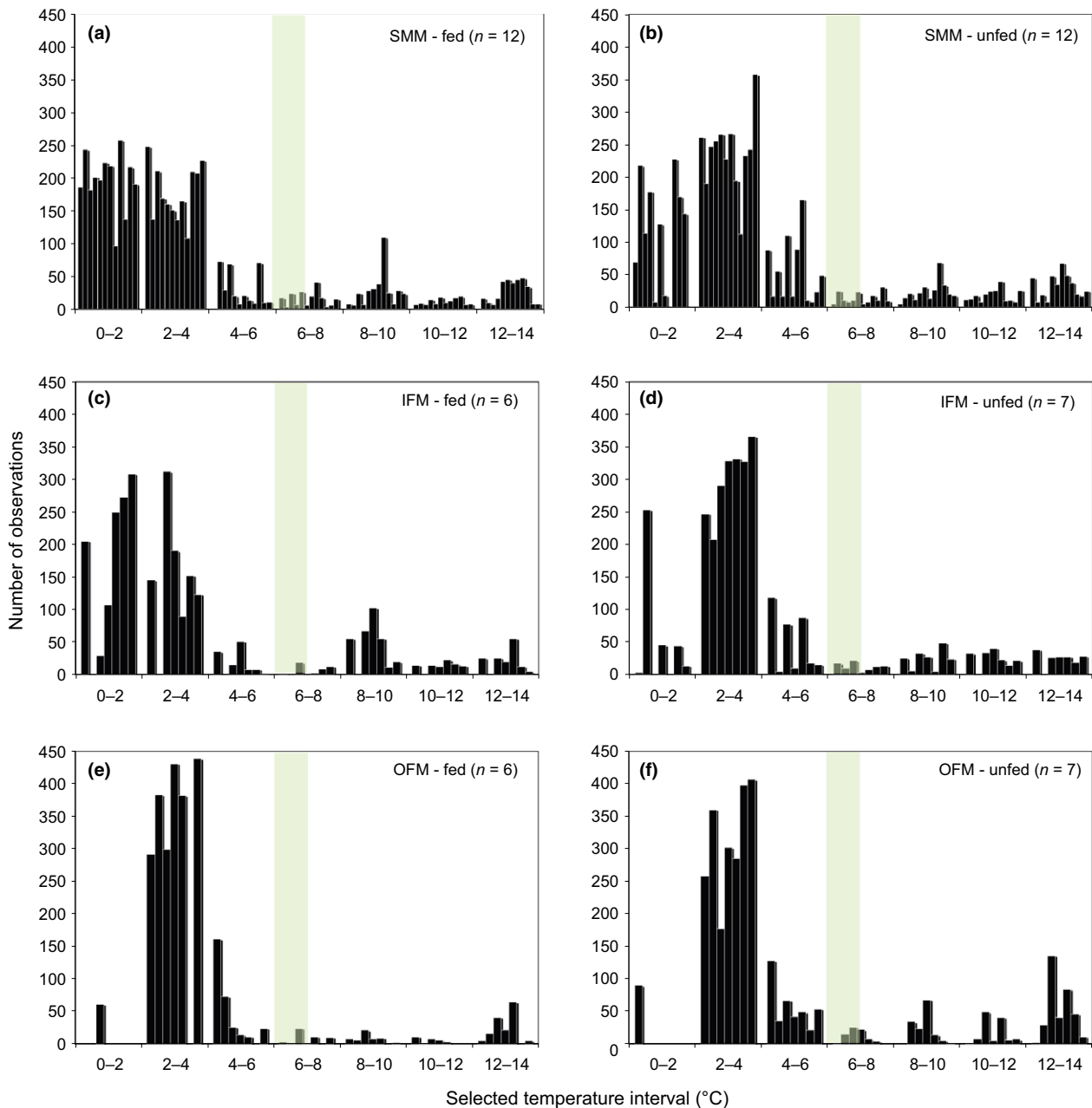


Figure 3 Number of observations within temperature intervals selected and recorded by introduced Kamchatka red king crab *Paralithodes camtschaticus* tested individually for 24 h in a thermal gradient ($1-14\text{ }^{\circ}\text{C}$). One observation corresponds to a time period of three min. SMM = sexually mature males, IFM = immature females, OFM = ovigerous females. All animals are shown to reveal individual variability, and they are ranked according to the order in which they were tested. The same order was used both for Fed and Unfed animals. Raw data for fed SMM are shown in Fig. 2. The vertical shaded bars indicate the stable acclimation temperature ($\sim 6.5\text{ }^{\circ}\text{C}$) of the holding tanks. See also Table 1 and Fig. 2 for variability in selected temperature.

Sundet, 2014). A recent tag-recapture study from the Barents Sea, on the other hand, revealed that most adult red king crabs cover a distance $< 30\text{ km year}^{-1}$ while some individuals may disperse $> 100\text{ km year}^{-1}$ (Windsland *et al.*, 2014). In other words, a conservative dispersal rate of 25 km year^{-1} corresponds *ceteris paribus* to a full latitude ($\sim 60\text{ nmi}$) every 4–5 years and about three decades for adult red king crab to reach the Arctic shelves north in the Barents Sea.

Whereas adult red king crabs actively explore new territory, the meroplanktonic larvae are subjected to and dispersed by the prevailing currents of the Barents Sea: Atlantic water feeds the northbound Spitsbergen Current on the west and the eastbound Murmansk Current on the north-east (cf. map in Boitsov *et al.*, 2012). A Lagrangian drift study based on the hydrography and the distribution of sexually mature red king crabs in years 1998–2000 showed that virtual larvae

were mainly advected eastward by the Norwegian Coastal Current (Pedersen *et al.*, 2006). Therefore, it is worrying to realise that a 'fast track advection' of larvae into the Arctic shelf areas is to be expected once ovigerous red king crabs enter the source of the Spitsbergen Current on Tromsøflaket Bank north of Troms County (Sætre & Aure, 2007; Boitsov *et al.*, 2012; Fig. 1).

