# Competition in benthic marine invertebrates: the unrecognized role of exploitative competition for oxygen

Nick Ferguson,[1] Craig R. White,[1] and Dustin J. Marshall[1,2,3]

[1]*School of Biological Sciences, The University of Queensland, 4079, Brisbane, Australia*
[2]*School of Biological Sciences, Monash University, 3800, Clayton, Australia*

*Abstract.* Competition is a ubiquitous structuring force across systems, but different fields emphasize the role of different types of competition. In benthic marine environments, where some of the classic examples of competition were described, there is a strong emphasis on interference competition: marine invertebrates are assumed to compete fiercely for the limiting resource of space. Much of our understanding of the dynamics of this system is based on this assumption, yet empirical studies often find that increases in density can reduce performance despite free space being available. Furthermore, the assumption that space is the exclusively limiting resource raises paradoxes regarding species coexistence in this system. Here, we measure the availability of oxygen in the field and in the laboratory, as well as the tolerance of resident species to low-oxygen conditions. We show that oxygen can be the primary limiting resource in some instances, and that exploitative competition for this resource is very likely among benthic marine invertebrates. Furthermore, growth form (and the associated risk of oxygen limitation) covaries with the ability to withstand oxygen-poor conditions across a wide range of taxa. Oxygen availability at very small scales may influence the distribution and abundance of sessile marine invertebrates more than is currently appreciated. Furthermore, competition for multiple resources (space and oxygen) and trade-offs in competitive ability for each may promote coexistence in this system.

Key words: *coexistence; interference competition; R\*; resource limitation theory.*

## Introduction

The relative abilities of species to exploit shared resources determine the structure of communities and species coexistence (Tilman 1982). Two types of competition among species are generally observed: interference competition occurs when an organism directly affects other organisms; exploitative competition occurs when an organism indirectly affects other organisms by reducing the resources available to them. The type of competition that dominates any one system will determine its dynamics, and processes such as invasibility and succession (Tilman 2004). Different fields place different emphases on these two types of competition. While exploitative competition is considered particularly common and strong in terrestrial plant communities, it has long been assumed to be less important in marine invertebrate communities (Schoener 1983).

The study of competition in benthic marine systems has been central to our understanding of competition more generally; indeed, some of the earliest and most influential demonstrations of competition come from studies of sessile marine invertebrates (Connell 1961, Sutherland 1974, Buss 1979, Russ 1982, Keough 1984*a*).

Today, more general insights about competition and community dynamics continue to stem from work in this system (Stachowicz et al. 2007, 2008, Clark and Johnston 2011). Studies of competition in marine invertebrates tend to place a strong emphasis on the role of interference competition over exploitative competition: species are thought to compete fiercely for the available space, and will overgrow or undercut each other to secure further space (Buss 1979). On the rare occasions that exploitative competition is considered in benthic marine systems, space again is thought to be the primary resource. For example, considerations of "preemptive" competition (sensu Schoener 1983) whereby a species secures a site and is able to persist despite the presence of other species can be considered a form of exploitative competition for space (Rubin 1985). It has become a paradigm in marine ecology textbooks that the primary limiting resource for sessile marine invertebrates is space (e.g., Witman and Dayton 2001), and many studies make this assumption explicitly when designing and interpreting studies of competition (Jackson 1977, Russ 1982, Marshall and Keough 2009, Clark and Johnston 2011). Furthermore, evolutionary considerations of marine life-histories assume that interference competition for space is a major factor in the evolution of coloniality (McKinney and Jackson 1991).

The emphasis on interference competition for space in benthic marine communities has created a significant

divide between terrestrial ecologists and marine ecologists in how competition is viewed and studied (Hart and Marshall 2012). For example, R* is emphasized in plant communities but has received little attention in marine communities (but see Byers 2000 for an example of exploitative competition in grazing snails). R* is defined as the minimum amount of a resource that an organism needs to maintain a stable population (Tilman 1982). When a system is at equilibrium, dominance is determined by those species that have the lowest R* (Tilman 2004, Fargione and Tilman 2006). In contrast, in marine systems, overgrowth ability is often measured as the primary determinant of competitive dominance while ability to survive at low resource levels has been largely ignored (Buss 1979, Russ 1982, Barnes 2003, Dunstan and Johnson 2005). These differences in underlying theory have also led to differences in the way marine systems are managed and exploited relative to terrestrial systems (Hart and Marshall 2012). For example, if interference competition is dominant, then invasions will occur because species are able to effectively seize resources from established individuals, but if exploitative competition is dominant, invasion occurs because invaders are able to more efficiently use resources in short supply (Persson 1985). Thus, the impact and mode invasion will differ dramatically depending on which type of competition is most influential in a particular system.

