REVIEWS

Environmental effects on fished lobsters and crabs

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Abstract The fisheries for crabs and lobsters (Reptantia, Decapoda) are shaped by environmental variation through the distribution ecology, productivity or even their market traits such as colour and size. Many crabs and lobsters have a wide latitudinal distribution and therefore are exposed to significant abiotic gradients throughout their geographic range. Environmental factors affect reptantians throughout their complex life cycle, including embryo development, timing and length of the spawning period, the duration and quality of the larval stages, the level and spatial distribution of the settlement, growth rates and size of the juveniles, size at maturity, and catchability. The most consistent environmental response is of growth and reproduction to temperature. Growth rates increase with increasing temperatures in a parabolic function, tapering and then declining as the boundaries of thermal tolerance are reached. With increasing temperature the intermoult duration decreases. Once the upper thermal boundary is reached, increases in temperature result in longer intermoult duration and smaller growth increments so that growth is reduced. Declines in temperature generally suppress moulting, and consequently reptantians rarely moult in winter. Increasing temperature decreases the time for egg incubation, larval development and the maturational age. Catchability increases with water temperature and also varies, although less predictably, with moon phase and wind strength. Catchability decreases with an increase in population density. Larval settlement of many reptantian species depends on current strength, increasing with the strength of certain local currents. Reptantians can tolerate a wide-variety of conditions and have flexible life-histories to respond to conditions throughout their broad geographic ranges. Information on environmental effects on reptantians not only assists in understanding probable effects of ocean warming and acidification, but also seasonal and interannual changes in fisheries production.

Keywords Catchability · Crabs · Lobsters · Temperature · Salinity · pH · Oxygen · Swell · Lunar cycle

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Introduction

Lobsters and crabs support valuable fisheries from the poles to the equator. Annual harvests in 2010 were 1,424,867 tons of crabs and 279,685 tons of clawed

and spiny lobsters, which has been steadily increasing since 2004, representing an annual revenue of US$6,209 million from worldwide fisheries (FAO 2010). Crabs and lobsters are grouped in the decapod suborder of Reptantia, which describes a group of animals with broadly similar life history and of significant commercial value.

A range of environmental factors affect both lobsters and crabs throughout their complex life cycle. The distribution and abundance of the pelagic larvae is mainly determined by abiotic factors (e.g. currents, wind, temperature and available settling habitat), whereas the benthic adult stage is governed by biotic factors (predation, food availability, competition) (Cobb et al. 1994). Phenotypic traits that vary in response to environmental change allow flexibility in recruitment strategies and therefore adaption to variable external conditions, encompassing trade-offs in age at reproduction and longevity, fecundity, degree of parental care, larval duration and post-settlement mortality (reviewed by Cobb et al. 1997).

Recruitment variability is assumed to be higher in spiny lobsters (Palinurids) and *Cancer* crabs than in clawed lobsters, as they typically have higher fecundity (1–4 orders of magnitude higher), smaller eggs, longer larval duration and therefore presumably lower larval survival (Cobb et al. 1997). Large number of poorly provisioned propagules, combined with variable survival and transport, have the potential for producing considerable variation in recruitment (Incze et al. 1997). Spatial and temporal variations in life history parameters are largely attributed to environmental heterogeneity (Shields 1991; Quinn et al. 2013). Identifying any long-term trends associated with the key environmental factors shaping the fisheries may aid in predictions of future biomass (Winemiller and Rose 1992). From a fisheries management perspective, changes in growth rate, natural mortality and catchability are three critical factors that can be included in the stock assessments. From a biological perspective, however, all species have specific tolerance limits for temperature and other environmental variables, which limit their geographic distribution.

Few attempts have been made to describe general patterns across species of how environmental variation and climate change will affect decapods crustaceans. The effects of environmental variables on larval recruitment of American lobster were reviewed by

Aiken and Waddy (1986), and the effects of temperature on crustacean growth were reviewed by Hartnoll (1982). This review will focus on the influence of environmental variables on reptantians with information summarised mainly from the commercial species that have received most research attention (Table 1). One of the challenges in producing a review with such a broad scope was to constrain the content to a manageable unit without excluding effects or trends of central importance to the overall understanding of "Environmental effects on fished lobsters and crabs". Each component of the environment could be a singular review, as could each species. We have focused on key fisheries species and described general trends, and then used specific examples to illustrate the trends. We focus mainly on the effects of temperature, wind and currents, salinity, oxygen on growth, reproduction, egg and larval development, natural mortality, catchability and disease. We finish with an overview of the effects of climate change, including ocean warming and acidification which are fast-growing and quickly changing fields of research.

Growth

A major determinant of the influence of environmental variation on reptantian crustaceans is their mode of growth. Crustaceans have a largely inextensible exoskeleton that is replaced intermittently in stepwise moults (or ecdysis) resulting in discontinuous growth (Hartnoll 1982). At each moult the old exoskeleton is shed, allowing the animal to expand before new exoskeleton hardens. This increase in size is termed the moult increment, while the intermoult period is the duration between two successive moults. Growth rate in crustaceans is thus a function of both moult increment and moult frequency and these two factors respond differently to environmental variation (Serfling and Ford 1975; Hartnoll 1982).

Temperature and growth

Temperature is a major factor influencing the physiological and ecological properties of marine species (Kinne 1970; Aiken and Waddy 1986). Temperature varies on both temporal (e.g., daily, seasonal) and spatial (depth and latitude) scales in aquatic systems although variation is generally less than in terrestrial

Table 1 Key commercial decapods species reviewed and their geographic range

Family	Species	Common name	Location
Nephropidae Clawed lobster	*Homarus americanus*	American lobster	East coast of North America from Labrador, Canada to North Carolina
	Homarus gammarus	European lobster	Continental shelf in North-Eastern Atlantic Ocean from Morocco to the Arctic circle, Mediterranean Sea and parts of the Black Sea
	Nephrops norvegicus	Norway lobster	North-east Atlantic Ocean and Mediterranean Sea
Palinuridae Spiny lobsters	*Panulirus argus*	Caribbean spiny lobster	Western Atlantic Ocean, North Carolina to Brazil and throughout the West Indies
	Panulirus cygnus	Western rock lobster	West coast of Australia
	Jasus edwardsii	Southern rock lobster	East and south Coast of southern Australia, New Zealand
	Jasus lalandii	Cape rock lobster	Western South Africa from Walvis bay, Namibia to Cape Province
	Palinurus elephas	European spiny lobster	Western Mediterranean Sea, North-East Atlantic Ocean, cost of North Africa, Canary Island and the Azores
Lithodidae	*Paralithodes camtschaticus*	Red king crab	Bering Sea, north Pacific Ocean, around the Kamchatka Peninsula, Gulf of Alaska, Barents Seas (introduced)
Cancridae	*Cancer magister*	Dungeness crab	West coast North America
	Cancer pagurus	Edible crab, brown crab	Continental shelf in North-Eastern Atlantic Ocean from Morocco to the Arctic circle, Mediterranean Sea and parts of the Black Sea
Portunidae	*Portunus trituberculatus*	Japanese blue crab	Coast of East Asia
	Portunus pelagicus	Blue swimmer crab	Africa, Southeast Asia, East Asia, Australia and New Zealand
	Callinectes sapidus	Atlantic blue crab	Western Atlantic Ocean, the Pacific coast of Central America, and Gulf of Mexico
	Scylla serrata	Mud crab	Africa, Australia and Asia
Orgeoniidae	*Chionoecetes opilio*	Snow crab	Northwest Atlantic Ocean and north Pacific Ocean, Barents Sea (introduced)
Majidae	*Maja brachydactyla*	Spider crab	British Isles to Senegal

See Phillips (2013) for more details of lobster distribution

ecosystems because of thermal buffering of water. Temperature influences the rate of metabolism and growth, and reproduction in poikilotherms such as crabs and lobsters, and has a major influence on development in early life history stages (Leffler 1972; Le Moullac and Haffner 2000; Tlusty et al. 2008). Variation in water temperature may alter absolute growth, food availability, timing of moulting, mating, spawning and recruitment, and the amount of growth, all of which can have cascading effects on population dynamics. Many crab and lobster species have a wide latitudinal distribution (Table 1) and are therefore exposed to significant temperatures throughout their geographic range. As with all living organisms, their geographical range is primarily governed by both an upper and a lower thermal limit (Rombough 1997), as well as the availability of contiguous habitat.

Growth rate is generally positively correlated to temperature amongst crustaceans within the thermal tolerance of each species (Hartnoll 2001). Elevated

(warm) temperature can accelerate growth by shortening the intermoult period, or increasing the moult increment, or both (Serfling and Ford 1975). There is an optimum temperature effect within the thermal tolerance of a species, whereby growth increases with increasing temperature to a maximum, before declining near the upper thermal limits as higher temperatures have negative effects (Hartnoll 1982). Above the thermal optimum both the intermoult period and the moult increment are negatively affected by temperature. The temperature range at which growth is optimal is specific to each species but also varies within a given population.