Besides ambient temperature, bathymetry is deemed a major threshold for marine zoobenthos (Brown & Thatje, 2014). In its native Pacific waters, red king crab occurs mainly at depths < 100 m (Stevens & Lovrich, 2014). In the Barents Sea, a sub-Arctic shelf sea with a mean depth ~ 230 m (maximum ~ 500 m), ovigerous red king crabs are known from the shallows to depths ~ 270 m (Pinchukov & Sundet, 2011; IMR, 2014). Interestingly, the realised bathymetric habitat for a range of benthic invertebrates is considerably shallower than that disclosed from experimental studies on the physiological thresholds to hydrostatic pressure for the same taxa (Brown & Thatje, 2014). Species of king crabs (Lithodidae) may reach the deep sea (Hall & Thatje, 2009), and it is conceivable that the introduced red king crab, a stenobar in its realised habitat, is a physiological eurybar capable of exploring greater depths. As a noteworthy analogue, king crabs of the Southern Ocean now reoccur in the warming waters on the Antarctic Shelf (1–2 °C) after they allegedly disappeared from the region during the cooling period some 15 Ma (Thatje *et al.*, 2005; Hall & Thatje, 2011; Smith *et al.*, 2012; Anosov *et al.*, 2015).

Contentious management policies imperil conservation aims

The introduced red king crab is monitored and managed by Norway and Russia (Sundet, 2014). In Norway, the management policy for red king crab is at odds because the species is handled both as a resource and a nuisance (Falk-Petersen & Armstrong, 2013): the fisheries for red king crab are regulated by quotas in the eastern part of Finnmark, and free fisheries are encouraged outside the regulated areas on the west. On one side, to serve socio-economic demands, red king crab is considered a valid and lucrative resource for the coastal fleet and in local aquaculture and the stock should be maintained at a sustainable level. On the other hand, to serve conservation aims and to honour international agreements (Keller *et al.*, 2011), the red king crab is viewed as a potentially harmful invasive species that should be eradicated. In Russia, the invasive red king crab is simply considered a valuable commercial resource, as intended by former Soviet authorities some 55 years ago.

