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Contrasting effects of hypoxic conditions on survivorship of planktonic larvae of rocky intertidal invertebrates

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ABSTRACT: Hypoxia is increasing in coastal zones worldwide, with acute effects on demersal fish and benthic invertebrate communities in shallow coastal and estuarine habitats. Less studied are the effects of hypoxia on planktonic larvae of open coastal habitats. Climate change projections suggest intensified hypoxia in open coast upwelling systems, such as the northern California Current Upwelling System, where there has been a recent rise of seasonally persistent inner-shelf hypoxia (dissolved oxygen [DO] < 1.43 ml l^{-1}) and anoxia (DO 0 ml l^{-1}). We examined survivorship of larval invertebrates exposed to low oxygen conditions in controlled laboratory experiments. Multiple-day hypoxic conditions, resembling DO levels in nearshore Oregon waters, were generated by bubbling seawater with nitrogen gas. Tolerance levels among species varied, from larvae of species with little tolerance to hypoxia (e.g. the shore crab *Hemigrapsus oregonensis*) to species with high tolerance (e.g. the California mussel *Mytilus californianus*). These contrasting responses among open-coast intertidal taxa suggest that chronic hypoxia or anoxia may have different effects on recruitment success among species and, consequently, on the structure and species composition of open coast intertidal communities.

KEY WORDS: Hypoxia · Survivorship · Planktonic larvae · Rocky intertidal · Coastal ecosystem · Oregon coast

INTRODUCTION

Hypoxia is increasing in frequency and severity worldwide with the number of coastal hypoxia sites rising exponentially since the 1960s (Vaquer-Sunyer & Duarte 2008) with over 500 reported cases globally (STAP 2011). Oxygen concentrations have declined faster in coastal waters than in open oceans (Gilbert et al. 2010), a phenomenon that has been cited as one of the fastest and most drastically changing environmental variables of ecological importance (Díaz 2001). Ecosystems experiencing severe hypoxia suffer from losses of fisheries and biodiversity, altered food webs, and slow recovery rates (Díaz 2001, Díaz & Rosenberg 2008, STAP 2011). Severe hypoxic events can lead to mass mortality of both fish and invertebrates and generate areas devoid of most life, often termed 'dead zones' (Díaz 2001). Hypoxic zones thus pose a global threat to coastal ecosystems and rank with overfishing and habitat loss as a major environmental problem (Díaz & Rosenberg 2008).

The best-known coastal hypoxic zones are those that are caused by the input of agricultural and industrial land-derived nutrients that increase primary

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production and promote high oxygen demand (e.g. Díaz 2001, STAP 2011). Others are caused by upwelled waters. One example is the novel occurrence of hypoxia in the nearshore waters of the northern California Current Large Marine Ecosystem (CCLME; Grantham et al. 2004), an Eastern Boundary Current region characterized by high biological productivity. This hypoxic zone is fueled by an increased supply of nutrient-rich upwelled waters resulting from variation in ocean–atmosphere processes at the basin scale (Chan et al. 2008).

From the 1950s to about 2000, severe hypoxia (<0.5 ml l^{-1}) was rare on the inner continental shelf (<50 m depth) (Chan et al. 2008). Since then, intensive monitoring has revealed a novel rise of severe hypoxia and even anoxia in these inner-shelf waters (Chan et al. 2008). In 2006, a particularly intense hypoxic episode spanned 3000 km^2, extending from the shelf break to the inner shelf, and occupied 80% of the water column. Such events have caused mass mortalities in fish and benthic invertebrates (Chan et al. 2008). They are predicted to intensify with climate change-driven increases in upwelling (Bakun et al. 2010, Iles et al. 2012), together with greater ocean deoxygenation (Keeling et al. 2010).

This system, thus, poses a unique opportunity to investigate the potential impact of a novel rise in nearshore hypoxia on rocky intertidal communities. In this study we ask:

Do the oxygen changes of nearshore waters have the potential to influence rocky intertidal communities via direct effects on the larval phase of the life cycles of rocky intertidal invertebrates? More specifically, does exposure to low oxygen waters result in differential larval survivorship among intertidal species?

We focus on the planktonic life stage of rocky intertidal invertebrates for 3 reasons:

(1) Larvae are considered to be the most sensitive life stage. The planktonic larval phase of marine invertebrate life cycles is widely considered to be most sensitive to environmental conditions. This planktonic dispersal phase often lasts weeks to months (e.g. larvae of *Pisaster ochraceus* can remain in the plankton for up to 228 d; Strathmann 1978) and exposes larvae to environmental conditions that vary in time and space. Environmental factors can have significant effects on larval development, metabolism, settlement success, and subsequent juvenile survivorship (e.g. Emlet & Sadro 2006, Giménez 2010). Documented cases of sensitivity in early life stages include the effects of pollutants (e.g. Hutchinson et al. 1998), ocean acidification (e.g. Dupont et al. 2010), temperature (e.g. Talmage & Gobler 2011), and hypoxia (e.g. Vaquer-Sunyer & Duarte 2008, STAP 2011).

(2) Hypoxia's effects on pelagic larvae of open coast species are not well understood. Hypoxia has been well documented to affect the benthic adult stages of a variety of invertebrate species (see reviews by Herreid 1980, Vaquer-Sunyer & Duarte 2008), but few studies have focused on the effects of hypoxia on pelagic larval stages. Most published studies focus on species that occur in estuarine and semi-enclosed, shelf-system habitats that experience human-caused hypoxia, such as studies of estuarine bivalves (Wang & Widdows 1991), and of decapods (shrimp, crabs) in bays and estuaries (Tankersley & Wieber 2000). The sensitivity of larval stages of open coast species from the CCLME to hypoxia has not been studied. In light of the novel rise of hypoxia in this system and the critical role of larvae to the dynamics and integrity of coastal ecosystems, determining larval sensitivity to hypoxia is an important research priority.