Temperature can affect growth in different ways before and after the onset of maturity. Faster juvenile growth in response to warmer water can be offset by reduced growth rates at maturity resulting in a smaller asymptotic maximum size and lower stock productivity. For example, size at maturity of western rock lobster, *Panulirus cygnus,* is smaller in the northern sites of the fishery, which appears to be linked to higher water temperatures, although it is confounded by high density in this region (Melville-Smith and De Lestang 2006). In laboratory experiments, the weight gain of post-pueruli *Panulirus cygnus* almost doubled at 23 °C compared to ambient temperature (between 15.6 °C and -23.1 °C) (Johnston et al. 2008). Year 1 juveniles showed a 50 % increase in weight at the higher temperature treatment whereas little difference was observed for year 2 juveniles (weight gain at 23 °C versus ambient: 23 versus 21 %) (Johnston et al. 2008).

Temperature and moulting

Metabolic processes in poikilotherms increase at higher temperatures including the mobilization of reserves and the preparatory stages needed for moulting (Hartnoll 2001). For example, moulting of adult *Homarus americanus* occurred 2 weeks earlier when temperatures were higher in 1994 (18.3–20 °C in July to September) compared to 1993 (15.1–17 °C in the same period) (Aiken 1973). The effect of temperature on intermoult period varies immensely between species and also between individuals of the same species. As a result, the timing of moulting for individuals of *Panulirus cygnus* from the same site can vary by several weeks (Caputi et al. 2009).

When measured within the species thermal tolerance range, increasing temperature almost universally

decreases the intermoult period in larvae, juveniles and adult lobsters and crabs. Lobster examples include *Jasus edwardsii* phyllosoma (Bermudes & Ritar, 2008), *Panulirus cygnus* (Liddy et al., 2004)*, Panulirus argus* (Lellis & Russell, 1990), *Panulirus homarus rubellus* (Kemp & Britz, 2008), *Jasus verreauxi* (Moss et al., 2001), *Homarus americanus* larvae (Templeman, 1935), *Panulirus japonicus* (Matsuda & Yamakawa, 1997), *Panulirus interruptus* (Serfling & Ford, 1975), and crab examples include *Paralithodes camtschaticus* (Stoner et al., 2010), *Pseudocarcinus gigas* (Gardner et al., 2004), *Carcinus maenas, Callinectes sapidus,* (Leffler, 1972, Fisher, 1999), *Hyas araneus* (Anger, 1983), *Cancer irroratus* (Johns, 1981), *Ranina ranina* (Minagawa, 1990), *Lithodes aequispinus* (Paul & Paul, 1999), and *Cancer magister* (Kondzela & Shirley, 1993).

When the effects of temperature on the intermoult were examined at the upper boundary of the species thermal range then the response to temperature was not consistent. A temperature increase towards the upper limit increased the intermoult period and mortality in *Jasus edwardsii* phyllosoma (Thomas et al., 2000, Bermudes & Ritar, 2008), *P. argus* (Lellis & Russell, 1990) and *Cancer magister* (Kondzela & Shirley, 1993). However the opposite was observed in *P. cygnus* and *P. argus* phyllosomsa and *C. magister* adults where higher temperature reduced moult increment (Lellis and Russell 1990; Kondzela and Shirley 1993; Liddy et al. 2004). These contrasting observations may be caused by differences in the nature of metabolic processes which begin to decrease above the upper thermal limit in poikilotherms due to energetic imbalance (e.g. reduced feed intake versus raised nitrogen excretion (Bermudes and Ritar 2004). At the lower thermal boundary growth is reduced to the point where moulting is completely suppressed. For example, *Homarus americanus* and *Callinectes sapidus* do not moult from November to April (Hartnoll 1982; Ju et al. 2001) and *C. magister* did not moult when temperature was 0 °C (Kondzela and Shirley 1993).

Frequency of moulting and the moult increment are influenced differently by changes in temperature which complicates interpretation of the effect of temperature on growth. Hartnoll (1982) reviewed four crustaceans where increasing temperature had no effect on moult increment, eight that displayed a reduced increment with raised temperature, and only

two showed an increase in moult increment with increased temperature. A decrease in temperature results in a delay of larval development in the spider crab *Hyas araneus* which is stronger than the acceleration caused by an equally great increase (Anger 1983). In *Cancer magister* the effect of temperature on growth was mainly through change in the intermoult duration (Kondzela and Shirley 1993). In species and life stage where moulting is annual, such as *J. edwardsii*, the intermoult period is less flexible so the effect of temperature on growth is mainly through the size of the moult increment (Gardner and Van Putten 2008). Moult increment in the Artic lyre crab *Hyas coarctatus* was observed to initially increase between 6 and 9 °C before decreasing between 9 and 18 °C (Anger 1984). Maximum growth increment of captive inbred Stage I *Jasus edwardsii* phyllosoma occurred at a mid-range temperature 18.2 °C, compared to the higher and lower temperatures (Bermudes and Ritar 2008). Increased temperature had an opposing effect on growth in *Carcinus maenus* by shortening the intermoult duration, but reducing the moult increment (Mohamedeen 1990). However, the general pattern appears to be that the effect of temperature on intermoult duration is more influential on growth than change in moult increment (Hartnoll 2001).

Salinity and growth

Hartnoll (1982) reviewed the effect of salinity on adult growth and concluded that there were minimal effects of a range of salinities on growth of reptantian crustaceans.

Reproduction and ontogeny

Temperature and timing of reproduction

Timing of reproduction within a season

The timing of reproduction is critical to the survival of a species. Firstly, individuals must time their spawning to coincide with reproductive ripeness in a mate, and secondly they must time it so their offspring have the best possible chance of survival. The timing of reproduction of most crustaceans relies on both photoperiod and temperature to ensure that spawning is synchronized (Lawrence and Soame 2004). Timing

larval release to match with abundance of food maximizes the chances of survival of the most number of larvae (match-mismatch hypothesis, Cushing 1972). Increasing sea temperatures may accelerate early egg or larval growth and increase recruitment to the fishery, assuming that when daily egg loss is constant, shorter incubation will result in more eggs hatching (Oviatt 2004). Concurrently, an increase in temperature may increase the period over which lobsters and crabs release their larvae (Tlusty et al. 2008). Timing of reproduction within a season and larval duration are inextricably linked. Snow crab *Chionoecetes opilio* is a cold water stenotherm, that is, it can only survive in a very narrow range of temperatures (Moriyasu and Lanteigne 1998; Kuhn and Choi 2011), with a reproductive cycle that is temperature dependent. Different temperature conditions at the time of egg extrusion in this species alter the length of the embryonic development, ranging from 1 year in multiparous females to 2 years in primiparous females (Moriyasu and Lanteigne 1998; Webb et al. 2007). At temperatures below 1 °C the 1-year reproductive cycle is replaced by a 2-year cycle (Webb et al. 2006).

Timing of first reproduction

Temperature stimulates early ovarian development (Annala et al. 1980), and so reproductive maturity is accelerated at higher temperatures. The size at onset of sexual maturity depends on other factors besides temperature, such as population density, food availability and other environmental and genetic variables (Annala et al. 1980). With the onset of sexual maturity, organisms face a trade-off between the amounts of energy used for reproduction and growth (Stearns 1976; Partridge and Sibly 1991; Zera and Harshman 2001). Consequently those starting reproduction earlier will have less energy available for growth than those that reproduce later. Female *Homarus americanus* mature between 55 and 110 mm carapace length (CL), aged generally 5–9 years (Waddy and Aiken 1992; Fogarty 1993). Warm-water spiny lobsters are younger (2–4 years) and smaller (40–75 mm CL) at maturity than cool-water species (5–7 years and 55–110 mm CL) (MacDiarmid 1989; Gardner et al. 2006; Frisch 2007). Likewise, *Cancer* crab females including *C. irroratus* and *C. pagurus*, in warm waters mature earlier and at smaller sizes than those in cool

waters (Shields 1991). There is wide variation in size at first reproduction (10–130 mm carapace width (CW)), but less in age at first reproduction (1–3 years) (Shields 1991). In the American lobster, *Homarus americanus,* the consequence of temperature increases within their thermal tolerance on growth is that the time to reach a particular stage of the life cycle (e.g. the end of larval development, or the onset of sexual maturity) is decreased, but the size on attaining that stage is also decreased. In simpler terms, the life span is shortened and the body size is decreased (Wahle and Steneck 1991). This pattern does not hold across all species though. The size at which female southern rock lobster mature in Tasmania follows a latitudinal decline from warmer water in the north to colder waters in the south (Gardner et al. 2006). However as the latitudinal trend in the same species is the opposite in New Zealand, factors additional to temperature appear to be involved.