It has been opined that invasive species are harmless to marine biota and may even add to local biodiversity (Briggs, 2013), but this and similar arguments were countered by Richardson & Ricciardi (2013). Following the impact categories outlined by Blackburn *et al.* (2014), the introduced red king crab is certainly not harmless after its outbreak as an invasive species in the 1990s (Matishov *et al.*, 2012), and

numerous studies convincingly demonstrate its massive and deleterious impact on native biota (Jørgensen & Primicerio, 2007; Falk-Petersen *et al.*, 2011; Oug *et al.*, 2011; Mikkelsen & Pedersen, 2012). The introduced red king crab displays all the biological features of a successful invader: high fecundity, high mobility, few natural enemies and a long life (~ 20 year) (Windsland *et al.*, 2013; Sundet, 2014). Overpopulated areas, food shortage and rising temperatures in its coastal core habitat are main factors likely to speed-up an invasion into colder waters even further.

It is problematic to codify native and invasive species because they form parts of a continuum in context of geographic scales and timelines (Preston, 2009; Webber & Scott, 2012). Range expansions and contractions of species are common and reoccurring natural processes in space and time (Thomas, 2010). But, mediated by climate change and direct human intervention, both tempi and scales of dispersal have increased disproportionately (Webber & Scott, 2012; Bellard *et al.*, 2013) and boreal and sub-Arctic marine organisms are rapidly entering Arctic waters in unprecedented numbers (CAFF, 2013). For example, snow crab *Chionoecetes opilio* (O. Fabricius, 1788) (Oregoniidae), a native to the North Pacific and the North American Atlantic, is a recent and abundant denizen to the Barents Sea and the species constitutes yet a confounding benthic top predator on the Euro-Arctic shelves (Alsøvåg *et al.*, 2009; IMR, 2014).

We argue that ecophysiological knowledge of species' constraints and options is weighty and necessary complements for biogeography, invasion biology and ensuing conservation actions (Lüttge & Scarano, 2004; Somero, 2010; Cooke *et al.*, 2014). The red king crab has a well-documented invasion history, but knowledge about environmental preferences and physiological thresholds is scarce still. We present the first study on the thermal behaviour of introduced adult red king crab and show how increasing sea temperature may trigger the spread of this invasive top predator onto the Euro-Arctic shelves. We emphasise that the FTP by invasive ectotherms is only one, although important, part in spread scenarios. Temperature acclimation may shift physiological thresholds in crustaceans (Ravaux *et al.*, 2012), and long-term laboratory studies are warranted to disclose the effect of acclimation on thermal preferenda and tolerances across life stages. Short-term challenge tests, on the other hand, show that introduced adult red king crab survives temperatures close to the freezing point of seawater (–2 °C) and ambient salinities as low as 8 (Matishov *et al.*, 2008; Ilyushchenko & Zenzerov, 2012). In other words, neither temperature nor mesohaline waters generated by riverine runoff to the Arctic shelf seas (McClelland *et al.*, 2012) seem to impede a dispersal of red king crab further north and east. Laboratory tests should be supplemented by field campaigns using biotelemetry and DSTs to document realised habitats by free-ranging animals (e.g. Hunter *et al.*, 2013).

From a conservation standpoint, we fully support the view that invasive species threaten native biodiversity and biota

(Richardson & Ricciardi, 2013), and we welcome the discourse on anthropocentrism vs. ecocentrism, cf. 'new conservation science' (Doak *et al.*, 2014a,b; Marvier & Kareiva, 2014). In the light of ocean warming and depleted feeding grounds in its extant habitat, we suggest that the introduced red king crab may invade the Euro-Arctic shelves in less than three decades. Scientific uncertainty is a hallmark in conservation biology and to enforce a strict precautionary approach towards Arctic marine biodiversity (CAFF, 2013), we find it urgent to brand the introduced red king crab a notorious pest and not an asset. It appears futile to eradicate an introduced species once it has turned into an established invader (Blackburn *et al.*, 2011). On the other hand, to counteract further spreading of the introduced red king crab, free fisheries on this species should be effectuated across its entire distributional range in the Northeast Atlantic. This would benefit local fisheries in the short-term and protect native biota in the long term.