(3) Larval supply plays an important role shaping adult communities, and understanding hypoxia's effects on interacting species within a community context is important. While most experimental studies focus on the effect of hypoxia on one or a small number of species, few have focused on a suite of species that interact as competitors or as predator and prey. Most benthic invertebrate species have a bi-phasic life cycle that includes a larval stage (Pechenik 1999). The nearshore hypoxic events of the CCLME occur during the summer upwelling season, when many rocky intertidal invertebrate species produce their planktonic larval phase. Thus, insights into how hypoxic events affect survivorship of larval invertebrates may help us understand their effects on larval supply to rocky intertidal communities and the subsequent effects on community composition.

This information will be well placed within a context of long-term studies of Oregon, USA, rocky intertidal communities dating from 1981 (Menge et al. 2011), and the larger context of ecosystem interactions studied across the CCLME. This body of research has fostered the development and testing of fundamental ecological concepts such as predator–prey dynamics and food web complexity (e.g. Paine 1966), competition (e.g. Connell 1961), disturbance (e.g. Sousa 1979), and community dynamics (e.g. Menge & Sutherland 1987).

Here, we focus on a suite of 10 rocky intertidal invertebrate species from 4 phyla representing the biodiversity found in this habitat. Based on prior published research, we expected to observe variability in survivorship across species, but, because of

previously documented evidence and the notion that early life history stages are more sensitive to environmental influences, we also expected most of these species to exhibit poor survivorship under severe hypoxia (Díaz 2001, Vaquer-Sunyer & Duarte 2008, STAP 2011).

MATERIALS AND METHODS

Species used in experiments

Experiments were conducted with 10 species and, for 3 species, several larval stages. The species (with phyla in parenthesis) included: *Anthopleura xanthogrammica* (cnidarian), *Balanus glandula*, *Pollicipes polymerus*, *Cancer antennarius*, *Hemigrapsus nudus*, *H. oregonensis* (arthropods), *Mytilus californianus*, *Onchidoris bilamellata* (mollusks), *Pisaster ochraceus*, and *Strongylocentrotus purpuratus* (echinoderms). Five of these species have important ecological roles in rocky intertidal communities. For example, 2 species, *M. californianus* (California mussel) and *B. glandula* (acorn barnacle), are important prey items, habitat engineers, and components in succession, and were studied as model organisms in competition studies in rocky intertidal communities (Menge 1992). In addition, *P. ochraceus* (ochre star) and *C. antennarius* (spotted rock crab) are predators in rocky intertidal habitats, and *P. ochraceus* is an important species in ecosystem studies investigating keystone predation and top down effects (Menge et al. 2004). Similarly, *S. purpuratus* (purple urchin) can be an important ecologically dominant species and herbivore (Dayton 1975).

Collection of adults and egg masses

All specimens were collected from sites on the Oregon coast during the spring, summer, and fall of 2009 (see Table S1 in the Supplement for collection locations and dates; www.int-res.com/articles/suppl/m478p139_supp.pdf) and transported to the Hatfield Marine Science Center (HMSC), Newport, Oregon, USA. The method of obtaining larvae from each species differed (refer to the Supplement, Tables S1 & S2; www.int-res.com/articles/suppl/m478p139_supp.pdf) and followed methods described in Strathmann (1987). Adults of the urchin *Strongylocentrotus purpuratus*, mussel *Mytilus californianus*, and brooding crabs (*Cancer antennarius*, *Hemigrapsus nudus*, and *H. oregonensis*) were collected in the field and brought back to the lab, where they were induced to spawn (urchin and mussel), held until larvae hatched (crabs), or conditioned for later spawning (mussel, conditioning details in the Supplement). For the barnacles (*Balanus glandula* and *Pollicipes polymerus*), ripe egg lamellae collected from adults in the field were induced to hatch in the lab. Egg masses of the nudibranch *Onchidoris bilamellata* were collected in the field and held in aquaria with running seawater until hatching. Gametes of the anemone *Anthopleura xanthogrammica* and the sea star *Pisaster ochraceus* were obtained by spawning captive individuals from the public aquarium at HMSC.

Larval culture

Larval culture (including spawning and fertilization) methods followed procedures outlined by Strathmann (1987; Table S2) with the exception of barnacle cultures, which followed Emlet & Sadro (2006). Cultures used offspring from more than one parent to account for individual variation. All larval cultures were reared in a temperature-regulated room at the HMSC facilities, using 3.5 l glass jars containing 3 l of filtered seawater and were stirred with a paddle apparatus (Strathmann 1987). Cultures were incubated at 8 to 10°C and kept on a 10:14 h light:dark photoperiod. Seawater used for all larval rearing and experiments was pumped from the Yaquina estuary at high tide, sand-filtered, then filtered to 1 µm using a cartridge filter, and finally UV-sterilized before use in larval cultures or delivery to the experimental system. Cleaning and feeding of cultures occurred every other day (see the Supplement for details). Species-specific larval culturing information, including diet types, is presented in Table S2.