Frequency of reproduction

Reptantians exhibit a variety of reproductive cycles depending mainly on water temperature and latitude. Clawed lobsters spawn every 1 or 2 years, spiny lobsters spawn once (temperate species) or several (tropical species) times per year, and most *Cancer* crabs spawn only once per year (Cobb et al. 1997) (Table 2). Life-time fecundity is a function of clutch size and number of broods, and some species such as *Jasus edwardsii* produce one clutch per year. Clawed lobsters have relatively low fecundity, producing small clutches once every year or 2 years and panulirids have an intermediate clutch size and 2–4 clutches per year (Table 2). At the northern end of its distribution, *Homarus americanus* have two different spawning strategies, similar to that of the snow crab described above (Webb et al. 2007). Larger females, most likely multiparous with a 2-year reproductive cycle, generally spawn earlier in the season. Smaller females, most likely primiparous, with a 1-year cycle generally spawn later (Gendron and Ouellet 2009). This results in different trajectories of egg development, and as a consequence larvae, from early spawning, multiparous and late spawning, primiparous females encounter different environmental conditions at hatching and during subsequent larval development. These two reproductive strategies spread larval production over time and provide greater capacity for successful recruitment despite environmental uncertainty (Gendron and Ouellet 2009). Similarly, at temperatures similar to those found at the centre of their range, *Cancer setosus* can produce three egg masses per year whereas they produce only one egg mass per year at temperatures similar to those at the northern and southern extent of their range (Fischer and Thatje 2008).

Salinity and maturation

There is evidence from *Callinectes sapidus* that maturation occurs at smaller size when salinity is higher (Fisher 1999).

Eggs and embryos

Temperature and egg development

Temperature is the major factor that controls embryonic development duration (time from fertilisation to larval hatching) and the larval development duration (time from larval hatching to metamorphosis with recruitment to the benthos) in lobsters and crabs. Embryonic development occurs once the eggs have been extruded and fertilised and attached to the pleopods on the external surface of the underside of the female's abdomen. In reptantians, the egg incubation period decreases with increasing temperature following a similar trajectory between species, according to the equation: $y = 0.5906x^2 - 29.725x + 429.09$, $R^2 = 0.8619$ (Fig. 1).

Incubation time in the sub-arctic blue king crab *Paralithodes platypus* ranged from 410 days at 6.1 °C to 434 days at 2.3 °C and increased with decreasing temperature (Stevens et al. 2008; Fig. 1). In the temperate *Cancer magister*, incubation time increased with decreasing temperature to 1 °C at which point all adults and eggs died before hatching occurred (Shirley et al. 1987). In the mud crab *Scylla serrate,* egg incubation period decreased exponentially from 30 to 10 days with increasing mean temperature in the range 20.3–30.0 °C (Hamasaki 2003). Time from fertilization to hatch was positively correlated to temperature in *Maja brachydactyla* (Martin & Planque, 2006). American lobster eggs will go into diapause if the temperature drops below 5° C (Perkins 1971), and eggs will be brought out of a developmental stasis only when temperatures rise back over 10 °C (Helluy and Beltz 1991). Given the

Table 2 Batch fecundity of key fisheries species

Species	Brood size	Broods per year	References
Homarus americanus	300–100,000	0.5–1	Estrella and Cadrin (1995), Wahle et al. (2013)
	17,000–220,000		Herrick (1896)
Homarus gammarus	2,000–50,000	0.5–1	Agnalt et al. (2007), Agnalt (2008)
	2,400–28,000		Lizarraga-Cubedo et al. (2003)
Nephrops norvegicus	1,000–5,000	1	Bell et al. (2013)
Jasus edwardsii	38,000–540,000	1	Annala and Bycroft (1987)
	43,900–660,000	1	Linnane et al. (2008), Green et al. (2009)
Jasus lalandii	33,000–490,000	1	Annala (1991), Jeffs et al. (2013)
Jases frontalis	61,000–524,000		Annala (1991)
Sagamariensis verreauxi	387,000–2,040,000	1	Annala (1991)
Most of the Cancer crabs	Up to 3,000,000	1–2	Cobb et al. (1997)
	18,200–2,208,000		Hines (1991)
Cancer pagurus	5,000–2,500,000	0.5–1	Ungfors (2007)
Cancer magister		0.5–1	Swiney et al. (2003)
Paralithoides camtschaticus			
Maja brachydactyla	125,000–530,300	1–4	Verísimo et al. (2011)
Pseudocarcinus gigas	830,000–2,500,000		Gardner (1997)
Panulirus cygnus	116,000–682,000	1	Chubb (2000)
Panulirus argus	160,000–1,600,000	1–2	Lipcius (1985), Cruz and de León (1991), Fonseca-Larios and Briones (1998)
Panulirus gracilis	76,700–1,115,000	2–4	Briones-Fourzan and Lozano-Alvarez (1992), Perez-Gonzalez et al. (2012)
Panulirus ornatus	120,000–800,000	3–4	Macfarlane and Moore (1986)
Panulirus inflatus		2–4	Briones-Fourzan and Lozano-Alvarez (1992)

This table is presented as a general indicator of the ranges. More detailed information is available in Annala (1991), Perez-Gonzalez et al. (2012) and Jeffs et al. (2013)

shape of the temperature—egg incubation curve (Fig. 1), it is crucial to consider the full thermal spectrum and not just maximal summertime temperature when evaluating the impact of ocean warming on crustaceans.
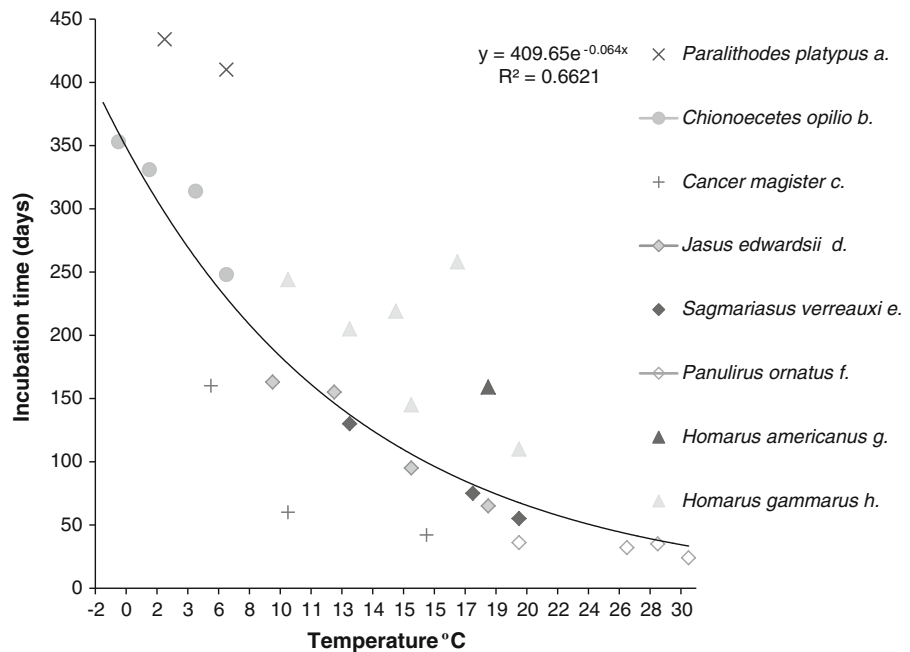
Temperature not only effects the time of development, but the bioenergetics of the developing embryos. Fatty acids are metabolized at a higher rate at lower temperature in *Cancer setosus* and *Panulirus japonicus* and at higher temperatures egg metabolism was largely based on protein (Fischer et al. 2009; Tokuda et al. 2013). In *Homarus americanus* changing seasons, simulated by changing temperatures in aquaria, changed the rate of embryo growth and lipid use, with highest lipid use occurring as temperature was falling at the beginning of embryo development, simulating winter (Sibert et al. 2004).

Salinity on eggs and embryos

Marine ecosystems generally have salinity around 35 ppt (except the Red and Baltic Seas, which have distinct haloclines), but this can fluctuate both seasonally or aseasonally due to rainfall, oceanic upwelling or downwelling. Salinity affects water density and therefore circulation and stratification, especially in estuaries (Johnson et al. 1991). Numerous chemical reactions follow changes in salinity as most equilibrium and rate constants are salinity dependent. For instance, higher salinity increases pH and reduces organic matter solubility (Cai et al. 1998).