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REFERENCES

Alsvåg, J., Agnalt, A.-L. & Jørstad, K.E. (2009) Evidence for a permanent establishment of the snow crab (*Chionoecetes opilio*) in the Barents Sea. *Biological Invasions*, **11**, 587–595.

Anosov, S.E., Spiridonov, V.A., Neretina, T.V., Uryupova, E.F. & Schepetov, D. (2015) King crabs of the western Atlantic sector of Antarctic and adjacent areas: new records, molecular barcode data and distribution (Crustacea: Decapoda: Lithodidae). *Polar Biology*, **38**, 231–249.

Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M. & Courchamp, F. (2013) Will climate change promote future invasions? *Global Change Biology*, **19**, 3740–3748.

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U. & Richardson, D.M. (2011) A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, **26**, 333–339.

Blackburn, T.M., Essl, F., Evans, T. *et al.* (2014) A unified classification of alien species based on the magnitude of their environmental impacts. *Plos Biology*, **12**, 1–11.

Boitsov, V.D., Karsakov, A.L. & Trofimov, A.G. (2012) Atlantic water temperature and climate in the Barents Sea, 2000–2009. *ICES Journal of Marine Science*, **69**, 833–840.

Briggs, J.C. (2013) Invasion ecology: origin and biodiversity effects. *Environmental Skeptics and Critics*, **2**, 73–81.

Brown, A. & Thatje, S. (2014) Explaining bathymetric diversity patterns in marine benthic invertebrates and demersal fishes: physiological contributions to adaptation of life at depth. *Biological Reviews*, **89**, 406–426.

CAFF. (2013) *Arctic biodiversity assessment. Status and trends in Arctic biodiversity*. Conservation of Arctic Flora and Fauna, Akureyri. Available at: <http://www.arcticbiodiversity.is/> (accessed 25 October 2014).

Christiansen, J.S. & Fevolden, S.-E. (2000) The polar cod of Porsangerfjorden, Norway; revisited. *Sarsia*, **85**, 189–193.

Christiansen, J.S., Schurmann, H. & Karamushko, L.I. (1997) Thermal behaviour of polar fish: a brief survey and suggestions for research. *Cybium*, **21**, 353–362.

Christiansen, J.S., Mecklenburg, C.W. & Karamushko, O.V. (2014) Arctic marine fishes and their fisheries in light of global change. *Global Change Biology*, **20**, 652–659.

Cooke, S.J., Killen, S.S., Metcalfe, J.D., McKenzie, D.J., Mouillot, D., Jørgensen, C. & Peck, M.A. (2014) Conservation physiology across scales: insights from the marine realm. *Conservation Physiology*, **2**, 1–15, DOI: 10.1093/conphys/cou024.

Cossins, A.R. & Bowler, K. (1987) *Temperature biology of animals*. Chapman and Hall, University Press, Cambridge.

Doak, D.F., Bakker, V.J., Goldstein, B.E. & Hale, B. (2014a) What is the future of conservation? *Trends in Ecology and Evolution*, **29**, 77–81.

Doak, D.F., Bakker, V.J., Goldstein, B.E. & Hale, B. (2014b) Moving forward with effective goals for conservation: a reply to Marvier and Kareiva. *Trends in Ecology and Evolution*, **29**, 132–133.

Faccia, I., Alyakrinsky, A. & Bianchi, C.N. (2009) The crab that came in from the cold: first record of *Paralithodes camtschaticus* (Tilesius, 1815) in the Mediterranean Sea. *Aquatic Invasions*, **4**, 715–718.

Falk-Petersen, J. & Armstrong, C.W. (2013) To have one's cake and eat it too: managing the alien invasive red king crab. *Marine Resource Economics*, **28**, 65–81.

Falk-Petersen, J., Renaud, P. & Anisimova, N. (2011) Establishment and ecosystem effects of the alien invasive red king crab (*Paralithodes camtschaticus*) in the Barents Sea – a review. *ICES Journal of Marine Science*, **68**, 479–488.