Experimental setup

The experimental system consisted of a gravity-fed mesocosm in which a 500 l header tank delivered seawater to four 50 l diffuser tanks (Nalgene polypropylene carboys). Each diffuser tank then delivered water via Tygon^{TM} tubing to four 1 l polycarbonate bottles, where larvae were held for treatments (Fig. 1). Water flowed into each 1 l bottle through a 6.25 mm inflow glass tube that delivered water at the base of the bottle. Water exited the bottle through a double-sided cylindrical filter covered with Nitex mesh. The mesh sizes used varied with larval sizes and were 80, 100, or 250 µm. For each treatment, one

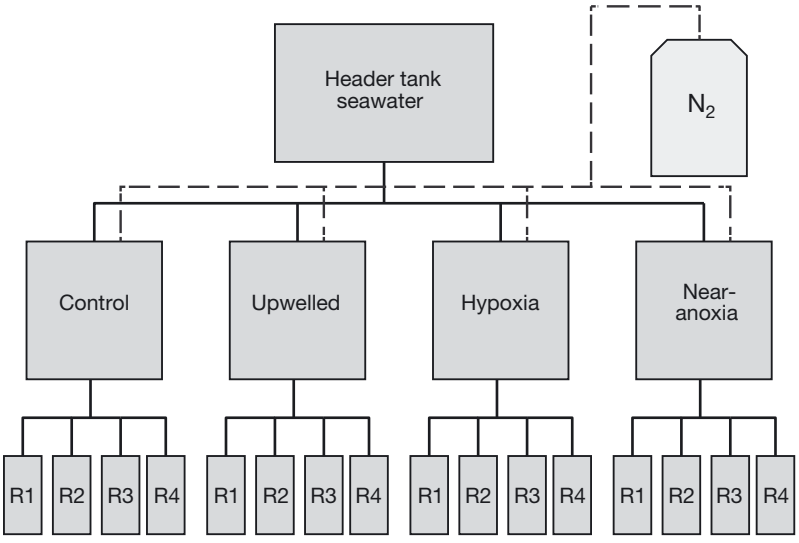


Fig. 1. Diagram of gravity-fed experimental set up, consisting of a 500 l header tank, four 50 l diffuser tanks, where water was bubbled with nitrogen gas, and sixteen 1 l containers. For ease of visualization, the 50 l diffuser tanks are labeled according to each treatment (upwelled dissolved oxygen [DO] 1.8–3.6 ml l^{-1}, hypoxia DO 0.5–1.4 ml l^{-1}, near-anoxia DO < 0.5 ml l^{-1}) and control (DO 5–7 ml l^{-1}), but note that control and treatments were assigned randomly at each experiment. Each diffuser tank supplies seawater to four 1 l containers, which serve as replicates

of the four 1 l bottle replicates fed into an additional 1 l bottle used for measuring dissolved oxygen (DO) and temperature of outflow water. The positions of these outflow bottles were assigned randomly in each trial. The rate of flow into the 1 l bottles was ~70 ml min^{-1}, generating a water turnover rate of 4.2 × h^{-1}.

Experiments

Experiments were conducted between May and December 2009 (Table S3 in the Supplement; www.int-res.com/articles/suppl/m478p139_supp.pdf). Experiments were performed within a temperature range of 8 to 10°C and kept on a 10:14 h light:dark photoperiod. Illumination was limited to the 1 l flow-through containers while the remainder of the experimental room remained dark. Low DO was generated by bubbling seawater with nitrogen gas through glass bonded silica diffusers (Sweetwater Air Diffuser, 9″ long × 1.5″ wide, 1/2″ national pipe thread [NPT], PE, Aquatic Ecosystems). Treatments, based on the hypoxic conditions observed on the Oregon coast (Grantham et al. 2004, Chan et al. 2008), included 2 DO-deficient treatments: an extreme low DO treatment called 'near-anoxia' (<0.5 ml l^{-1}) and a low DO treatment called 'hypoxia' (>0.5 and <1.4 ml l^{-1}). A third treatment, 'upwelled water' (1.8–3.6 ml l^{-1}), represented the DO levels of waters upwelled into the inner shelf during normal summers on the Oregon coast (Grantham et al. 2004). The fourth treatment, 'control' (5–7 ml l^{-1}), had levels representative of DO in the upper 10 m of the water column on the Oregon coast (Grantham et al. 2004, Chan et al. 2008). Experimental trials were conducted with either 4 replicates of 4 DO levels (control, upwelled water, hypoxia, and near-anoxia) or with 8 replicates of the 2 most extreme treatments: control and near-anoxia.

DO was monitored with an YSI Professional Optical Dissolved Oxygen (ProODO™) instrument (YSI), which was calibrated daily in water-saturated air, following user manual instructions. Initially, DO was measured hourly for each treatment for 24 h on the first and last day of a pilot experimental run. In these measurements, the 99.5% CI of treatment means all fell within the desired DO range. This high level of stability suggested that in subsequent experiments, measuring DO twice daily (morning and afternoon) would capture the relevant variability. In each trial, larvae were not introduced into the system until DO reached required treatment levels. Once DO treatments were established, they remained stable within 10% of the set value.

Since bubbling with nitrogen gas affected the pH of experimental seawater (raising the pH to 8.3 in the near-anoxia treatment versus 8.1 in the control treatment), an additional set of experiments was conducted to check for an effect of higher pH (see the Supplement for details). The pH levels of low DO treatments (pH 7.5, 8.1, and 8.3) did not affect larval survivorship ($p > 0.05$, post-hoc Tukey's honestly significant difference [HSD]) as determined by experiments using sensitive crabs (see the Supplement). Results were similar across low DO treatments with pH levels of 7.5, 8.1, and 8.3 ($p > 0.05$, post-hoc Tukey's HSD), where crab larval survival was significantly lower than in the control treatment with normal DO levels ($p < 0.0001$, post-hoc Tukey's HSD) (see the Supplement).

On the Oregon coast, hypoxia can persist in nearshore waters for days to months (Grantham et al. 2004, Chan et al. 2008). Larvae of all species were initially exposed in a 24 h pilot trial to determine their sensitivity. Based on the results of this trial, animals

were exposed to longer (3 d and 6 d) or shorter (12 h) treatments. Six day experiments were chosen to approximate, as closely as possible, a field-based scenario, where larvae may be caught in a low DO water mass (Grantham et al. 2004, Chan et al. 2008). Trials were conducted for 6 d if the larvae were large (>100 µm) and/or could be fed an algal diet. Only 3 d exposures were possible for small larvae or larvae that required non-algal foods (e.g. brine shrimp *Artemia*) because the mesh filters clogged.