Many crustacean fisheries occur in coastal and estuarine areas where salinity fluctuates due to rainfall and freshwater in-flow. Lobsters and crabs are generally restricted by a lower salinity threshold value

Fig. 1 Egg incubation temperature and the resultant incubation time for select commercial crustaceans. *a* Stevens et al. (2008), *b* Webb et al. (2006), *c* Shirley et al. (1987), *d* Tong et al. (2000), *e* Moss et al. (2004), *f* Sachlikidis et al. (2010), *g* Helluy and Beltz (1991), *h* Charmantier and Mounet-Guillaume (1992), Schmalenbach and Franke (2010)

$y = 409.65e^{-0.064x}$
$R^2 = 0.6621$

× *Paralithodes platypus a.*
Chionoecetes opilio b.
+ *Cancer magister c.*
Jasus edwardsii d.
◆ *Sagmariasus verreauxi e.*
Panulirus ornatus f.
▲ *Homarus americanus g.*
▲ *Homarus gammarus h.*

(Gibson and Najjar 2000) so that both adults and larvae avoid low salinity by modifying behaviour such as migration (Charmantier et al. 2001). Other species such as *Hemigrapsus edwardsii* and *Hemigrapsus crenulatus* are euryhaline crabs, with eggs and larvae capable of tolerating salinities ranging from 3 to 45 ‰ so that they can survive in tidal and estuarine areas (Taylor and Seneviratna 2005).

Branchial differentiation and excretory organs used in adult osmoregulation are not developed until after the early larval stages, yet embryos and early larval stages of euryhaline crabs are able to tolerate a range of salinities nonetheless (Taylor and Seneviratna 2005). There are contradictory interpretations of responses of different life stages to changes in salinity. On the one hand, a fairly recent review of adaptation to salinity throughout the life cycle of Homarids (Charmantier et al. 2001) suggested that embryos are osmoconformers that maintain osmotic concentrations in their body fluids identical to the osmotic concentrations of the ambient medium but are osmotically protected by the egg membrane. On the other hand, Aiken and Waddy (1986) suggested that embryonic development of *Homarus americanus* is affected by salinity as embryos have higher osmotic pressure and take longer to adapt to low salinities than larvae. It appears that crustacean embryos employ a range of

strategies to survive in a variable salinity environment, and can osmoconform or osmoregulate (that is, regulate the osmotic concentration of their extracellular body fluid at a concentration different from the ambient medium). Other reviews have been produced specifically on the ontogeny of osmoregulation and salinity tolerance in crustaceans, and we recommend these for further details (Charmantier 1998; Charmantier et al. 2001).

Oxygen on eggs and embryos

In addition to salinity and temperature, the amounts of dissolved gases (mostly oxygen and carbon dioxide) are the most important components of sea water that influence reptantian eggs and embryos. Dissolved oxygen is required for respiration, and in adult marine animals is extracted from water flowing over gill filaments. Oxygen levels can reach over 20 ppm in temperate marine waters but decline with increasing temperature and increase with declining salinity (Weiss 1970).

In the early life stages of crustaceans there are different pathways for adjusting to changes in oxygen concentration compared with adults. Early life stages may use a range of relatively passive options to counter a fluctuating oxygen environment and regulate

oxygen uptake, by adjusting cardiovascular parameters like heart rate, stroke volume, haemolymph flow, ventilation and changes in O_2-binding properties of respiratory pigments (McMahon 2001). The eggs of *Carcinus maenas* and *Cancer pagurus* show some oxyregulatory ability which disappears after hatching (Wheatly 1981; Naylor et al. 1999). In most reptantian species, females brood their eggs on the underside of their abdomen, and therefore can actively control the oxygen environment of the offspring by fanning eggs and moving their abdomen. Female *Cancer pagurus* can detect oxygen levels and in response adjust their fanning rates and abdomen movement (Naylor et al. 1999). Egg mass oxygen demands in *C. pagurus, C. setosus* and *N. norvegicus* increase with ontogeny and active egg mass ventilation is increased accordingly (Naylor et al. 1999; Baeza and Fernandez 2002; Eriksson et al. 2006). Embryos in the centre of eggs masses of brachyuran crabs *Cancer setosus* and *Homalaspis plana* have lower oxygen supply and consumption and thus slower development than embryos at the periphery, causing asynchrony in development and hatch (Fernández et al. 2003). Adult Norway lobster, *Nephrops norvegicus,* inhabit areas where oxygen deficiency (<30 % oxygen saturation) frequently occurs during autumn in bottom waters (Baden et al. 1990). In a laboratory examination of female behaviour and embryo responses to a range of oxygen conditions, females increased the ventilation of their eggs in normoxic (>90 % oxygen saturation) and hypoxic condition (30 % oxygen saturation) (Eriksson et al. 2006). Although early and late hatching embryos survived acute exposure to 5–95 % oxygen saturation, late hatching embryos emerged with incomplete development (<16 % oxygen saturation) and decreased survival rate (<7 % oxygen saturation) (Eriksson et al. 2006).

Lobsters and crabs use changes in maternal behaviour and also physiological adaptation to escape unfavourable conditions during egg development. These methods appear to provide eggs with greater tolerance to hypoxia than later life stages (Eriksson et al. 2006).

Hatching and early development

Temperature on hatching and early development

The temperature thresholds for hatching and early development have been determined in many cases using tank experiments where the only variable changed is temperature. The reality of temperature change in the field is that it influences a range of other variables such as food availability, predator activity and water clarity. Consequently it is valuable to verify laboratory based observations with research in the wild that includes co-varying factors. For example, the degree of synchrony between phytoplankton blooms and larval hatching is thought to be a primary determinant of early life stage survival for many species, according to the 'match–mismatch' hypothesis (Cushing 1972; Burrow et al. 2011).

Hatching The timing of larval hatching varied interannually in *Cancer magister* and appeared to be related to degree days during the egg incubation period (Park and Shirley 2008). Larvae hatched later in 1997 and 2002 when temperatures were colder, and earlier in 1998 when temperatures were warmer (Park and Shirley 2008). Development rates of *Paralithodes platypus* embryos held at higher than normal temperatures were not constant over time (Stevens et al. 2008). Moreover the crabs exhibited a slowing of development, or diapause, at lower temperatures. Similar patterns were also exhibited by snow crab *Chionoecetes opilio* (Moriyasu & Lanteigne, 1998) and Tanner crab *C. bairdi* (Swiney, 2008). These findings suggest that there is often flexibility in development rates that reduces variance in hatch timing caused by environmental variation.

There is considerable flexibility or plasticity in the responses to temperature. For example, after 80 % of the embryonic development time has elapsed in the American lobster, *Homarus americanus,* embryos appear to be able to either complete their development if they are in a suitable thermal environment (>11 °C), or remain in stasis until the temperature is high enough (Helluy and Beltz 1991). Despite halting development, the embryo is still metabolically active, using up valuable yolk reserves. The longer the embryos remain in stasis, the less energy reserve available to the larvae upon hatching (Cowan et al. 2007).

Development Larval development time is the time taken to progress through larval stages from hatch to the first juvenile stage. Larval development stages vary between reptantian species with some undergoing direct development and hatching from the egg as juveniles. However, they more commonly pass

through a number of planktonic stages generally termed zoea (or phyllosoma in the Achelata—slipper lobsters and rock lobsters). There is also commonly an intermediate or post-larval stage between the planktonic larval stage and benthic juvenile stages, which is termed megalopae in crabs, glaucothoe in anomurans, and puerulus in the Achelata.

It is closely linked to growth, which is discussed above under the section: Growth, with generally similar patterns. Larval development time generally declines with increasing temperature, where changes at the low end of range are more consequential, as reported for *Scylla serrata* (Hamasaki, 2003) and *Cancer magsiter* (Sulkin & McKeen, 1996, Sulkin et al., 1996). In *Homaraus amercicanus*, larval development is optimised at temperatures above 12 °C and at lower temperatures development slows down (Templeman 1936; Harding et al. 1982; Mac-Kenzie 1988); Fig. 2. Rate of larval development in *Homarus americanus*, from MacKenzie (1988). Figure 2). In situ observations of larvae from the Gulf of Maine show that they have a preference for temperatures above 12 °C (Annis 2005). Recent observations on *H. americanus* larval development from the northern extent of their range, found 38 % shorter development time at 10 °C and 47, 50 and 100 % longer development times at warmer temperatures (14, 18 and 22 °C respectively) than those found by Mackenzie 1988, above (Quinn et al. 2013). The temperature—larval development relationship was different in these northern larvae from most other published studies, and from Fig. 2 (Templeman 1936; MacKenzie 1988; Annis 2005; Quinn et al. 2013). *H. gammarus* had similar rates of development along a temperature gradient as described in the Mackenzie study.
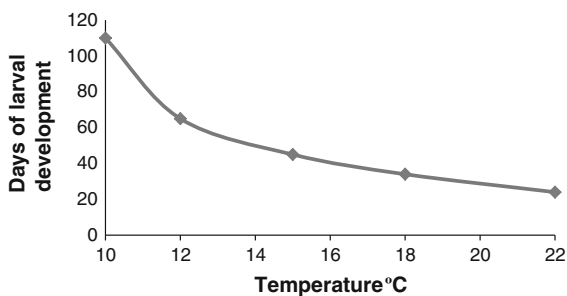

Fig. 2 Rate of larval development in *Homarus americanus*, from MacKenzie (1988)

A prolonged intermoult period at lower temperatures increased the overall food consumption during the intermoult period in *Jasus edwardsii* and *J. verreauxi* phyllosoma compared to larvae reared at higher temperatures (Tong et al. 2000; Moss et al. 2001). Tong et al. (2000) also found that although early to mid-stage *J. edwardsii* phyllosoma from the highest temperature treatments progressed through larval stages rapidly, they were significantly smaller. Tong et al. (2000) attributed the smaller size of these larvae to reduced food consumption combined with a higher metabolism at higher temperatures.