Fernandez, L., Kaiser, B.A. & Vestergaard, N. (2014) *Marine invasive species in the Arctic. TemaNord 2014: 547*. Nordic Council of Ministers, Copenhagen. Available at: <http://norden.diva-portal.org/> (accessed 25 October 2014).

Fordham, D.A., Brook, B.W., Moritz, C. & Nogués-Bravo, D. (2014) Better forecasts of range dynamics using genetic data. *Trends in Ecology and Evolution*, **29**, 436–443.

Franklin, J. (2013) Species distribution models in conservation biogeography: developments and challenges. *Diversity and Distributions*, **19**, 1217–1223.

- Fry, F.E.J. (1947) Effects of the environment on animal activity. *University of Toronto Studies, Biological Series 55. Publication of the Ontario Fisheries Research Laboratory*, **68**, 1–62.
- Golovanov, V.K. (2013) Ecophysiological patterns of distribution and behaviour of freshwater fish in thermal gradients. *Journal of Ichthyology*, **53**, 252–280.
- Grant, W.S., Zelenina, D.A. & Muge, N.S. (2014) Phylogeography of red king crab: implications for management and stock enhancement. *King crabs of the world: biology and fisheries management* (ed. by B.G. Stevens), pp. 47–72. CRC Press, Boca Raton.
- Hall, S. & Thatje, S. (2009) Global bottlenecks in the distribution of marine Crustacea: temperature constraints in the family Lithodidae. *Journal of Biogeography*, **36**, 2125–2135.
- Hall, S. & Thatje, S. (2011) Temperature-driven biogeography of the deep-sea family Lithodidae (Crustacea: Decapoda: Anomura) in the Southern Ocean. *Polar Biology*, **34**, 36–370.
- Havel, J.E., Kovalenko, K.E., Thomaz, S.M., Amalfitano, S. & Kats, L.B. (2015) Aquatic invasive species: challenges for the future. *Hydrobiologia*, DOI: 10.1007/s10750-014-2166-0.
- Hochachka, P.W. (1991) Temperature: the ectothermy option. *Phylogenetic and biochemical perspectives – biochemistry and molecular biology of fishes* (ed. by T.P. Mommsen and P.W. Hochachka), pp. 313–322. Elsevier Science Publishers, Amsterdam, The Netherlands.
- Hollowed, A.B., Planque, B. & Loeng, H. (2013) Potential movement of fish and shellfish stocks from the sub-Arctic to the Arctic Ocean. *Fisheries Oceanography*, **22**, 355–370.
- Hunter, E., Eaton, D., Stewart, C., Lawler, A. & Smith, M.T. (2013) Edible crabs “Go West”: migrations and incubation cycle of *Cancer pagurus* revealed by electronic tags. *PLoS One*, **8**, 1–9.
- Ilyushchenko, A.M. & Zenzerov, V.S. (2012) New data on the tolerance of Barents Sea red king crabs to low salinities. *Russian Journal of Ecology*, **43**, 177–178.
- IMR. (2014) *Institute of Marine Research, Norway*. Available at: <http://www.imr.no> (accessed 25 October 2014).
- Jiménez-Valverde, A., Lobo, J.M. & Hortal, J. (2008) Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distribution*, **14**, 885–890.
- Jobling, M. (1981) Temperature tolerance and the final preferendum – rapid methods for the assessment of optimum growth temperatures. *Journal of Fish Biology*, **19**, 439–455.
- Jørgensen, L.L. & Primicerio, R. (2007) Impact scenario for the invasive red king crab *Paralithodes camtschaticus* (Tilesius, 1815) (Reptantia, Lithodidae) on Norwegian, native, epibenthic prey. *Hydrobiologia*, **590**, 47–54.
