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Synthesis and comparative analysis of physiological tolerance and life-history growth traits of marine aquaculture species

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ABSTRACT

Aquaculture is one of the fastest growing industries in the world, and marine-based farming in particular is growing the fastest. With the ever-increasing demand for seafood, marine aquaculture (mariculture) has great potential to help meet this demand. Due to the highly diverse and variable nature of marine environments, it is critical to understand species-level trade-offs that can influence the suitability of a species or species groups for certain ocean conditions. Particularly for mariculture, physiological tolerance of a species to temperature fluctuations and low dissolved oxygen (DO) and its capacity to grow quickly are important attributes. Although there has been extensive research pertaining to the respective fields of tolerance and growth of marine organisms, there has been little overlap between the seemingly separate, yet related fields. More specifically, a relationship between traits of tolerance and growth is not well understood – especially across multiple taxonomic groups. In order to explore and compare possible tolerance and life-history relationships of mariculture species, we complied information on temperature tolerance range, minimum dissolved oxygen observations, growth parameters (asymptotic size and rate), trophic level (TL), taxon, region, and market value for 178 distinct marine farmed species, which included finfish ($n = 101$), crustaceans ($n = 20$), molluscs ($n = 52$), and other aquatic invertebrates ($n = 5$), including a cephalopod, a cordate, and three echinoderms. Using descriptive statistics and regression modelling, we found a significant inverse relationship between temperature tolerance range and minimum DO observations (i.e., a positive trend between thermal and hypoxia tolerance, as defined). We also found evidence of a possible trade-off between overall tolerance ability and growth. Specifically, larger, slower growing species tend to have wider temperature ranges and lower minimum DO levels, but potentially at the cost of being less ecologically sustainable (as measured by TL). In addition, tropical species appear less resilient when accounting for both thermal extremes and lower observed DO levels compared to subtropical and temperate species. These patterns highlight associations and uncertainties of traits important for mariculture practices, including species and trait selection, as well as adaptive capacity of regional ventures relative to climate change.
Statement of relevance: Potential trade-offs of adaptive tolerance and growth.

1. Introduction

Aquaculture has grown nearly exponentially over the past 50 years (Bostock et al., 2010), now accounting for over half of all seafood worldwide (FAO, 2014). The continuing global demand for seafood drives the need for aquaculture growth (Godfray et al., 2010). Despite the significant expansion of aquaculture in recent years, there remains strong prospects to expand farther into the ocean environment, where aquaculture currently occupies only a small fraction of all potentially suitable growing areas (Duarte et al., 2009; FAO, 2014; Holmer, 2010). While marine aquaculture, henceforth referred to as mariculture, can have significant environmental impacts (Goldburg et al., 2001), many of these concerns can be mitigated through best management practices and optimized site and species selection. Therefore, in order to increase sustainable marine production, it is critical to first understand the potential capacity and diversity of farmed marine species, as well as the trade-offs associated with their suitability to tolerate and thrive in a range of environmental conditions.

Species selection is an important component of aquaculture development (Alvarez-Lajonchère and Ibarra-Castro, 2013), particularly in the context of a changing global climate. Most species selection approaches tend to revolve around identifying new species for a specific region (e.g., Caribbean) and concentrate on one group of organisms (e.g., finfish) (Alvarez-Lajonchère and Ibarra-Castro, 2013; Cao et al., 2007; Quéméner et al., 2002). Although such approaches offer insight into farming potential at the local level, assessment has not been

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Table 1
Ranges of the six continuous physiological and life-history variables for all fish, crustaceans, molluscs, and other aquatic invertebrates.

	Fish	Crustacean	Mollusc	Aq. invert
Maximum upper temperature (°C)	42.5	35.0	45.0	30.00
Minimum upper temperature (°C)	12.0	17.2	9.0	19.7
Maximum lower temperature (°C)	26.5	27.0	30.0	24.9
Minimum lower temperature (°C)	0	5.0	−1.6	7.0
Maximum TTR (°C)	33.3	21.0	26.0	20
Minimum TTR (°C)	2.5	3.9	1.5	3.9
Maximum DO minimum (mg L^{-1})	5.9	5.3	5.9	5.1
Minimum DO minimum (mg L^{-1})	0.4	0.9	0.7	4.0
Maximum L_∞ (cm)	800.0	33.6	137.0	49.0
Minimum L_∞ (cm)	10.9	3.7	5.0	6.0
Maximum K (yr^{-1})	2.13	5.4	2.3	1.4
Minimum K (yr^{-1})	0.04	0.03	0.02	0.3
Maximum TL	4.5	3.7	2.0	4.0
Minimum TL	2.0	2.3	2.0	2.0

applied at a global scale. More specifically, investigation into an array of species across multiple taxonomic groups and regions has not been examined. Such a comparison could provide valuable information concerning broader trade-offs that cannot be gleaned from smaller scale evaluations. Furthermore, most selection processes do not consider the adaptive capacity of a species and thus the production stability of a farm. Conditions in the ocean are expected to become increasingly warm and more variable due to climate change (Altieri and Gedan, 2015; Best et al., 2015), suggesting the aquaculture industry should select species that can withstand such variability in order to optimize stable production over time.