Temperature effects on larval reptantia size vary. Increasing temperatures reduced larval size for a given developmental stage in *Homarus americanus* (Mac-Kenzie, 1988) and *Jasus edwardsii* (Tong et al., 2000). However this pattern is not consistent for all reptantians. First stage larvae of *Cancer magister* were larger in the cooler offshore areas than in inshore waters, possibly due to low temperatures, although it could also have been due to food availability (Sulkin et al. 1996). *Jasus edwardsii* stage I phyllosoma kept at 18 °C had more rapid development but significantly reduced levels of the omega-3 fatty acid, eicosapentanoic acid ($20:5n$-3), and sterols compared to individuals kept at either (10.5 °C) or ambient (11.7 °C, range 9.5–13 °C). Ascorbic acid reserves were highest in the coldest incubated larvae. The results were interpreted to mean a detrimental effect of warm incubation temperature on embryonic development on Stage I phyllosoma (Smith et al. 2002). As this temperature is above typical natural temperatures at the time of larval release this response may also be a stress response.

Numerous studies have demonstrated the profound influence of temperature on the development of reptantia larvae in terms of instar duration, morphology, feeding rate, size, incidence of deformity and survival (Johns 1981; Shirley et al. 1987). It is important to note that reptantian larvae do not usually experience temperature passively, they actively adjust their depth in response to both absolute temperature and rates of temperature change, as observed in *Rhithropanopeush arrisii, Neopanope sayi* (Forward, 1990) and *Pseudocarcinus gigas* (Gardner et al., 2004) The effect of temperature on vertical migration is covered in two comprehensive reviews (Sulkin 1984; Queiroga and Blanton 2005). Many of the above examples are drawn from aquaculture examples which

have limited utility in defining thermal tolerances and expected field responses to temperatures as they can test responses of animals outside their normal range, and do not contain enough information to account for geographic variation in broodstock source and therefore any local adaptation that might have occurred. Behaviour of reptantian larvae in response to temperature can be important because they actively move in and out of water bodies of different temperatures. In laboratory studies, *Homaraus americanus* postlarval settlement was greater in an unstratified water column than in the presence of a thermocline (Boudreau et al. 1991). In the wild the thermocline may act as a natural barrier to settlement. Temperature can affect recruitment of reptantian larvae beyond that which would be predicted from observation of their response to absolute temperature values.

Lunar effects on hatching

Lunar rhythms influence tides on daily and monthly cycles, as well as the amount of light at night, and through these effects can influence biological rhythms in marine species. This can be particularly useful in synchronizing mating and egg hatching, which has been reviewed for crustaceans by Ferrero et al. (2002). Daily tidal rhythms have been noted in sub-tidal crustaceans such as fiddler crabs (*Uca*) and land crabs (*Chiromantes haematocheir*), where hatching is often linked to high-tide (DeCoursey 1979; Saigusa 1980; Bergin 1981). Monthly patterns of hatching occur, coinciding with full or new moons, in the brachyuran land crab *Chiromantes haematocheir* (Saigusa, 1980) and clawed lobster, *Homarus gammarus* (Ferrero et al., 2002). However, hatching does not follow lunar cycles in all species, including mud crab, *Scylla serrata* (Hai, 2001, Davis et al., 2004).

Larvae and postlarvae

Temperature on settlement

Water temperature has the potential to shape larval survival and settlement patterns in reptantians, as coastal temperatures regimes are either unsuitable or unappealing to larvae searching for settlement habitat. *Homarus americanus* lobsters settled in higher numbers at a site with temperatures above 12 °C compared to a site with lower temperatures, despite similar

availability of planktonic larvae (Annis et al. 2013). Recruitment in the southern rock lobster, *Jasus edwardsii* declined in periods of cold upwelling (Linnane et al. 2010). Thermal sensitivity of larvae and juveniles may determine these patterns (Sanford et al. 2006).

Effects of currents and wind on larvae

Wind-driven and geostrophic currents influence delivery of larvae to suitable settlement habitat and thus influence larval duration, successful settlement and recruitment. Reptantian eggs are attached and brooded by the female until hatching so current and wind effects are mainly on the larvae rather than eggs and embryos.

As crustacean larvae have limited horizontal swimming capability (Ennis 1986), their position in the water is traditionally assumed to be primarily governed by currents. Postlarvae on the other hand appear to actively swim horizontally which is considered to be essential to lobster and crab dispersal (Charmantierdaures and Charmantier 1991). There is new evidence suggesting local retention of larvae on small-scales in *Homarus gammarus* by retention of water masses below a halo-cline (Oresland and Ulmestrand 2013).

Homarus americanus larvae concentrate in areas of downwelling, where currents come together (Aiken and Waddy 1986) and in windrows, which are zones of strong surface motion (Harding et al. 1982). *Jasus edwardsii* larvae are dispersed over periods of up to 24 months and concentrate in fronts at the interface of currents and slower moving water (Bruce et al. 2007). It is unclear whether larvae are actively or passively involved in maintaining position in these locations and whether transport is a combination of passive horizontal movement and active vertical movement. Onshore wind combines with current movement especially in relation to larval transport of lobsters from offshore locations to coastal sites (Sheehy and Bannister 2002).

Current systems substantially influence fisheries production and species abundance through their effects on recruitment. The relationship between settlement and current strength has been particularly well studied in the western rock lobster *P. cygnus*, and this offers a good example of the relationship between broad-scale oceanic currents and settlement and

condition of pueruli. The strength of the Leeuwin Current flow varies according to ENSO events, and are stronger during La Niña years and weaker during El Niño years, which consequently affects puerulus settlement strength (Pearce and Phillips 1988; Caputi et al. 2001). This effect of the Leeuwin Current on recruitment is thought to be either through temperature and thus growth effects from a stronger Leeuwin Current in April or through the current strength influencing larval retention and transport across the continental shelf (Caputi et al. 1996). As pueruli swim across the predominant direction of flow of the Leeuwin and adjacent currents, their success in reaching inshore nursery areas will be influenced by variations in the strength of the currents, prevailing westerly winds, proximity to eddies and water conditions especially temperature (Pearce and Phillips 1988; Caputi et al. 1996; 2001; Limbourn et al. 2009).

The effects of current and wind advection on *P. cygnus* larval dispersal was studied with oceanographic modelling by Griffin et al. (2001) who concluded that the high variation in natural settlement could be primarily attributed to non-advective effects of the Leeuwin current, such as temperature and primary production. Biochemical analyses of puerulus is consistent with this because the puerulus stage relies on stored energy during its settlement onto near-shore habitats (Limbourn et al. 2009). Thus currents that create warm-core eddies tend to have increased food supply for phyllosoma, which in turn increases lipid and protein content and quality in pueruli (Limbourn et al. 2009). Experimental studies have also shown that that nutritional factors may be important in initiating metamorphosis of phyllosoma to the puerulus stage (Rotllant et al. 2001; McWilliam and Phillips 2007) presumably linked to the need for puerulus to have sufficient energy reserves to sustain the cross shelf migration to setting habitat (Fitzgibbon et al. 2013).

Current strength and spatial distribution typically has seasonal patterns with distinct shifts in Spring and Autumn. This affects larval dispersal and development as observed in the change in *Cancer magister* megalopae abundance in Coos Bay, Oregon which was significantly higher when the spring transition and associated change in the California Current was early (March) and low when it was late (May or later). This environmental effect on recruitment strength affects commercial catch in Coos Bay which was positively correlated to settlement strength of megalopae 4 years

earlier (Shanks and Roegner 2007). Interestingly, the opposite was observed for *Pagurus* spp., *Hemigrapsus* spp., and *Porcellanid* crab where there was a stronger recruitment pulse in late spring transition years. As the larvae of those crab taxa remain close to shore, they may be carried offshore with the Davidson Current waters during the spring transition. In total the variation in the spring transition date, which marks a key annual shift in coastal currents, explained 90 % of the annual variation in the annual abundance of megalopae of all four species of crabs investigated (Shanks and Roegner 2007). Furthermore, as the spring transition occurs nearly simultaneously from Washington to Point Conception, California (Strub et al. 1987), the significant correlations between the timing of the spring transition and commercial catch can be observed over the entire West Coast (1,700 km long).