- Jørstad, K.E., Smith, C., Grauvogel, Z. & Seeb, L. (2007) The genetic variability of the red king crab, *Paralithodes camtschaticus* (Tilesius, 1815) (Anomura, Lithodidae) introduced into the Barents Sea compared with samples from the Bering Sea and Kamchatka region using eleven microsatellite loci. *Hydrobiologia*, **590**, 115–121.
- Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species’ ranges. *Ecological Letters*, **12**, 334–350.
- Keller, R.P., Geist, J., Jeschke, J.M. & Kühn, I. (2011) Invasive species in Europe: ecology, status, and policy. *Environmental Sciences Europe*, **23**, 1–17.
- Killen, S.S. (2014) Growth trajectory influences temperature preference in fish through an effect on metabolic rate. *Journal of Animal Ecology*, **83**, 1513–1522.
- Lagerspetz, K.Y.H. & Vainio, L.A. (2006) Thermal behaviour of crustaceans. *Biological Reviews*, **81**, 237–258.
- Leppäkoski, E., Gollasch, S., Gruszka, P., Ojaveer, H., Olenin, S. & Panov, V. (2002) The Baltic – a sea of invaders. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1175–1188.
- Lüttge, U. & Scarano, F.R. (2004) Ecophysiology. *Brazilian Journal of Botany*, **27**, 1–10.
- Marvier, M. & Kareiva, P. (2014) The evidence and values underlying ‘new conservation’. *Trends in Ecology and Evolution*, **29**, 131–132.
- Matishov, G.G., Zenzerov, V.S., Emelina, A.V. & Muraveiko, V.M. (2008) Temperature resistance of the red king crab *Paralithodes camtschaticus* from the Barents Sea. *Doklady Biological Sciences*, **420**, 198–200.
- Matishov, G., Moiseev, D., Lyubina, O., Zhichkin, A., Dzhenyuk, S., Karamushko, O. & Frolova, E. (2012) Climate and cyclic hydrobiological changes of the Barents Sea from the twentieth to twenty-first centuries. *Polar Biology*, **35**, 1773–1790.
- McClelland, J.W., Holmes, R.M., Dunton, K.H. & Macdonald, R.W. (2012) The Arctic ocean estuary. *Estuaries and Coasts*, **35**, 353–368.
- Mikkelsen, N. & Pedersen, T. (2012) Invasive red king crab affects lump sucker recruitment by egg consumption. *Marine Ecology Progress Series*, **469**, 87–99.
- Miller, A.W. & Ruiz, G.M. (2014) Arctic shipping and marine invaders. *Nature Climate Change*, **4**, 413–416.
- National Geographic. (2004) National Geographic News, 9 March 2004. Available at: <http://news.nationalgeographic.com> (accessed 15 October 2014).
- Orlov, Y.I. & Ivanov, B.G. (1978) On the introduction of the Kamchatka king crab *Paralithodes camtschatica* (Decapoda: Anomura: Lithodidae) into the Barents Sea. *Marine Biology*, **48**, 373–375.
- Oug, E., Cochrane, S.K.J., Sundet, J.H., Norling, K. & Nilsson, H.C. (2011) Effects of the invasive red king crab (*Paralithodes camtschaticus*) on soft-bottom fauna in Varrangerfjorden, northern Norway. *Marine Biodiversity*, **41**, 467–479.
- Pedersen, O.P., Nilssen, E.M., Jørgensen, L.L. & Slagstad, D. (2006) Advection of red king crab larvae on the coast of North Norway – a Lagrangian model study. *Fisheries Research*, **79**, 325–336.
- Pinchukov, M.A. & Sundet, J.H. (2011) Red king crab. *The Barents Sea. ecosystem, resources, management. Half a*