Despite the strong emphasis on interference competition for sessile marine communities, there is evidence to suggest that exploitative competition for resources other than space plays a role in this system. Flow regimes have repeatedly been implicated as important factors in determining the distribution and abundance of benthic invertebrates at a range of scales, suggesting that the delivery rate of water-borne resources may be important (Kim and Lasker 1997, Palardy and Witman 2011). Noncontact competition (i.e., a negative interaction in the absence of overgrowth) has been demonstrated in a number of studies (e.g., Dalby 1995, Allen et al. 2008), and in other studies, space does not appear to be the primary limiting resource, leading to surprising outcomes of experimental manipulations (Clark and Johnston 2011). When exploitative competition for resources other than space is considered at all in sessile marine invertebrate communities, it is food that is assumed to be the resource under competition. Generally however, competition for food is thought to be less important than competition for space and these two resources are thought to covary strongly (Buss 1979, Buss and Jackson 1981, Lohse 2002). Resource limitation theory predicts that for any community, the resource in shortest supply is the most important determinant of community dynamics (Loreau 2010). Food availability is therefore rarely considered in discussions of species coexistence in benthic marine communities, because of its assumed secondary importance to space. Interestingly, the crucial resource of

oxygen is sometimes an important factor that determines the distribution of marine communities at larger spatial scales (Theede et al. 1969, Verberk et al. 2011) and like food, will be affected by flow, but oxygen has rarely been considered as resource for which sessile marine invertebrates compete at small scales.

If oxygen rather than space is limiting in sessile marine invertebrate communities, then our view of competition in this system needs to change. Most considerations of competition and coexistence among marine invertebrates focus on the single limiting resource of space, and stable coexistence is assumed to occur because of a trade-off between competitive ability for space and ability to colonize new habitats (Keough 1984b, Edwards and Stachowicz 2010). Consideration of a second potentially limiting resource (oxygen) could complicate our view of competition in this system, but will also provide a broader parameter space for species coexistence and resolve some long-standing paradoxes about species coexistence (Tilman 1982, Loreau 2010). For example, how can two species with different abilities to compete for space, but similar fecundities and dispersal abilities, coexist in this system? When two resources are limiting, two apparently similar species can coexist if each is a better competitor for a different resource. Thus a species may be a poorer competitor for space and an equivalent colonizer but still persist because it can tolerate lower oxygen conditions. Multi-resource competition is thought to be common in terrestrial and freshwater systems, and may be an important maintainer of coexistence (Loreau 2010), but is rarely considered in benthic marine systems. More generally, oxygen availability and hypoxic events are increasingly recognized as important factors in determining benthic dynamics (Altieri 2006, 2008), but the degree to which individuals compete for oxygen is less well explored.

There are good reasons for suspecting that oxygen may be a resource for which sessile marine invertebrates compete. Because of its salinity, seawater dissolves less oxygen than freshwater, and so oxygen directly adjacent to a respiring organism can be depleted very quickly (Hill et al. 2005). The low-flow conditions typical of many subtidal habitats, together with high topographical complexity of sessile communities may combine to create a significant boundary layer as well as "skimming flow" (sensu Vogel 1996), in which oxygen replenishment is limited, creating a low-oxygen microenvironment. Given that benthic marine communities can be very dense, oxygen demands within these communities could outstrip supply. The few studies that have examined oxygen use in marine invertebrates have found that the microenvironment adjacent to the organism can be depleted to remarkably low levels (Gardella and Edmunds 1999, Osinga et al. 1999, Dodds et al. 2007), but it is unclear whether these levels are limiting and subject to competition. Similarly, numerous studies have demonstrated that photosynthetic corals

can generate too much oxygen adjacent to colonies, suggesting that gas exchange within the benthic boundary layer is highly limited (Finelli et al. 2007, Lenihan et al. 2008). Determining whether oxygen levels are limiting requires estimates of the tolerance of resident species to reduced oxygen levels: if oxygen levels fall below tolerance, then oxygen can be considered limiting. There are, however, few estimates of the ability to withstand reduced oxygen levels in marine invertebrates (Frederich and Portner 2000, Lannig et al. 2008; but see Dodds et al. 2007) and only one has linked this ability to competition for oxygen (Altieri 2006). Thus, two things are required in order to understand the role of oxygen in sessile marine communities: first, accurate measures of oxygen levels at relevant (small) spatial scales and second, estimates of the ability to withstand reduced oxygen.