Studies on interannual variation in recruitment of the Dungeness crab (*Cancer magister*) have identified correlations with ENSO conditions and wind-forced larval transport (Botsford 2001). Recruitment strength on a daily scale appears to be driven by upwelling winds that interacts over 100-km spatial variability with coastal topography (Botsford 2001). When abundance time series were compared to mean daily wind stress, maximum daily tidal range, and mean daily temperature residual, variation in wind stress had little effect on crab megalopae abundance in *Cancer magister*, *C. productus, C. oregonensis*, *Hemigrapsus oregonensis* and *Pachygrapsus crassipes*. Crab recruitment appeared to be primarily controlled by tidal forcing for these species (Roegner et al. 2007).

Tilburg et al. (2005) examined larval transport and recruitment of the blue crab (*Callinectes sapidus*) in Delaware Bay. Timing of larval settlement was primarily driven by wind stress, however the model failed to fit observations in all years, indicating that small-scale physical events as well as larval behaviour also determine the timing and strength of larval settlement (Tilburg et al. 2005). Onshore winds and sea surface temperature were also correlated with settlement of the European lobster *Homarus gammarus* (Sheehy & Bannister, 2002).

Salinity on larvae and postlarvae

Salinity tolerance in adults and juveniles is determined largely by efficient regulation of the volume, and often

the osmolarity, of the body fluids by specialised branchial epithelia and excretory organs (Taylor and Seneviratna 2005). These are less well developed in larvae which tend to be osmoconformers or less commonly hyper-osmoconformers that maintain a slight positive difference in osmolarity with the environment. Shore crabs, such as *Libinia emarginata* can weakly osmoregulate as larvae, which is an unusual ability early in ontogeny (Charmantier 1998). Survival of larvae is often reduced at lower salinities for stenohaline species, for example, *Homarus americanus* could not be cultured to stage four below 17 ppt (Templeman 1936). Rapid osmotic adjustment is important to planktonic crustacean larvae exposed to low salinity surface water following heavy rainfall. For instance in *Homaraus americanus* stage three larvae adapted to diluted water in 3 h and stage four larvae in 6 h (Charmantier et al. 1988). Temperature interacts with salinity tolerance and can improve salinity tolerance and survival. For example, the mud crab *Scylla serrata* larvae have a broader salinity tolerance when they are held at optimum temperatures of 21 °C (Nurdiani and Zeng 2007).

Natural mortality

Survival of juveniles and adults

Reptantian crustaceans most commonly have a planktonic larval development phase after which they settle into benthic habitats often similar to their adult habitat. For many species this is a site-attached or sedentary phase and so the occurrence of a species in a region is determined by the presence of appropriate water conditions and habitat. In research on the barriers to the natural range of Dungeness crab (*Cancer magister*), reasons for their absence from suitable habitats with adequate supply of larvae were identified (Sulkin et al. 1996). Late stage larvae and juveniles were raised at the range of temperatures reflecting those from the areas they were absent. Survival of megalopae was not affected by the experimental temperatures, however, juvenile crabs had reduced growth rate and high mortality at 22 °C, supporting the hypothesis that summer water temperature exceeding 18 °C controls distribution of commercial stocks because of higher mortality of newly settled juveniles (Sulkin et al. 1996). Moult increment in juvenile *C. magister*

did not vary significantly between 5 and 15 °C and juvenile Dungeness crabs are exposed to this temperature range along their geographic range (Kondzela and Shirley 1993). Testing a similar hypothesis on minimum temperature thresholds rather than maximum thresholds, winter mortality of Chesapeake Bay blue crabs (*Callinectes sapidus*) was measured to assess whether harsh winter conditions could be a significant source of stock loss (Rome et al. 2005). *C. sapidus* suffered highest winter morality rates (6.0–14.5 %) when bottom water temperature fell below the February average. Similar thresholds were identified in laboratory tests where highest mortality occurred in the lowest temperature (1 °C) and salinity (8 ppt) treatments (Rome et al. 2005). Mature females were less tolerant than juvenile crabs and of the juvenile stages, recruits (<15 mm carapace width) were least tolerant to winter conditions. In the early 1980s an increase in survival and growth rates of juvenile *Homarus americanus* was attributed to an increasing sea temperatures near Halifax, which gave rise to increased recruitment to the fishery throughout coastal Nova Scotia during the mid- to late 1980s (Campbell et al. 1991). In laboratory experiments *Callinectes sapidus* were capable of maintaining their metabolic rate between 20 and 27 °C, which was taken to be an evidence of acclimation (Leffler 1972). Although it appears that they still make adjustments at higher temperatures, their metabolic rate increased at temperature above 27 °C (Leffler 1972).

Numerous studies on different reptantian crustaceans have shown that life span becomes shortened and total body size decreased with increasing temperature, for example in crabs, *Portunus trituberculatus* (Kim et al.), *Cancer magister* (Terwilliger & Dumler, 2001) *Callinectes sapidus* (Fisher, 1999) (Darnell et al., 2009) *Portunus pelagicus* (De Lestang et al., 2003) *Paralithodes camtschatica* (Stevens, 1990) and lobsters including *Homarus americanus*, (Landers et al. 2001) and *Panulirus cygnus* (Johnston et al., 2008).

Salinity on juveniles and adults

Lower salinity water has lower density and overlays more saline waters so benthic juvenile and adult stages rarely encounter hyposaline conditions (Aiken and Waddy 1986). Juveniles and adults tend to be osmoconformers, but hyper-osmoregulation occurs at lower spectra of the salinity tolerance range which involves

expenditure of energy to maintain osomolarity above ambient (Charmantier et al. 1984; Dall 1970). Juvenile *H. gammarus* require 24 h (Charmantier et al. 1984) and adults 75 h (Dall 1970) to adjust to changes in salinity. Low salinity is more stressful at higher temperatures (Jury et al. 1994), and the combination of temperature and salinity change has a synergistic effect. For example, for *H. americanus,* salinity was lethal at 6 ppt at 5 °C and 16.4 ppt at 25 °C (Mcleese 1956). Lobsters are capable of detecting salinities and prefer higher (20–25 ppt) over lower salinities (10–15 ppt) and appear to avoid these (Jury et al. 1994).

Catchability and catch rates

Catchability in reptantian crustaceans is usually in relation to trap fisheries where it measures the probability of an animal being captured by a randomly applied trap. There is often an assumption in estimates of biomass based on catch per unit effort that catchability remains constant (Morgan 1974; ArreguinSanchez 1996). Catchability can vary with population density, and is assumed to decrease as the population density increases. c/f = qD, where c/f is catch rate, number of animals per trap, D = absolute density, animals per square metre, and q is the catchability coefficient, square metres per trap (Miller 1990). Catchability also varies with environmental changes that are unrelated to changes in stock abundance so that assessment methods such as depletion models can be improved by incorporation of catchability information (Wright et al. 2006). Understanding the environmental factors affecting catch rates provides a way of standardising these catch rates to provide a more reliable abundance index and hence an improved stock assessment and management (Srisurichan et al. 2005).

The catchability of lobsters is influenced by a variety of environmental and endogenous parameters, on an annual basis as well as over shorter periods. Environmental factors can interact to influence catchability. Monthly catchability (q) of a population of the western rock lobster (*Panulirus cygnus*) was examined and increased with increasing water temperature and salinity in adults and juveniles, and decreased with percentage of lobsters in pre-moult condition (Chittleborough 1970; Morgan 1974). Similarly, catchability and activity rates increased with water temperature for *Homarus americanus* throughout the range of temperatures normally

encountered by the lobster (McLeese and Wilder 1958). Activity and catchability increased with water temperature in *Homarus gammurus* (Smith et al., 1999). Habitat heterogeneity influenced catchability of *Homarus americanus*, with decreased catchability in higher-relief sites compared to low-relief sites, possibly due to increased shelter or decreased dispersal of bait odour plume (Tremblay and Smith 2001).

Wind and swell effects on catchability

Wind affects catchability of *Homarus americanus*, principally due to its influence on ocean bottom temperatures, consistent with the classical Ekman response (Drinkwater et al. 2006). Eastward wind produces warmer water by forcing the warmer upper layers shoreward and causing downwelling, whereas westward winds causes upwelling of colder water, hence resulting in colder bottom temperatures and reduced lobster catchability (Drinkwater et al. 2006).

Swell increased catchability of legal-sized *P. cygnus*, especially in shallow water and with greatest effect at a lag of 1 day (Srisurichan et al. 2005). Effects were also strongly seasonal with null effects in summer months November to January (Srisurichan et al. 2005). Similar effects of swell on catchability have been reported in *P. japonicas*, but not for *P. argus* and *J. edwardsii* (Table 3).