During experiments, all larvae except the anemone *Anthopleura xanthogrammica* were fed, as indicated in Table S2. For species receiving an algal diet, food was added to the header tank and monitored daily in the outflow containers to ensure it was at the desired food levels (see Table S2). In the case of experiments with crab larvae, brine shrimp were added directly into the 1 l containers at the start of experiments. The *A. xanthogrammica* larvae were not fed during experiments because their diet requires incubation with excess *Artemia* nauplii homogenate, promptly followed by cleaning, a prohibitively time-consuming process (see the Supplement). Due to these logistical constraints, anemone larvae were not fed, and for this reason, experiments with anemone larvae only lasted 3 d.

In most cases, experiments were carried out with late larval stages (2 wk or older). However, for crabs, experiments were conducted on stage I zoeas because we were unable to rear larvae in sufficiently high numbers to later stages. The density of larvae exposed to each treatment varied, based primarily on larval size (Table S3). We estimated survivorship following low DO exposures based on larval movement. If larvae were swimming or moving in any way (e.g. moving limbs, beating cilia, or showing internal ciliated gill movement in the case of bivalves), they were considered alive. Experiments were either conducted with 100 or fewer larvae per replicate (in these experiments all larvae were counted) or with 1500 larvae per replicate (for these, subsamples were counted). Larval counts of subsamples were repeated until 3 were within a coefficient of variation (CV) of 10%. Most experiments were repeated 2 to 3 times, using different batches of larvae, from May 2009 until December 2009 (Table S3). Between experiments, the whole experimental system was cleaned thoroughly.

Statistical analysis

Analyses of larval survivorship were conducted separately for each of the 10 species or larval stages. We used a mixed effects model ANOVA of survivorship with each DO treatment (control, upwelled water, hypoxia, near-anoxia) as a fixed factor and the date of the experimental trial as a random effect. In 13 of 14 species/stage combinations, treatment effects did not vary by trial date (i.e. survivorship patterns for each of the 4 treatments were similar across trial dates), so survivorship for each treatment was averaged across dates of separate trials. Multiple pairwise comparisons were carried out using Tukey's HSD to determine differences among treatments ($\alpha = 0.05$). In order to adhere to the assumptions of ANOVA, percent survivorship values of larvae from treatments were converted to proportions and logit transformed (i.e. $\log_e[p/(1-p)]$ where p is the proportion). While all analyses were carried out with logit-transformed data, the results are presented as untransformed percent survivorship values rather than transformed proportion values for ease of interpretation. All analyses were performed using R version 2.12.2 (R Development Core Team 2011). Constraints of the system resulted in replicates sharing a common water source; therefore, the experiments were pseudo-replicated. However, we attempted to minimize the importance of this issue by randomly assigning treatments among the diffuser tanks for each experiment. For each experiment, the sequence with which larvae were introduced into treatments/replicates was also randomly assigned.

RESULTS

Crabs – species with low hypoxia tolerance

Hemigrapsus nudus, *H. oregonensis*, and *Cancer antennarius* were all sensitive to low oxygen conditions. All species exhibited high mortality in hypoxia and near-anoxia treatments within a 12 h period ($p < 0.0001$, see Table 1, Fig. 2). Mean survivorship in hypoxia treatments was between 25 and 50% but was less than 25% in the near-anoxia treatment (Fig. 2). All crab species showed high survivorship (>95%) in control and upwelled water treatments.

Species with high tolerance of hypoxia

In contrast, all remaining species examined in this study were tolerant to low oxygen conditions for 3 and 6 d exposure periods (see Table 1, Fig. 2, and Table S4 in the Supplement; www.int-res.com/articles/suppl/m478p139_supp.pdf), and trends in survivorship held across larval stages for the sea star,

Table 1. Summary of effects of low seawater oxygen concentrations on rocky intertidal invertebrate larvae. Duration of each experimental trial, number of experimental trials repeated over time, and the number of replicates per experiment (reps.) are shown for each treatment. The significant effects ($p < 0.05$) of 4 dissolved oxygen (DO) treatments are indicated with lowercase letters (Tukey's honestly significant difference [HSD]). Negative signs indicate where survival was significantly lower than other treatments. The letters NA (not applicable) are included for the upwelled and hypoxia treatments when only the 2 most extreme treatments were tested

Species	Duration	No. trials	No. reps.	Control (5–7 ml l^{-1})	Upwelled (1.8–3.6 ml l^{-1})	Hypoxia (0.5–1.4 ml l^{-1})	Near-anoxia (<0.5 ml l^{-1})	*F*	p
Cnidarian									
Anthopleura xanthogrammica planula	3 d	2	8	a	NA	NA	a	0.62	0.436
Arthropods									
Balanus glandula stage IV	6 d	2	4	ab	a –	b	b	5.55	0.004
Balanus glandula stage V	6 d	1	4	a	NA	NA	a	0.20	0.669
Balanus glandula stage VI	6 d	1	8	a	NA	NA	a	3.98	0.067
Pollicipes polymerus stage IV	6 d	1	4	a	NA	NA	a	2.46	0.141
Cancer antennarius zoea I	12 h	2	4	a	a	b –	c –	242.24	<0.0001
Hemigrapsus nudus zoea I	12 h	3	4	a	a	b –	c –	195.46	<0.0001
Hemigrapsus oregonensis zoea I	12 h	3	4	a	a	b –	c –	149.33	<0.0001
Mollusks									
Mytilus californianus pediveliger	6 d	2	4	a	a	a	a	1.13	0.355
Onchidoris bilamellata veliger	3 d	2	8	a	NA	NA	a	0.38	0.543
Echinoderms									
Pisaster ochraceus bipinnaria	3 d	2	8	a	NA	NA	a	1.12	0.299
Pisaster ochraceus brachiolaria	6 d	2	4	a	a	a	a	0.41	0.749
Strongylocentrotus purpuratus 6-arm pluteus	3 d	2	4	a	NA	NA	a	0.15	0.708
Strongylocentrotus purpuratus 8-arm pluteus	6 d	2	4	b –	a	a	a	35.16	<0.0001

urchin, and acorn barnacle. For each of these species, both younger and older larval stages showed high tolerance of hypoxia and near-anoxia after 3 or 6 d exposures.