The most common estimate of tolerance to low oxygen is the critical partial pressure of oxygen for aerobic metabolism ($P_c$), which represents the lowest level of oxygen at which aerobic metabolism is independent of the ambient partial pressure of oxygen ($PO_2$; Hochachka and Somero 2002). At levels of $PO_2$ below $P_c$, metabolism cannot be supported by aerobic processes entirely and metabolic rate decreases; anaerobic processes that are relatively inefficient and produce potentially toxic end-products become increasingly important (Hochachka and Somero 2002). The importance of $P_c$ is exemplified by studies of mobile species that show behavioral avoidance of oxygen levels below their $P_c$ (Burleson et al. 2001). Behavioral avoidance is less available to sedentary species (though some can temporarily avoid short-term hypoxia by ceasing to filter water), but we know little about the availability of oxygen for sessile marine invertebrates.

Here we measure oxygen availability at the appropriate scale in benthic marine invertebrate assemblages in both the laboratory and the field, and then examine the physiological tolerances of 15 species from five phyla to determine whether the availability of oxygen is a limiting resource for which they compete. We first measured oxygen availability in the laboratory on artificial settlement plates that bore six-week-old, field-developed assemblages. We then measured the availability of oxygen on six week-old plates in situ in the field, and the availability of oxygen in well-established assemblages growing directly on artificial structures. Finally, we measured how much individual species reduce the availability of oxygen in their immediate surrounding area.

## MATERIALS AND METHODS

### Study site and organisms

All oxygen measurements and species collections were done at Manly Boat Harbour, Brisbane, Australia (27°27.6′ S, 153°11.2′ E) between April 2010 and November 2011. The harbor (approximately 600 m by 800 m; average depth is 4 m) is sheltered by a breakwater, and floating pontoons extend throughout the site. We used an AC10000 handheld digital flow meter and AC10002 30-mm vane wheel flow probe (Loligo Systems, Tjele, Denmark) to measure water flows at our site. In the most exposed part of the marina adjacent to the main channel, flow rates averaged 20 cm/s both 1 cm and 1 m below the surface. In more sheltered areas between marina pontoons (where we conducted our experiments and where our study organisms occur), no flow was detectable using our equipment (published minimum detection limits for this system are 2 cm/s). Multiple dye release observations at our site indicated that flow rates rarely exceed 5 cm/s adjacent to the fouling assemblage. The fouling assemblage is typical of most harbors around the world with a suite of cosmopolitan invaders that are common throughout the year.

We examined the respiration characteristics of 15 species across five phyla. These were two arborescent bryozoans (*Bugula neritina* and *B. stolonifera*), three encrusting bryozoans (*Hippopodina indicia*, *Schizoporella* sp., and *Watersipora subtorquata*), two tube-dwelling polychaetes, the serpulid *Hydroides diramphus* and the spirorbid *Janua pagenstecheri*, a barnacle *Balanus amphitrite*, two sponges (*Sycon* sp. and *Porania* sp.), a solitary ascidian *Styela plicata*, and four colonial ascidians (*Botrylloides* sp., *Diplosoma listerianum*, *Didemnum* sp., and *Botryllus* sp.).

### Generating communities and collecting individuals

To measure oxygen availability within communities, we first needed to generate communities on a substratum that was amenable to measurement. We therefore deployed settlement plates into the field face down to accumulate a fouling community. We used standard methods that resulted in a representative community after six weeks in the field (Marshall and Keough 2009). These plates were then used in our estimation of oxygen availability in the laboratory and in the field. Across all of our plates, unoccupied space varied between 20% and 70% such that the plates were never fully saturated with organisms. Initially, we had hypothesized that the availability of free space and the availability of oxygen adjacent to a settlement plate would be correlated but pilot studies showed that oxygen availability varied at much smaller scales such that there was no correlation at the scale of settlement plates (see *Results*).

To collect individuals in order to measure oxygen consumption rates and $P_c$, we also deployed pre-roughened acetate sheets to collect settlers for between four and six weeks as per standard methods (Hart and Marshall 2009). We then identified our target species, returned the sheets to the laboratory and removed the focal species (with a small piece of acetate attached) from the rest of the sheet.

### Measuring oxygen availability: general approach

We used three approaches to estimate the availability of oxygen within our marine invertebrate assemblages.