Temperature and catchability

Catchability of reptantians often increases with temperature (Table 3) due to increased metabolic demand for food and also because the rate of diffusion of bait molecules increases with temperature (Morrissy 1975). Fishers report that day-to-day catch rates are affected by temperature although this interacts with the type of bait, sea swell, wind strength, tidal movement and water turbidity (Koeller 1999).

Catchability in some species of lobsters is more complex than abiotic environmental effects alone. In *Jasus edwardsii*, catchability was influenced by water temperature (Ziegler et al. 2002) but was more strongly influenced by biotic effects such as moulting, mating and density (Ziegler et al. 2003, 2004) (Table 3). There is often higher catchability of larger individuals, for example *Homarus americanus* and *Cancer irroratus* (Miller, 1990), *Jasus edwardsii* (Frusher & Hoenig, 2001) and *J. lalandii* (Pollock & De B. Beyers, 1979)

Table 3 The effect of environmental conditions on catchability

Species	Increasing water temperature	Increasing salinity	% in pre-moult condition	Increasing swell	Increasing wind speed	Full moon	Increase in population density	References
Panulirus cygnus	Increase	Increase	Decrease	Increase		Decrease		Morgan (1974), Wright et al. (2006), Srisurichan et al. (2005)
Panulirus cygnus juvenile	Increase						Increase	Chitleborough (1970), Wright et al. (2006)
Panulirus argus						Null		Lopeztegui et al. (2011)
Panulirus japonicus				Increase				Yamakawa et al. (1994)
Jasus edwardsii	Increase, decrease			Decrease		Null, increase	Decrease	Ziegler et al. (2002), Ziegler et al. (2003, 2004), Ihde et al. (2006)
Homarus americanus	Increase, decrease				Decrease, null		Decrease	McLeese and Wilder (1958), Koeller (1999), Drinkwater et al. (2006), Tremblay et al. (2006), Pickering et al. (2010), Courchene and Stokesbury (2011)
Homarus gammarus	Increase							Schmalenbach (2009)

due to the agonistic exclusion of smaller individuals by larger animals (Scrivener 1971; Ihde et al. 2006). Catchability differed markedly between legal-sized male and female *J. edwardsii*, although catchability of both sexes generally declined in winter and was elevated in summer (Ziegler et al. 2003, 2004). For male *J. edwardsii*, water temperature had a greater influence on seasonal catchability than moulting and mating, although these also had strong effects (Ziegler et al. 2003). For females, moulting and mating occur at around the same time and had a profound effect on catchability although water temperature remained an important driver of catchability. The effect of water temperature was strongest in colder southern regions where it described 9–52 % of the seasonal variation in catchability in different years, while in northern warmer areas, temperature accounted for only 1–19 % of the seasonal variation (Ziegler et al. 2003). *Nephrops norvegicus* catch rates have declined with increased temperature in the Mediterranean (Tzanatos et al. 2014).

Lunar cycle and catchability

Kanciruk (1980) reviewed the impact of lunar cycles on the catchability of a number of spiny lobster species and reported that catchability of *P. japonicus* and *P. argus* were affected by the lunar cycle in addition to other processes including temperature and wave height (Yamakawa et al. 1994). In contrast, there was no correlation between lunar cycle and catchability in *P. argus* from the Gulf of Batabano, Cuba (Lopeztegui et al. 2011). These inconsistent observations on the effect of moon phase on catchability suggest other local environmental effects have greater influence so that there isn't a consistent trend between fisheries for this species. Catchability of *P. cygnus* varied through the lunar cycle with the minimum during the full moon period and maxima near the new moon period, a pattern most apparent in larger, legal-sized lobsters in shallow water (Srisurichan et al. 2005).

Disease

Environmental stressors of marine organisms such as change in temperature can increase the frequency of disease and the severity of its impacts as resilience is reduced (Wernberg et al. 2011). Disease will limit

food production from future crustacean aquaculture and fisheries (Bondad-Reantaso et al. 2012; Stentiford et al. 2012). Not surprisingly, disease is of concern to reptantian crustacean fisheries because of loss of productivity from mortality caused by pathogens, and also through indirect effects such as reduced growth and reproduction (Shields 2012).

Pearce and Belcom (2005) predicted that the incidence of disease of *H. americanus* will increase with higher temperatures and similar patterns are predicted for decapods in general with climate change (Stentiford et al. 2012). In the summer of 2002 Long Island Sound populations of *H. americanus* declined due to a new disease, excretory calcinosis, which led to fatal respiratory failure due to reduced effective surface area of the gills (Dove et al. 2004). No significant pathogens were observed and the disease was attributed to prolonged thermal stress (Dove et al. 2004). Experimental work on thermal stress showed that elevated temperature led to a depression of haemolymph pH and reduced phagocytic activity, which was consistent with hyperthermic acidosis and lower immunocompetence (Dove et al. 2005).

Another disease that affects *H. americanus* is bacterial epizoic shell disease and this has also been linked to increasing bottom water temperatures (Glenn and Pugh 2006). Both the incidence of shell disease occurrence and the bottom water temperature increase from north to south in Massachusetts Bay, which suggested that temperature may be linked to disease prevalence because warmer temperatures favour bacterial growth (Glenn and Pugh 2006). The effects of this disease on post-settlement mortality were strong enough that it obscured the effect of variable settlement strength on cohort strength or population size (Wahle et al. 2009).

The first records of luminous *vibriosis* in spiny lobsters was observed in *Jasus verreauxi* phyllosoma reared in experimental hatchery tanks with evidence that incidence increased at higher temperatures (Diggles et al. 2000). Higher temperatures were also linked to an infection of a parasitic dinoflagellate of the genus Hematodinium, which affected the *Cancer pagurus* fishery in Ireland (Chualáin et al. 2009).

Climate change: ocean warming and acidification

Previous sections of this review have described the response of crustaceans to environmental change within the daily, seasonal and annual cycles crustaceans were likely to experience. This section expands that to address the effects of longer term changes to environmental variables through climate change, including ocean warming and acidification. For an extensive review on the effects of climate change on fisheries see Pörtner and Peck (2010) and Salinger (2013) and on lobster fisheries, Caputi et al. (2013).

Water temperature

Climate change is shifting temperature beyond the thermal envelope many species are adapted to within their current range. As discussed above, higher water temperatures can be expected to affect many biological parameters such as moult frequency and increment (thus growth), natural mortality, settlement of first benthic stages, catchability, and reproduction. Global average air and sea surface temperature have increased by 0.4–0.8 °C in the last century with both larger and smaller changes at smaller scales (Harley et al. 2006). Climate change is responsible for poleward shifts in the distribution of many marine species and the condition of the 'rear-edge' populations provides a guide for the future of current population centres (Hampe and Petit 2005). Climate change can also have impacts on fisheries through the fishery assessment and management cycle. Many inputs into assessment processes are assumed to be constant through time, such as natural mortality and seasonal patterns in catchability however these can vary with temperature (Ziegler et al. 2003; Caputi et al. 2010), which trends through time under climate change.

A common assumption in stock assessment and management decision making in reptantian fisheries is that recruitment varies around a constant mean through time. One of the ways that climate change is expected to alter recruitment is through the "match-mismatch" effect. The timing of hatching affects recruitment strength because organisms have generally evolved to coincide reproduction with peak availability of suitable food for survival and development of the offspring (Cushing 1972, 1990). Lobsters and crabs do not have endogenous mechanisms to delay larval hatching to coincide with optimal external conditions for larval development (Schmalenbach and Franke 2010), so it is predicted that an increasing mismatch between larval peak appearance and optimal

food conditions will have a negative effects on growth and reproduction (Schmalenbach and Franke 2010). An example where timing of larval release appears to be vulnerable to climate change is in the North Sea where annual mean surface water temperatures have risen by almost 1.5 °C from 1962 to 2005 (Wiltshire et al. 2008) and has been most pronounced in winter (Franke et al. 1999). Climate change scenarios forecast warming to continue, with a further increase in North Sea water temperatures by 2–3 °C over the 21st century (IPCC 2007). Laboratory tests of these effects on European lobster *H. gammarus* suggest that a 2 °C increase in water temperature during the incubation period reduces incubation time (Schmalenbach and Franke 2010). Larval development in turn will commence at lower seasonal temperatures and will need more time to metamorphosis, which prolongs the high risk larval period, increasing exposure to predators and subsequently increasing mortality (Schmalenbach and Franke 2010). A climate regime shift in the North Pacific in 1989 is also believed to have caused a dramatic decline in the catch of the Hawaiian spiny lobster *P. marginatus* (Polovina et al., 1999, Hare & Mantua, 2000, Polovina, 2005).

Many reptantian crustacean fisheries have been studied for decades, which suggest they are well placed to detect significant changes in stock abundance, distribution and biological parameters as a result of climate change. The response of reptantian crustacean fisheries to climate change is a research issue that requires much further effort, especially as changes will also occur through complex ecosystem interactions (Lindley and Kirby 2010).