- century of Russian-Norwegian Cooperation (ed. by T. Jakobsen and V.K. Ozhigin), pp. 160–166. Tapir Academic Press, Trondheim.
- Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A. & Richardson, A.J. (2013) Global imprint of climate change on marine life. *Nature Climate Change*, **3**, 919–925.
- Preston, C.P. (2009) The terms 'native' and 'alien' – a biogeographical perspective. *Progress in Human Geography*, **33**, 702–713.
- Ravaux, J., Léger, N., Rabet, N., Morini, M., Zbinden, M., Thatje, S. & Shillito, B. (2012) Adaptation to thermally variable environments: capacity for acclimation of thermal limit and heat shock response in shrimp *Palaemonetes varians*. *Journal of Comparative Physiology B*, **182**, 899–907.
- Ricciardi, A., Steiner, W.W.M., Mack, R.N. & Simberloff, D. (2000) Toward a global information system for invasive species. *BioScience*, **50**, 239–244.
- Richardson, D.M. & Ricciardi, A. (2013) Misleading criticisms of invasion science: a field guide. *Diversity and Distributions*, **19**, 1461–1467.
- Richardson, D.M. & Whittaker, R.J. (2010) Conservation biogeography – foundations, concepts and challenges. *Diversity and Distributions*, **16**, 313–320.
- Sætre, R. & Aure, J. (2007) Characteristic circulation features. *The Norwegian coastal current – oceanography and climate* (ed. by R. Sætre), pp. 99–114. Tapir Academic Press, Trondheim.
- Schurmann, H. & Christiansen, J.S. (1994) Behavioural thermoregulation and swimming activity of two Arctic teleosts (subfamily Gadinae) – the polar cod (*Boreogadus saida*) and the navaga (*Eleginus navaga*). *Journal of Thermal Biology*, **19**, 207–212.
- Siikavuopio, S.I. & James, P. (2015) Effects of feed intake, growth and oxygen consumption in adult male king crab *Paralithodes camtschaticus* held in captivity and fed manufactured diets. *Aquaculture Research*, **46**, 602–608.
- Smith, C.R., Grange, L.J., Honig, D.L., Naudts, L., Huber, B., Guidi, L. & Domarck, E. (2012) A large population of king crabs in Palmer Deep on the west Antarctica Peninsula shelf and potential invasive impacts. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1017–1026.
- Somero, G.N. (2005) Linking biogeography to physiology: evolution and acclimatory adjustments of thermal limits. *Frontiers in Zoology*, **2**, 1–9.
- Somero, G.N. (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *The Journal of Experimental Biology*, **213**, 912–920.
- Stevens, B.G. & Lovrich, G.A. (2014) King crabs of the world: species and distributions. *King crabs of the world: biology and fisheries management* (ed. by B.G. Stevens), pp. 1–29. CRC Press, Boca Raton.
- Sundet, J.H. (2014) Red king crab in the Barents Sea. *King crabs of the world: biology and fisheries management* (ed. by B.G. Stevens), pp. 477–492. CRC Press, Boca Raton.
- Thatje, S., Anger, K., Calcagno, J.A., Lovrich, G.A., Pörtner, H.-O. & Arntz, W.E. (2005) Challenging the cold: crabs reconquer the Antarctic. *Ecology*, **86**, 619–625.
- Thomas, C.D. (2010) Climate, climate change and range boundaries. *Diversity and Distributions*, **16**, 488–495.
- Timofeev, S.F. (1999) Reviews. *Crustaceana*, **72**, 714–716.
- Ware, C., Berge, J., Sundet, J.H., Kirkpatrick, J.B., Coutts, A.D.M., Jelmert, A., Olsen, S.M., Floerl, O., Wisz, M.S. & Alsos, I.C. (2014) Climate change, non-indigenous species and shipping, assessing the risk of species introduction to a high-Arctic archipelago. *Diversity and Distributions*, **20**, 10–19.
- Webber, B.L. & Scott, J.K. (2012) Rapid global change: implications for defining natives and aliens. *Global Ecology and Biogeography*, **21**, 305–311.
- Windsland, K., Hvingel, C., Nilssen, E.M. & Sundet, J.H. (2013) Evaluation of von Bertalanffy growth curves for the introduced red king crab (*Paralithodes camtschaticus*) in Norwegian waters. *Fisheries Research*, **145**, 15–21.
- Windsland, K., Hvingel, C., Nilssen, E.M. & Sundet, J.H. (2014) Dispersal of the introduced red king crab (*Paralithodes camtschaticus*) in Norwegian waters: a tag-recapture study. *ICES Journal of Marine Science*, **71**, 1966–1976.

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