First, we measured the availability of oxygen on artificial settlement plates in the laboratory under conditions of flow that represented the upper range of flows observed in the field (2 cm/s). The plates had been placed in the field for approximately six weeks such that an average of ~50% of the available space was occupied by sessile marine invertebrates. Using this approach, we were able to use fiber-optic oxygen sensors to sample oxygen availability within the community at a very fine scale ($<1$ mm$^2$), and were able to sample intensively within and among settlement plates in order to determine the scales at which oxygen availability varied. We then measured oxygen availability under field conditions on artificial plates that again had accumulated a community for approximately six weeks and haphazardly on artificial structures (pontoons and pilings) that had very established communities. In the field, on both substrates (plates and pontoons), we used equipment that were more robust to field conditions, but had less spatial resolution ($<1$ cm$^2$).

All of our field measures of oxygen availability were collected during the day and all of our flume measures were conducted in ambient light such that photosynthesis may increased oxygen availability. We focused daytime measures because we wanted a conservative measure of oxygen availability rather than collecting measurements when oxygen availability was likely to be at its lowest (at night in the absence of photosynthesis). We took care to leave out probes in situ for extended periods during each measurement so as to capture any variation in oxygen availability that may have been associated with variation in the activity patterns of our focal species.

### Measuring oxygen availability in the laboratory

To create conditions of flow in the laboratory, we used a small flume (300 × 150 × 100 mm, with the settlement plate placed face-up at the midway point along the flume. Water was drawn from 20-L aerated tank recirculated, and maintained at a constant flow rate of 2 cm/s with a Thermaltake P500 pump (PC Case Gear, Melbourne, Australia). To measure oxygen at fine scales we used a fiber-optic oxygen microsensor housed inside a glass Pasteur pipette and mounted to a micromanipulator. The probe was connected to a Microx TX3 Microsensor Oxygen Meter (Presens, Precision Sensing GmbH, Regensburg, Germany), which was interfaced with a computer running OxyView-TX3 V5.31 (Presens). These sensors were selected over the more commonly used oxygen microelectrodes because they do not consume oxygen, and for their improved accuracy and prior use in aquatic systems (Klimant et al. 1995, Gatti et al. 2002). The oxygen sensors measured oxygen saturation at a frequency of 1 Hz. The sensors were calibrated using air-saturated seawater (100% saturation) and seawater containing 2% sodium sulfite (0% saturation). Small areas of bare space that were surrounded by organisms were sampled haphazardly,

and care was taken to lower the probe to a distance of $<4$ mm from the surface as pilot studies indicated that above this putative boundary layer, oxygen levels were more variable. We chose $<4$ mm because the majority organisms in our system do not protrude more than 4 mm above the substrate, particularly immediately after settlement, and so oxygen conditions in this region are those that are most likely to be experienced by newly settled organisms. Up to five samples were taken for each of 46 settlement plates.

### Measuring oxygen availability in the field

The oxygen saturation of water to which communities were exposed in the field was measured using a fiber-optic oxygen sensor probe (FOXY-R; Ocean Optics, Dunedin, Florida, USA) connected to a temperature-compensated O$_2$ meter (TauTheta MFPF-100–2; Ocean Optics), which was interfaced with computer running OOISensors and Tau Theta software (Ocean Optics). The FOXY-R probe consists of a 1-mm optic fiber housed in a 152.4 mm long, 1.587 mm outer diameter, stainless steel ferrule with a beveled tip. Measurements were made either by mounting the probe to the back of a settlement plate and inserting it through a predrilled hole in the center of the plate, or by manually placing the probe at haphazardly selected positions within established assemblages on artificial structures. After placement, the probe was left in situ until oxygen readings had stabilized ($\sim$5–10 minutes after placing the probe) so that the influence of any disturbance on the surrounding community had subsided and equilibrium levels of oxygen had been reestablished. For each measure, after a period of stable measures, we then manually generated high water flow in the vicinity of the probe to check that it had not been inadvertently buried in sediment or covered, before allowing the reading to stabilize again. The sensors were calibrated using air-saturated seawater (100% saturation) and either seawater containing 2% sodium sulfite (0% saturation) or N$_2$-equilibrated seawater (0% saturation).