Assessing the physiological requirements and limitations of marine species provides a fundamental baseline for evaluating the potential of mariculture across the globe. Unlike wild organisms that have the capacity to avoid unfavorable conditions, farmed species are constrained to particular areas and the associated physical conditions. Thus, a species' ability to withstand environmental extremes could have important implications for production. In particular, tolerance to a range of temperatures and dissolved oxygen (DO) conditions can influence the level of impact of these external stressors on individual growth and survival of a species (Altizer et al., 2013; Bickler and Buck, 2007; Gislason et al., 2010; Harvell et al., 2002; Vaquer-Sunyer and Duarte, 2011, 2008). Moreover, thermal and DO tolerance are rarely explored in unison, even though both stressors can and do co-occur (McBryan et al., 2013). As a result, investigating mariculture potential needs to account for the physiological constraints of the species themselves.

Size and growth of species are important considerations in aquaculture, yet our understanding of how these traits relate to temperature and DO tolerance is not clear. Relationships between size, growth, and other life-history traits (e.g., reproduction) are well documented in the literature (King and McFarlane, 2003; Pauly, 1998; Winemiller, 2005; Winemiller and Rose, 1992). However, there is a lack of overlap and investigation into the relationships between growth attributes and adaptive tolerance to multiple stressors across multiple species (Roze et al., 2013). Existing literature suggests that some individual salmonids are more sensitive to higher temperatures at larger sizes (Clark et al., 2012; Roze et al., 2013), while larger reef fish tend to be more tolerant to reduced DO conditions (i.e., hypoxia) (Nilsson and Ostlund-Nilsson, 2008). At the species level, invertebrates appear to be more hypoxia tolerant than fish (Vaquer-Sunyer and Duarte, 2008). Investigation into growth and tolerance is even scarcer in the literature, with only a few publications describing genetically-selected faster growing individuals showing decreased tolerance to low DO (Sundt-Hansen et al., 2007), but lower sensitivity to higher temperatures (Molony, 2001; Roze et al., 2013). Although providing some insight into potential life history and tolerance trade-offs, the sparse nature and individual-level focus of the literature makes it difficult to infer trade-offs across multiple species and taxonomic groups. In addition, with aquaculture practices tending to select for faster growth (Gjedrem et al., 2012), it is even more important to explore the possible trade-offs and consequences associated with selection for a specific trait.

This study evaluates and compares physiological tolerance and life-history traits of successfully farmed marine species. Using a variety of online databases, as well as gray and primary literature, specific information on species temperature tolerance range, minimum oxygen observations, growth, trophic level, geographic region, and market value

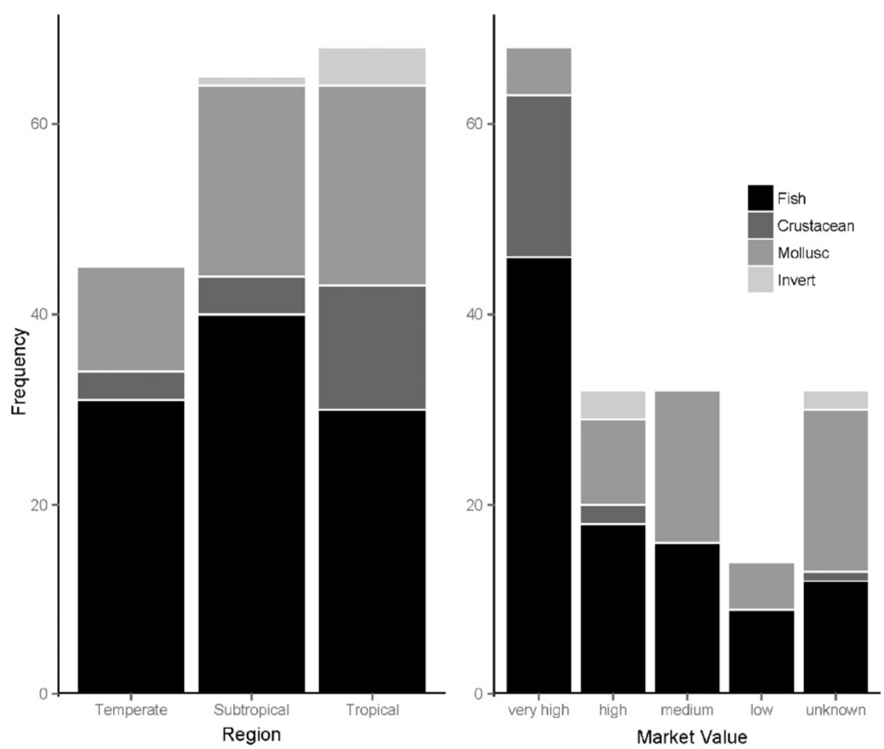

Fig. 1. Frequencies of species associated with a given region (*left panel*) and market value (*right panel*). Relative number of specific taxonomic groups is differentiated.