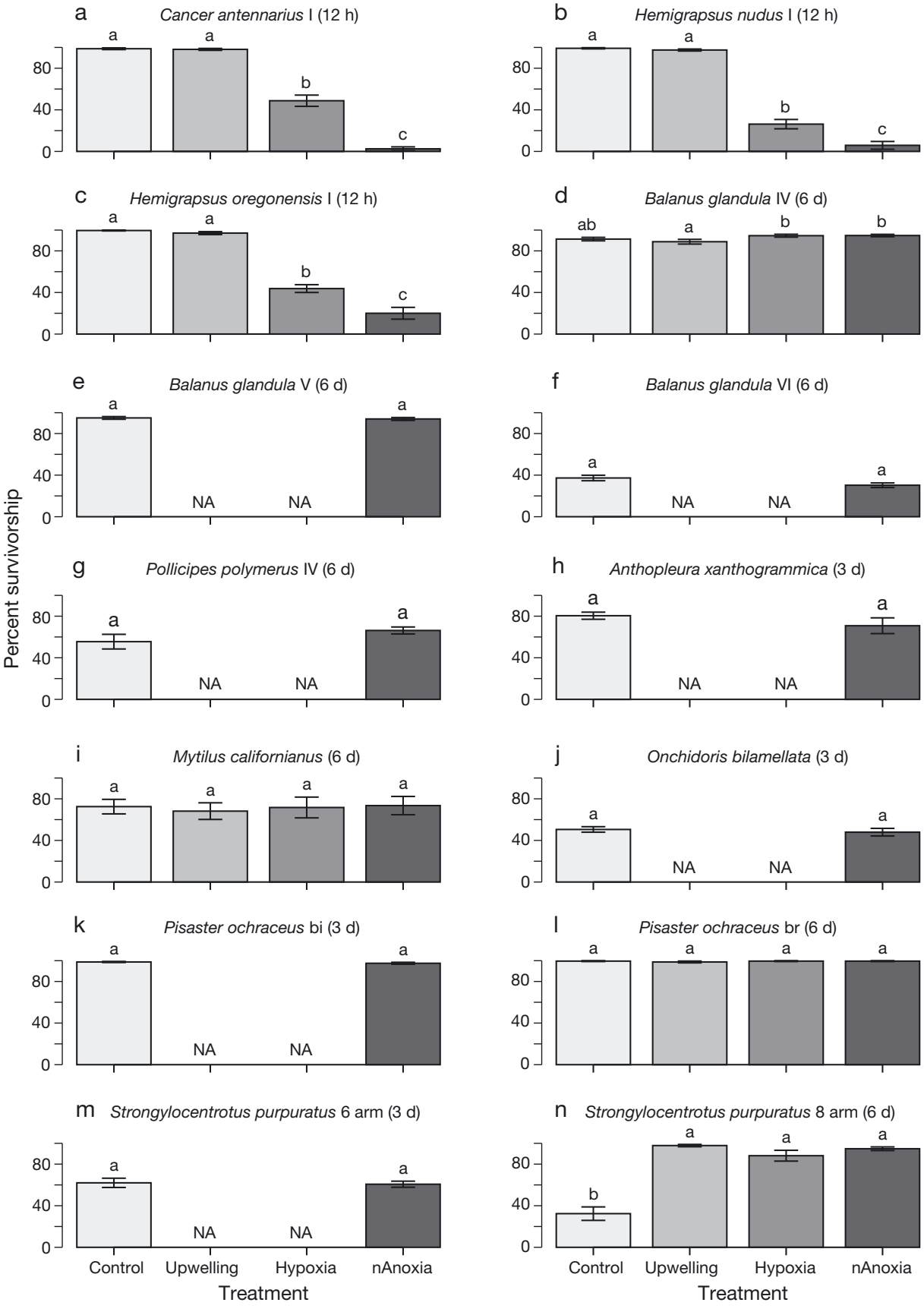
High tolerance following 3 d exposures to hypoxia

Following 3 d exposures, survivorship in control and near-anoxia treatments did not differ for planula larvae of *Anthopleura xanthogrammica* ($p = 0.436$), veliger larvae of *Onchidoris bilamellata* ($p = 0.543$), bipinnaria larvae of *Pisaster ochraceus* ($p = 0.299$), or the 6-arm pluteus larvae of *Strongylocentrotus purpuratus* ($p = 0.708$).