### Critical partial pressure of oxygen and $V$O$_2$

To measure the rate of oxygen consumption ($V$O$_2$, mL/s) and critical partial pressure of oxygen ($P_c$) of each of our species, we used closed-system respirometry (Köster et al. 2008). Our study organisms were first cut out of the acetate sheets collected from the field and placed in 5-mL vials, with filtered seawater, while the dissolved oxygen in the vial was measured for up to 24 h on 48 channels simultaneously using a SensorDish Reader (Presens) in constant darkness. Our observations of oxygen depletion over extended periods indicated that oxygen consumption rates were relatively constant (above $P_c$) suggesting that activity levels did not vary substantially over time. Each run of 48 vials included four vials that contained acetate with no organisms attached to act as controls for background rates of oxygen consumption. The oxygen reader was situated on
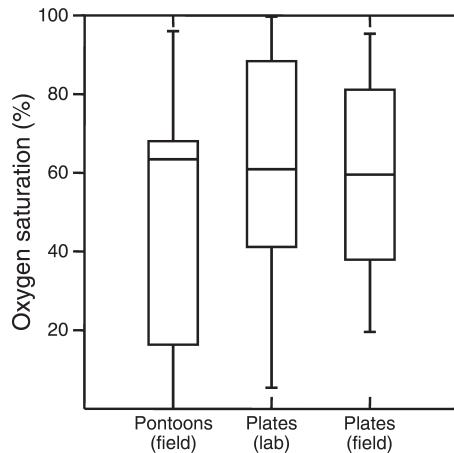
FIG. 1. Distribution of oxygen availability across three different marine environments. Box plots show the mean and distribution of oxygen availability in the laboratory, in the field on pontoons, and in the field on settlement plates. Boxes represent data within one standard deviation of the mean; whiskers represent data beyond one standard deviation of the mean.

an orbital shaker (Ratek OM1; Ratek Instruments, Boronia, Australia) in an incubator (SEM RI90-DOP; ProSciTech, Thuringowa, Australia) to allow for agitation of the seawater in the vials and to maintain a stable temperature (25°C ± 1°C). Seawater was previously filtered, aerated, and placed in the same incubator as the SDR at least 24 hours before use to allow it to reach the same temperature. Rate of oxygen consumption ($VO_2$, mL/s) was calculated from the slope of the line relating oxygen saturation and time for the vials containing organisms ($m_o$, %/s), the equivalent slope for the control vials ($m_c$), the oxygen capacitance of air-saturated seawater ($\beta O_2$, 4.88 mL/L; Cameron 1986), and the volume of the vial, minus that taken up by the organism and acetate ($V$, L) following Alton et al. (2007):

$$VO_2 = [(m_o - m_c)/100] \times V \times \beta O_2$$

$P_c$ was then determined as the lowest $PO_2$ at which $VO_2$ was independent of $PO_2$ (Hill et al. 2005, White and Seymour 2011). The wet mass of each organism was determined by first weighing the organism on the acetate, to the nearest milligram (Sartorius A 200 S; Sartorius, Göttingen, Germany), and then subtracting the mass of the acetate alone. Rate of oxygen consumption was divided by mass to determine mass-specific $VO_2$.

### Species-specific oxygen reductions in the laboratory

$R^*$ theory predicts that those species that have the lowest $R^*$ also deplete resources to the greatest degree (Loreau 2010). To test this prediction, we measured how much individual species reduced the availability of oxygen in their immediate area. We used the same equipment and methods as described above for measuring oxygen availability in the laboratory but rather than

targeting bare space among different species, instead we sampled within 1 mm of our target species, directly above it or adjacent to it. Individuals of the target species were sampled haphazardly and we recorded the level of oxygen once it had stabilized and remained constant for >5 s.

### Data analyses

Our target species varied substantially in their growth form (some species grow only along the surface [e.g., encrusting bryozoans such as *Hippopodina* and *Watersipora*] though in California, *Watersipora* tends to show a more foliose growth form; J. J. Stachowicz, *personal communication*), while others have an erect growth form where they grow outward from the substratum (e.g., *Bugula*). We hypothesized that species that have flatter growth forms are likely to be more tolerant of low oxygen conditions than species with more erect growth forms. To test this hypothesis, we allocated species to two categories (flat and erect), according to their growth form. The appendix shows the list of species and their classification in growth form. While some species obviously fit into one category, others had more intermediate form or had the potential for change. For example, species such *Hydroides diramphus* initially grow along the substrate but can occasionally grow out into the water column. We classified these species with an intermediate growth form according to their relative height from the substratum, those that grew >5 mm away from the substratum within a few weeks of settlement were classed as erect, those that typically were less than 5 mm were classed as flat. Importantly, the inclusion or exclusion of the species with an intermediate growth from did not affect the qualitative outcomes of our analyses (*unpublished analyses*). All analyses were done in Systat version 12 (Systat, Cranes Software International, Bangalore, India).