Case study: Tasmanian rock lobster fishery

The implications of climate change on the *J. edwardsii* fishery off the east coast of Tasmania has been examined in detail because change is expected to be substantial in this region. The east coast of Australia is experiencing ocean warming, and there has already been an increase in surface temperature of 2.28 °C over the last century (Ridgway 2007a). The current rate of warming in this area is 3.8 times the global average (Lough and Hobday 2011). Climate models predict a strengthening of the East Australia Current (EAC), which would bring warmer water further south along the eastern Tasmanian coast (Ridgway 2007b). This would be expected to affect puerulus settlement

because this depends on the position of the sub-tropical convergence (STC), where the warm EAC meets the cold Southern Ocean (Bruce et al. 2007). Further change in recruitment is predicted through the effects of acidification, which is expected to occur rapidly in this area (Fabry et al. 2008).

Projections of change in the fishery in response to climate change included the effect of temperature on growth and recruitment and predict an initial gain in biomass due to the positive correlation between temperature and growth rate (Pecl et al. 2009). However puerulus settlement is predicted to decline, adversely affecting recruitment to the fishery (Pecl et al. 2009). Consequently there was expected to be a trade-off between opposing short-term increases in lobster growth against long-term recruitment decline.

One of the limitations of model based prediction of climate change effects is that it is not field-tested. Some field-based information was collected in the Tasmanian *J. edwardsii* fishery where a large-scale translocation experiment moved 30,000 slow-growing lobsters from deep cold water to inshore areas along the east coast of Tasmania where growth is faster. For the lobsters at the southern extent of their range (poleward) this equatorward translocation represented a change in mean water temperature that reflects changes predicted by climate scenarios for 50 years hence (IPCC 2007). Lobster growth increased beyond that of the resident inshore lobsters within the first moult (Chandrapavan et al. 2010; Green et al. 2010), resulting in an improved reproductive output (Green et al. 2010). Nutritional condition of the deep water lobsters also improved (Chandrapavan et al. 2009). These positive changes suggest that southern rock lobster is plastic enough to accommodate a changing climate in at least some parts of its range.

Ocean acidification

As a result of increasing carbon dioxide (CO_2) emissions, the world's oceans are slowly becoming more acidic (Caldeira and Wickett 2003; Orr et al. 2005). During the last century, the pH of global oceans has dropped by an average of 0.1, an equivalent to a 25 % increase in acidity, and models predict pH to decline by 0.2–0.4 by the year 2100 (Caldeira and Wickett 2003; Dupont et al. 2008). A decline in pH results in a decrease in carbonate saturation state, and a lower concentration of carbonate ions for the

biosynthesis of calcium carbonate (Keppel et al. 2012). This puts marine calcifiers especially at risk of impact (Mayor et al. 2007; Dupont et al. 2008; Arnold et al. 2009; Pelejero et al. 2010; Sheppard Brennand et al. 2010; Walther et al. 2010). Manipulative experiments on marine calcifers, including echinoderm, bivalve, coral and crustacean species, have shown that ocean acidification negatively affects growth, physiology, fertilization, cleavage, larval development, settlement and reproductive success (Kurihara 2008).

The effects of increased acidification has been examined in several reptantian crustaceans. Dry weight of European lobster larvae, *Homarus gammarus,* decreased at exposures of 1,200 ppm CO_2, but no differences were detected in the period of planktonic development (Arnold et al. 2009). Lower dry weight might also indicate a thinner and less calcified exoskeleton (Arnold et al. 2009), causing greater susceptibility to predators, disease and possibly a reduced capacity for feeding due to decreased claw strength (Keppel et al. 2012). *Homarus americanus* larvae had reduced growth, increased development time and decreased survival when reared in water with a pH of 7.7 (Keppel et al. 2012). Similarly, red king crab, *Paralithodes camtschaticus,* embryos had smaller yolks, longer mean hatch duration, resulting in longer larvae with lower survival at pH of 7.7, compared to ambient (pH 8.0) (Long et al. 2013). Spider crab (*Hyas araneus*) larvae had reduced dry weight and C/N ratio decreased at 710 ppm CO_2 (Walther et al. 2010). Prior to moulting, larval metabolism appears to switch from lipid storage to an increasing production of protein (enzymes and structural proteins relevant during moulting), which is reflected in decreasing C/N ratios (Anger and Harms 1990). Measuring C:N ratio also enables temperature effects to be separated from CO_2 effect (Walther et al. 2010). CO_2 is thought to affect these metabolic processes through metabolic depression (Portner et al. 2004). Juvenile *H. americanus* did not have an altered calcification in response to decreased pH (Ries et al. 2009). Shell and skeletal mineralgy is expected to change in some calcifers, but not all, depending on the Mg/Ca ratios (Ries 2011).

Increased CO_2 (decreased pH, as a measure of ocean acidification) reduced the tolerance of the spider crab *Hyas araneus* and the edible crab *C. pagurus* to extremes of high and low temperature with an as yet unclear mechanistic background (Metzger et al. 2007;

Walther et al. 2009, 2010). High CO_2 concentrations caused a delay in development in *Hyas araneus* (Walther et al. 2010). Walther et al. (2010) identified the megalopa stage as well as reproducing females as the bottleneck in the life cycle of *H. araneus* as the physiological tolerance for temperature and pH is smallest for those stages.

Overall, small changes in the pH of seawater are having a range of negative effects on the early life history stages of reptantians. These are the most vulnerable stages to a wide range of environmental factors. This field of experimentation with ocean acidification has arisen recently, and for reptantians is currently limited to observations in the laboratory. The observations comprise of physiological or survival changes in response to a number of levels of acidification. In contrast, in reef fishes, serious behavioral responses to ocean acidification include impaired homing behavior and predatory responses have been documented (Cripps et al. 2011; Allan et al. 2014; Chivers et al. 2014), which have the potential to influence recruitment. Applying this level of complex experimental probing to reptantians to understand the effects of changing pH levels on the homing and predator escape behavior in species with exoskeletons will provide the first indications of the challenges faced by crab and lobster fisheries in the future.

Conclusion

Fisheries management for crabs and lobsters could be enhanced by understanding the natural fluctuations in biomass caused by response of these species and their ecosystems to environmental change. Interactions between environmental variables and the ecosystem are complex and may lead to unexpected responses. This review shows that there are some clear trends when variables are assessed independently, such as temperature increasing growth rates of all life stages until the species-specific lethal limits are reached. However, when environmental variables are assessed in combination, reflecting what is likely to be experienced in the wild, the effects are often synergistic, the impacts of the response may be negative or positive and the direction and the magnitude are species specific. That is to say, the responses are not easily predictable or generalizable. There are few strong environmental predictors of recruitment or

catchability in reptantians, the two main sources of natural variation in catch or biomass in commercial fisheries. There is a large body of work on environmental influences on crustacea using single or double variable experiments and these are generally conducted for understanding biological processes rather than directly for informing fisheries management. Such an applied outcome typically requires additional field studies or analysis of trends in fisheries data.

In trap fisheries, which rely on the animal voluntarily entering the pot, there is a large amount of unexplained variation in catchability and catch rates. Catchability increases with increasing temperature, but environmental variation such as temperature generally only explains a small amount of the variation in catchability. Catchability is one of the more poorly understood factors in crustacean fisheries science and of interest because of the common use of catch rate data as a proxy for abundance.

Understanding sources of variation in recruitment is almost as elusive as catchability. While the effect of single variables on growth, quality, and survival of embryos and larvae has received much research attention, information on the effect of environmental factors in the field are missing for most species. The bet-hedging reproductive strategy of many marine species of producing hundreds to millions of larvae each year in the hope one or two might survive, coupled with seasonal and interannual variation in environmental variables makes it hard to predict short term changes in biomass of a fishery. Changing climate increases the need for better understanding of the effect of environmental processes on larval stages and ultimately recruitment strength.

Often in early life history studies proxies for recruitment are in fact aquaria studies on responses of experimentally maintained animals to single variables. The temperature thresholds for hatching and early development in reptantians have been determined in many cases using tank experiments where the only variable changed is temperature. This is a useful first step in the process to understand physiological thresholds, but it does not explain how temperature change in the field will influence survival of individuals or cohorts of recruits. Temperature change in the wild influences a range of other variables such as food availability, predator activity, metabolic rate and water clarity. Consequently it is valuable to corroborate laboratory based observations with research in the wild that includes co-varying factors. For example, the degree of synchrony between phytoplankton blooms and larval hatching is thought to be a primary determinant of early life stage survival for many species, according to the 'match–mismatch' hypothesis (Cushing 1972; Burrow et al. 2011). It is time to take a broader approach to environmental fluctuations and its effects on recruitment using large-scale, long-term datasets on recruitment coupled with fine-scale oceanographic and biophysical modelling to start generating testable hypothesis.

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