High tolerance following 6 d exposures to hypoxia

In 6 d exposure experiments, survivorship did not differ among any of the experimental treatments (control, upwelled water, hypoxia, near-anoxia) for pediveliger larvae of *Mytilus californianus* ($p = 0.355$) or the brachiolaria stage of *Pisaster ochraceus* ($p = 0.749$). Mean survivorship across treatments for both these species was high, at ~70% for *M. californianus* and >95% for *P. ochraceus*. In contrast, survivorship of stage IV nauplii of *Balanus glandula* ($p = 0.004$) and the 8-arm pluteus larvae of *Strongylocentrotus purpuratus* ($p < 0.0001$) differed among treatments; however, survivorship in near-anoxia and hypoxia treatments was not lower than in the control treatment. For *B. glandula*, the difference was due to lower survivorship in the upwelled water treatment (mean survivorship 89%) in contrast to control

Fig. 2. Percent survivorship of larval species and stages in each dissolved oxygen (DO) treatment: control (DO 5–7 ml l^{-1}), upwelled water (DO 1.8–3.6 ml l^{-1}), hypoxia (DO 0.5–1.4 ml l^{-1}) and near-anoxia (written 'nAnoxia' in figure, DO < 0.5 ml l^{-1}). Data were pooled across experiments for each species, larval stage, and treatment. The species are grouped by taxa in the following sequence: (a–g) arthropods, (h) cnidarian, (i,j) mollusks, and (k–n) echinoderms. Length of experimental exposure (6 d, 3 d, or 12 h) is indicated in parentheses beside species names. Treatments that were not tested are indicated by NA (not applicable). Significant differences ($p < 0.05$, Tukey's HSD) are indicated with letters above each bar. Error bars are shown as standard errors


a Cancer antennarius I (12 h)
b Hemigrapsus nudus I (12 h)
c Hemigrapsus oregonensis I (12 h)
d Balanus glandula IV (6 d)
e Balanus glandula V (6 d)
f Balanus glandula VI (6 d)
g Pollicipes polymerus IV (6 d)
h Anthopleura xanthogrammica (3 d)
i Mytilus californianus (6 d)
j Onchidoris bilamellata (3 d)
k Pisaster ochraceus bi (3 d)
l Pisaster ochraceus br (6 d)
m Strongylocentrotus purpuratus 6 arm (3 d)
n Strongylocentrotus purpuratus 8 arm (6 d)
Percent survivorship
NA
Control
Upwelling
Hypoxia
nAnoxia
Treatment

(91%), hypoxia (95%), and anoxia (95%). In *S. purpuratus*, the difference was due to higher survivorship in the upwelled water (98%), hypoxia (88%), and near-anoxia (95%) treatments, in contrast to the control (32%). This result occurred both times the experiment was conducted, but we do not know the causal mechanism for low control survivorship.

Given the high tolerance of stage IV *Balanus glandula* nauplii to 6 d exposures, in further experiments with larval stages V and VI of *B. glandula* and with stage IV nauplii of *Pollicipes polymerus* we tested only the most extreme low DO treatment (near-anoxia) along with the control. Survivorship did not differ between control and near-anoxia treatments following 6 d exposures for stage V nauplii of *B. glandula* ($p = 0.669$), for stage VI nauplii of *B. glandula* ($p = 0.067$), and for stage IV nauplii of *P. polymerus* ($p = 0.141$) (see Fig. 2). Survivorship for *B. glandula* was high (>90%) across control and near-anoxia treatments for stage V nauplii but lower (30–37%) for stage VI nauplii. For stage IV *P. polymerus* nauplii, mean survivorship values for the control and near-anoxia treatments were 55 and 66%, respectively.

DISCUSSION

Larvae as the most sensitive life stage

Our results supported our hypothesis of differential effects of hypoxia among species; however, we were surprised to find that the planktonic larval stages of most of these rocky intertidal invertebrates were tolerant of hypoxic and near-anoxic conditions. Prior laboratory studies indicate a wide range in median mortality times of larvae exposed to hypoxia and anoxia (e.g. Vaquer-Sunyer & Duarte 2008, Table 2). For example, under anoxic conditions, the median mortality time (LT_{50}) ranges from 1.3 h for blue crab *Callinectes sapidus* megalopae to 131 h in recently settled oyster *Crassostrea virginica* spat (Table 2). We expected to see a similar range in rocky intertidal invertebrate larvae, and also expected to see higher mortality following prolonged exposures to near-anoxia. Our finding of species tolerance to 6 d (144 h) low oxygen exposures is in the upper range of reported larval hypoxia tolerance (Table 2).

Table 2. Examples of published laboratory experiments investigating time to 50% mortality in bivalve, decapod, and polychaete larvae exposed to low dissolved oxygen (DO) concentrations. Ax: anoxia; Hx: hypoxia

Species	Stage	Habitat	DO (ml l^{-1})	Median mortality time (h)	Reference
Bay scallop *Argopecten irradians irradians*	Larvae with mean shell length 108 and 140 µm	Jiaozhou Bay, China	<0.05 (Ax)	<15	Wang & Zhang (1995)
Oysters *Crassostrea virginica*	Recently settled spat	Chesapeake Bay, USA	1.05 (Hx) <0.05 (Ax)	131 (Hx) 84 (Ax)	Baker & Mann (1992)
Oysters *Crassostrea virginica*	Settlers (pre-metamorphosis)	Chesapeake Bay, USA	<0.05 (Ax)	87 (Ax)	Baker & Mann (1994)
Oysters *Crassostrea virginica*	Prodissoconch pediveliger	Chesapeake Bay, USA	<0.05 (Ax)	11 (prodissoconch) 51 (pediveliger)	Widdows et al. (1989)
Blue crabs *Callinectes sapidus*	Megalopae	Newport River estuary, USA	1.05 (Hx) 0.5 (Hx) <0.05 (Ax)	12.3 (Hx) 4 (Hx) 1.3 (Ax)	Tankersley & Wieber (2000)
Ragworm *Hediste diversicolor*	Postlarvae	Wismar Bay, Germany	<0.05 (Ax)	14 (Ax)	Gamenick et al. (1996)
White shrimp *Metapenaeus monoceros*	Zoea mysis	Seto Inland Sea, Japan	1.05(Hx)	28 (zoea) 68 (mysis)	Kang & Matsuda (1994)
Mussels *Mytilus edulis*	Early prodissochonch, later veliconch	Whitsand Bay, UK	<0.05 (Ax)	15 (prodissoconch) 39 (veliconch)	Wang & Widdows (1991)