### RESULTS

### Oxygen availability among environments

The availability of oxygen within the microenvironment was highly variable both within assemblages measured in the laboratory and in the field, and ranged between 100% and 0% of air-saturated seawater (Fig. 1). The coefficient of variation in oxygen saturation varied between 0.4 (field plates) and 0.614 (field pontoons) but neither the mean nor the variance were significantly different among environments (mean $F_{2, 130} = 2.848$, $P = 0.062$; variance $F$ test, $P = 0.581$). There was a trend for the highest levels of oxygen being available on field plates where species cover tended to be lightest. In the laboratory under conditions of flow, there was marginally significant variation in oxygen availability among different settlement plates ($F_{41, 37} = 1.78$, $P = 0.049$), but there was also substantial variation within plates (average CV within plates, 0.3).

The mean oxygen availability was similar among the different environments that we examined, but the lowest

TABLE 1. ANOVA for effect of species identity and growth form on (a) critical partial pressure of oxygen for aerobic metabolism ($P_c$); (b) in situ $O_2$ depletion surrounding each species; and (c) mass-specific respiration rate ($VO_2$) for several species of marine invertebrates.

| Source | df | MS | F | P |
|---|---|---|---|---|
| a) Critical $PO_2$ | | | | |
| Growth form | 1 | 1999 | 8.60 | 0.013 |
| Experimental run | 8 | 1103 | 4.82 | <0.001 |
| Species(growth form) | 12 | 232 | 1.01 | 0.434 |
| Error | 331 | 228 | | |
| b) Local $O_2$ depletion | | | | |
| Growth form | 1 | 9308 | 8.23 | 0.017 |
| Species(growth form) | 10 | 1130 | 1.19 | 0.300 |
| Error | 138 | 947 | | |
| c) $VO_2$ | | | | |
| Growth form | 1 | 0.008 | 1.276 | 0.281 |
| Species(growth form) | 12 | 0.006 | 0.99 | 0.457 |
| Error | 340 | 0.006 | | |

*Note:* Models are reduced after testing for nonsignificant interactions between fixed and random factors.

oxygen levels were more commonly encountered in the field pontoon environment; this was also the most heavily occupied environment with only ~20% bare space available. Around 20% of the microsites surveyed on the pontoon habitat had oxygen levels of less than 10% of saturation, while less than 5% of microsites on field plates had oxygen levels less than 10% of saturation. In the laboratory, around 20% of microsites had oxygen level of less than 20%.

## Variation in $P_c$ and $VO_2$ among species and growth forms

The average $P_c$ across all species was 18.74% of air-saturated seawater. There was a strong association between growth form and $P_c$: species with a flat growth form had ~45% lower $P_c$ than species with an erect growth form (Table 1, Fig. 2). Within growth forms, there was no significant variation in $P_c$ among species (Table 1), though this lack of a species level effect appears to be driven by substantial variation within
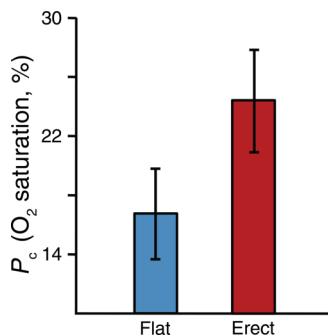


FIG. 2. Effect of growth form on critical partial pressure of oxygen ($P_c$) for benthic marine invertebrates. Bars represent mean (±SE) $P_c$ for species with a flat growth form (shown in blue) and for those with an erect growth form (shown in red).
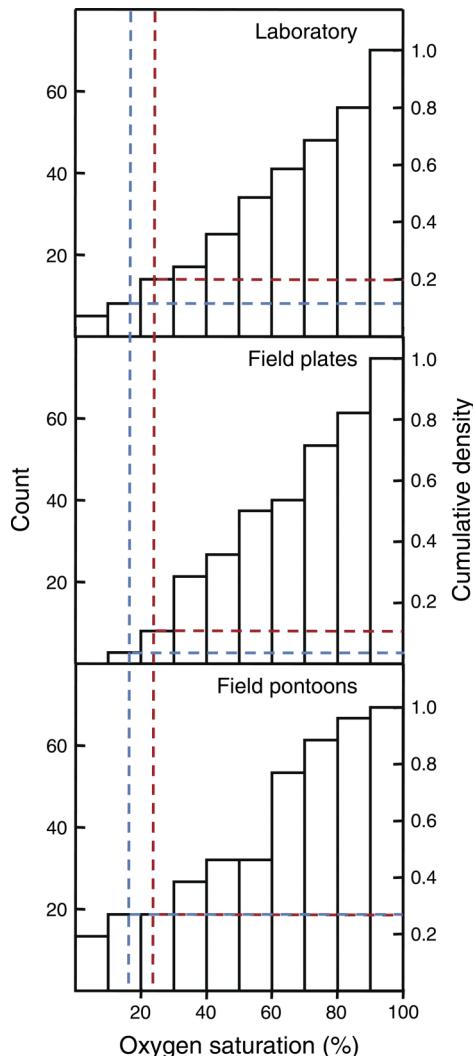