In their synthesis of hypoxia thresholds across benthic organisms, Vaquer-Sunyer & Duarte (2008) found that earlier life stages had lower survival rates than did later life stages. For example, Miller et al. (2002) reported that larvae were more sensitive than postlarvae or juvenile stages for 5 crustacean species from coastal and estuarine waters of Virginia, USA. In the white shrimp *Metapenaeus monoceros*, the LT_{50} of the zoeal stage was 28 h, whereas the later mysis stage had a LT_{50} of 68 h (Kang & Matsuda 1994). For the eastern oyster *Crassostrea virginica*, the LT_{50} of early prodissoconch larvae (shell length of 82 µm) was reported to be 11 h, whereas the later pediveliger larvae (shell length of 312 µm) and juveniles had a LT_{50} of 51 and 150 h, respectively (Widdows et al. 1989). For the bay scallop *Argopecten irradians irradians*, tolerance to anoxia increased as larvae grew and developed (Wang & Zhang 1995). Given these published results, our finding that the majority of larval species in our experiments were tolerant to 6 d (144 h) low oxygen exposures was unexpected.

Effect of hypoxia on larval invertebrates of open coast species

Most of the above-cited studies on tolerance of larvae to hypoxia were on estuarine or bay species. In coastal upwelling systems, where hypoxia arises from nutrient inputs and oxygen-poor waters brought by coastal upwelling, hypoxia studies have been generally field based and focused on benthic adults. In these systems, hypoxia can lead to a reduction in the biomass, density, and diversity of adult communities (Tarazona et al. 1988, Gutiérrez et al. 2000). As noted in the 'Introduction', however, few studies have investigated the impact of hypoxia on the larval stages of open coast species. Laudien et al. (2002) conducted one of the few laboratory investigations into the early life stage of an open coast species, the intertidal surf clam *Donax serra*, which lives in exposed sandy beaches of Namibia. This system is part of the Benguella upwelling system and experiences hypoxic conditions in nearshore areas (Laudien et al. 2002). They found the LT_{50} of post-settlement juvenile stages of *D. serra* to be 110 h under severe hypoxia (0.34 ml l^{-1}).

In our system, evidence for hypoxia impacts on benthic marine communities comes from remotely operated video surveys of demersal fish and benthic communities. These revealed a high mortality of fish and invertebrates during a hypoxic event in 2002 that lasted from July to September (Grantham et al. 2004). These survey observations, however, were of adult individuals, not larvae. Thus, our study supplements the current knowledge of hypoxia impacts on planktonic species of the CCLME and offers new insight by revealing that a larger-than-expected number of larvae species are tolerant to hypoxic conditions.

Adaptations of open coast species to hypoxia

In contrast to estuarine and semi-enclosed habitats, where larval hypoxic studies have generally been focused, the wave-exposed, intertidal zones of Oregon's coast are considered to be well oxygenated (Grantham et al. 2004, Chan et al. 2008). Prior to 2000, no severe hypoxia had been reported in the inner shelf (Chan et al. 2008). Thus, it seemed likely that organisms would be exposed to low oxygen infrequently and might lack adaptations to hypoxia; however, rocky intertidal adult invertebrates do experience emersion on a near-daily basis due to tidal fluctuations. During emersion, many intertidal organisms, including *Strongylocentrotus purpuratus* (Burnett et al. 2002), the intertidal porcelain crab *Petrolisthes eriomerus* (Stillman & Somero 1996), and intertidal acorn barnacles of the genus *Chthamalus* and *Semibalanus* (Davenport & Irwin 2003) experience a drop in the oxygen levels of their internal tissues. In brooding invertebrates, the embryos in large broods or egg masses can also experience drops in oxygen levels (e.g. intertidal barnacle *Balanus balanoides*; Crisp 1959).

Regular exposure to air at low tide may have led to adaptations to hypoxic conditions in open coast intertidal invertebrates. A survey of the literature reveals hypoxia tolerance in some intertidal adult animals within the same animal infraclass or class of species that we studied. The LT_{50} of adult barnacles, *Austromegabalanus psittacus*, can range between ~8 and ~4 d during emersion and anoxia (Lopez et al. 2003). For the intertidal barnacle *Jehlius cirratus*, LT_{50} values have been reported to range from 25 d under emersion hypoxic conditions to ~8 d under anoxic submersion (Castro et al. 2001). In the blue mussel *Mytilus galloprovincialis*, LT_{50} in anoxic conditions (<0.1 ml l^{-1}) was reported to be 5 d (Babarro et al. 2007), whereas another intertidal mussel, *Perna perna*, survived up to 30 d of anoxia (<0.05 ml l^{-1}) exposure (Hicks & McMahon 2005). Such tolerances to hypoxia and anoxia by these intertidal species may reflect adaptations to hypoxic conditions experienced during shell closure at the time of emersion.

Larval stages may also encounter seawater with lower DO levels during their dispersal stage, depending on their distribution in the water column. Larvae of some species, such as the bivalve *Mya arenaria*, have been reported to occur at high densities in deep nearshore waters (Shanks et al. 2003). Larvae of *Balanus glandula*, *B. crenatus*, and *Semibalanus cariosus* can be found as deep as 30 to 40 m in nearshore waters of the Oregon coast (Shanks & Shearman 2009), where oxygen levels can drop to 2–3 ml l^{-1} during the upwelling season (Grantham et al. 2004).

High sensitivity of crab larvae to hypoxia

In the present study, crab larvae were less tolerant of hypoxia than were other invertebrate larval taxa. This low tolerance is in agreement with published findings for crustaceans (Vaquer-Sunyer & Duarte 2008). Many larval crustaceans ranging from crabs to shrimp experience more than 50% mortality in less than 24 h under hypoxic (<1.4 ml l^{-1}) conditions (e.g. Vargo & Sastry 1977, Martinéz et al. 1998, Miller et al. 2002). This sensitivity may be related to the higher mobility of adult and larval crabs. In their review of hypoxia thresholds of fish and invertebrate species, Vaquer-Sunyer & Duarte (2008) found that fish and crustaceans had the lowest tolerance to reduced oxygen levels. They also found that the mobility of organisms accounted for variability in their oxygen tolerance thresholds. As mobile animals, crab larvae may depend to a greater degree on avoidance behaviors that reduce their exposure to hypoxic waters. The swimming speeds of crab larvae, which use muscular locomotion, are many times faster than those of larvae from other taxa, which use ciliary locomotion (Chia et al. 1984). For example, *Cancer magister* megalopae are reported to have swimming speeds up to 8.5 cm s^{-1} (Fernandez et al. 1994), whereas the swimming speeds of *Strongylocentrotus purpuratus* blastula are only approximately 0.045 cm s^{-1} (McDonald & Grünbaum 2010).

Sublethal effects and implications

An important next step in studying the impact of hypoxia on CCLME species would be an investigation of the sublethal effects of hypoxia/anoxia on larvae, which have been shown to lead to reduced larval settlement in *Crassostrea virginica* oysters (Baker & Mann 1992), reduced ingestion rates in *C. virginica* larvae (Baker & Mann 1994), delayed metamorphosis in *Callinectes sapidus* (blue crab) megalopae (Tankersley & Wieber 2000), reduced feeding and growth rates of *Mytilus edulis* mussel larvae (Wang & Widdows 1991), inhibited embryonic development, and altered swimming behavior and disintegration of the larval velum of the bay scallop *Argopecten irradians irradians* (Wang & Zhang 1995).

Survivorship of most of the species we tested was not affected by reduced oxygen, but we do not know how larval growth, development, metabolism, feeding behavior, or swimming behavior were affected. Negative impacts on these aspects of larval biology may increase the time period that larvae spend in the plankton and increase the chances of mortality due to predation and environmental stress (Pechenik 1999). Additionally, sublethal effects on planktonic larvae could eventually translate into reduced settlement, recruitment, and juvenile growth (Emlet & Sadro 2006, Giménez 2010).

The community context

Community-wide impacts of periodic hypoxic events include lower community biomass and species richness (e.g. Dauer 1993, Nilsson & Rosenberg 1994). Our results indicate that impacts on rocky intertidal communities may occur through plankton mortality events that differentially affect recruitment of various species (Pechenik 1999, Navarrete et al. 2005). With the exception of *Pollicipes polymerus*, all of the species in the present study have a planktonic larval phase during the upwelling season when the nearshore hypoxic events of the CCLME occur. These hypoxic events, which may last days to months (Grantham et al. 2004, Chan et al. 2008), have a high probability of overlapping with planktonic larval periods of these species, which often last weeks to months (Strathmann 1987), thus exposing all species to hypoxia.

Crabs are much less likely than other intertidal invertebrate species to survive prolonged anoxia. This could result in proportionally fewer crabs recruiting to adult communities than for other species. Fewer crab recruits may be of concern because of their many roles in benthic and intertidal community interactions. Crabs interact directly and indirectly with other crab species; for instance, juvenile *Hemigrapsus oregonensis* are a dominant competitor for refuge space with the commercially important *Cancer magister* (Visser et al. 2004). Crabs are also

important intertidal predators on species such as mussels and snails (Ellis et al. 2007, Shinen et al. 2009), and *C. antennarius* commonly prey on the dominant space occupier of the rocky intertidal, *Mytilus californianus*, as well as another common mussel species, *M. trossulus* (Shinen et al. 2009). Thus, hypoxic events in the CCLME may have a differential top-down impact on intertidal communities by removing the larval stages of predators while not removing the larvae of prey species.

Conclusions and implications of climate change

This investigation makes 4 contributions to our understanding of the likely ecological impacts of hypoxia. First, we provide novel insights into how the planktonic larval stage of open coast intertidal species in the CCLME may be affected by the recent onset of hypoxic events. Our experiments provide valuable understanding of the possible effects of hypoxia and near-anoxia on larval survivorship. Second, our research expands the limited knowledge of tolerance of open-coast larvae to hypoxia. Most hypoxia studies focus on the impacts of hypoxia on adults. Of the existing larval studies, most focus on species of estuarine and bay systems. Third, in contrast to the widely held view that earlier life stages are more sensitive to hypoxia than are later life stages, our findings suggest that the larval stages of several CCLME species are highly tolerant of hypoxic and near-anoxic conditions over periods of 6 d of exposure. Finally, our multispecies study provides insights into the possible community-wide impacts of hypoxia. Differential mortality of crabs suggests that intertidal communities may experience the effects of hypoxia through top-down effects. Less crab recruitment might result in lower crab abundances and less predation (Ellis et al. 2007, Rilov & Schiel 2011).

As the reported cases of coastal hypoxia continue to rise and with climate change scenarios predicting an increased likelihood of hypoxic events due to water stratification (Díaz & Rosenberg 2008) and more intensive upwelling in coastal ocean upwelling systems (Bakun et al. 2010), understanding how component species respond to hypoxic events might be important in predicting how coastal communities will change with global warming. This study contributes toward developing this understanding by providing novel insights into the impacts of hypoxia on the larval stages of a suite of species that play key roles in the rocky intertidal communities of the Pacific Northwest.

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