FIG. 3. Distribution of oxygen availability across three different marine environments. Histograms show cumulative density plots of oxygen availability in each environment. The vertical blue dashed line and the red dashed line indicate the mean $P_c$ of species with a flat growth form and species with an erect growth form, respectively. The horizontal lines correspond to the percentage of microsites that are uninhabitable due to oxygen limitation for each growth form in each environment.

species reducing our power to detect such an effect (within-species coefficients of variation exceeded 0.6 for all species). Based on our measurements of oxygen availability in the field and the laboratory, around 25% of the total area on pontoons in the field, 15% of the area on our settlement plates in the laboratory and 5% of our sites on our field plates have insufficient oxygen to support species of either growth form and these percentages are even greater for species with an erect grow form (Fig. 3).

We detected no significant difference in the mass-specific respiration rates between growth forms (Table 1). While flat species tended to have lower respiration

rates, species-level variation in respiration rates was much higher. The species with the greatest mass-specific respiration rates, *Hydroides diramphus*, had a respiration rate more than six times greater than that of the species with the lowest respiration rate, an orange sponge; both were classified as flat growth forms.

### Variation in local oxygen depletion among species and growth forms

In the laboratory, under conditions of flow, species with a flat growth form depleted the local oxygen to a greater degree (20%) than species with an erect growth (Table 1). Again, within growth forms, we detected no significant variation among species in the degree to which they depleted oxygen but again, variation within species was substantial (average within-species coefficient of variation, 0.45).

### DISCUSSION

Our results suggest that oxygen, rather than space, has the potential to be the primary limiting resource in sessile marine invertebrate communities. We measured oxygen availability under field conditions as well as in the laboratory, and found that oxygen levels were sometimes so low as to preclude the persistence of some species despite free space being available. Traditionally, it would be assumed that a benthic marine community with free space available is not saturated and that recruitment limitation or a recent disturbance is responsible for an area remaining unoccupied. Our results suggest that in some instances, bare space may persist because oxygen levels in the immediate area will not support sessile macroinvertebrates.

The thickness of the boundary layer and therefore water flow is likely to be a strong determinant of oxygen limitation in our system. We measured oxygen availability in a manmade harbor; an environment where water flow is minimized and oxygen limitation is therefore most likely. Much of the work on competitive interactions in marine environments comes from sites like ours (Sutherland 1974, Edwards and Stachowicz 2010, Clark and Johnston 2011), and we suspect that competition for oxygen has played an unrecognized role in this habitat particularly. Our estimates of flow were similar to several other estuarine environments (Altieri and Witman 2006, Rittschof et al. 2007) suggesting oxygen competition is likely in these areas also. Oxygen competition is probably not restricted to highly modified habitats however, and we predict that it is more common than is currently appreciated. For example, there are indications that oxygen is limited in corals (at night) and among sponges (Osinga et al. 1999, Dodds et al. 2007), raising the potential for oxygen competition. Furthermore, rocky subtidal habitats can have flow rates similar to those measured in our study (Mendola et al. 2008). Conversely, it seems unlikely that water flows in exposed habitats such as rocky intertidal reefs will ever be so low as to result in oxygen limitation and

therefore competition for oxygen is unlikely. Nevertheless, calm conditions could occasionally result in oxygen limitation and competition; local depletion of dissolved carbon dioxide by intertidal macroalgae occurs in rock pools at low tide under calm conditions (Pearson et al. 1998), and analogous depletions of oxygen might be likely for intertidal animals. Overall, we suggest that future studies estimate oxygen availability at the scales that are most relevant to organisms: the conditions immediately adjacent to them. Interestingly, our results came from day time measures of oxygen availability; at night we would expect ambient levels to be lower due to a lack of photosynthesis and as such, our measures are probably a conservative estimate of oxygen limitation in our habitat. An important next step will be to measure oxygen availability at night.

Our results suggest that we may need to change the way we view and study competition in sessile marine communities on manmade structures at least. We found that growth form was strongly related to $P_c$; those species with a flat growth form had much lower $P_c$ than species with an erect growth form. Such differences might be expected given the conditions that each growth form is likely to experience: flat species will often be well within the oxygen-depleted boundary layer while the erect species (at least once they have achieved sufficient size) will often project out of the boundary layer and into the more oxygen-rich water. Interestingly, species with an erect growth form tend to have lower space requirements (Hart and Marshall 2012): they grow out from the substratum and can achieve a much higher biomass for a given amount of space. It appears therefore that there is a species-level trade-off in competitive ability in for these two important resources: erect species can survive with less space availability, while flat species can survive at lower levels of oxygen.

Traditionally, coexistence in benthic marine invertebrates has thought to be maintained via species-level trade-offs in their ability colonize vs. their ability to compete via interference competition (Jackson 1977). Indeed, many considerations of benthic marine invertebrate competition focus strongly on whether a species is able to overgrow another; if such overgrowth is possible, then that species is considered a superior competitor (Barnes 2003, Dunstan and Johnson 2005). The coexistence of species with very similar colonization abilities, but very different (interference) competitive abilities have therefore been difficult to reconcile with traditional theory in this system. The differential use of oxygen and space could explain why some species with seemingly similar colonization abilities can coexist despite substantial differences in their ability to compete for space. Because different growth forms have different $R^*$ for space and oxygen, coexistence between these two forms should be promoted in the absence of any differences in colonization ability (Tilman 1982). Based on our estimates of $P_c$, many flat species will not be limited by oxygen availability (despite encountering low

oxygen environments more often), but will be limited by space whereas erect species in our study will be limited more by oxygen availability than space (particularly as new settlers). Thus, we suggest that new insights may be gained by viewing marine sessile communities in an $R^*$ framework.

The ability of species to deplete oxygen from the adjacent area was related to growth form and $P_c$, and this finding fits well with an $R^*$ view of competition in this system (Tilman 1982). Flat species not only were able to tolerate lower levels of oxygen, they also reduced oxygen to a lower level immediately surrounding them relative to erect species. Covariance between resource depletion and $R^*$ is predicted by theory but not often demonstrated (Loreau 2010). For bryozoans, at least, this difference in oxygen consumption between growth forms may be due to differences in the density of respiratory structures within the colony: flat species tend to have much more densely packed lophophores (the feeding and respiratory structure) than arborescent species (Grunbaum 1997).

Our estimates of $P_c$ for marine invertebrates show a similar range as published estimates for other aquatic species, which typically vary among species from almost 0 to ~50% air saturation (Childress and Seibel 1998, Hill et al. 2005, White and Seymour 2011). The $P_c$ of a species is generally matched to the minimum oxygen level encountered in the environment in which it lives (Childress and Seibel 1998). Thus, the $P_c$s of species from environments with low oxygen levels are lower than those from more oxygenated environments, and oxygen availability is an important determinant of broad-scale ecological patterns (Verberk et al. 2011). From our data, it would seem that similar matching occurs at smaller scales between $P_c$ and the microhabitat that a species inhabits. The impact of climate warming on oxygen availability and subsequent competition dynamics (Vaquer-Sunyer and Duarte 2011) would appear to be fruitful line of research as our data would indicate an advantage for species with a flat growth form in more oxygen limited conditions.

If competition for oxygen does occur often in our study habitat, then this has some surprising implications for competition among sessile and mobile species. Mobile and sessile species in marine habitats are typically thought to interact through predation (both mobile species consuming sessile species and vice versa) and trampling of sessile species by mobile species. Our results suggest that despite often utilizing different food sources, sessile and mobile species may compete for the common limiting resource of oxygen. Competition between these groups has not been anticipated or explored and presents an exciting opportunity for future research.

Overall, our results suggest that exploitative competition for multiple resources is more common than previously thought in marine benthic communities. In some instances, oxygen is a more limiting resource than

space, and the degree to which oxygen is limiting depends on growth form. Whether competition for oxygen is widespread in the marine environment remains unclear, and further studies are needed across a range of habitats and taxa.

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SUPPLEMENTAL MATERIAL

**Appendix**

Classification of study species into different growth forms (*Ecological Archives* E094-011-A1).