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ARTICLE

Suitability of Insulin-Like Growth Factor 1 (IGF1) as a Measure of Relative Growth Rates in Lingcod

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Abstract

The effectiveness of spatial management strategies is typically evaluated through traditional biological measurements of size, density, biomass, and the diversity of species inside and outside management boundaries. However, there have been relatively few attempts to evaluate the processes underlying these biological patterns. In this study, we take the first step toward developing a relative index of body growth for lingcod *Ophiodon elongatus* using plasma insulin-like growth factor 1 (IGF1) with the ultimate goal of measuring spatial differences in relative growth rates. Insulin-like growth factor 1 is one of the principal hormones that stimulates growth at the cellular level in all vertebrates and shows significant relationships with body growth in many fishes. In the laboratory, we found that the level of IGF1 was related to the instantaneous growth of juvenile lingcod. In the field, we measured size, condition, and plasma IGF1 level in 149 lingcod from eight locations inside and outside marine protected areas in the San Juan Islands, Washington. The IGF1 levels in wild lingcod were highly variable from site to site for both genders, and we were able to detect differences in IGF1 across space in males. Multivariate analyses showed that the spatial patterns of IGF1 differed from those of traditional biological measurements. More work is needed to validate the relationship between IGF1 and growth in larger individuals, but our research shows the potential for IGF1 to be used as an ecological indicator.

The rate of somatic growth in fish integrates the physiological and environmental conditions experienced by individuals and can be an important indicator of relative success at multiple levels of organization. At the level of an individual fish, faster growth usually confers greater survivorship, particularly for young fish (Meekan and Fortier 1996; Booth and Hixon 1999; Bergenius et al. 2002), because the risk of predation decreases as fish grow (e.g., Werner et al. 1983). At the population level, body growth is directly coupled with population dynamics via size-dependent fecundity (Werner and Gilliam 1984; Roff 1992) because larger individuals produce greater numbers of eggs and larvae (Morita et al. 1999; Osborne et al. 1999). In addition, somatic growth can influence the nature of density-dependent interactions (Lorenzen and Enberg 2002; Craig et al. 2007;

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Lorenzen 2008) because larger individuals often outcompete smaller individuals for food, habitat, or mates (Mittelbach and Osenberg 1993; Booth 1995; Post et al. 1999). Moreover, recent research argues that density-dependent growth can negate much of the proposed benefit to fisheries yields by spatial management strategies such as the establishment of marine protected areas (MPAs) (Gardmark et al. 2006). Thus, understanding how growth rate varies across time and space is fundamental to understanding how populations are regulated and may provide necessary information for evaluating management strategies.

Despite the potential importance of body growth to population dynamics and the success of spatial management strategies, measurements of growth are rare, especially in exploited species. For most teleost fishes, it is difficult to measure growth or feeding rates of individuals in situ. Analysis of otolith microstructure has been successfully used to assess growth (Pannella 1971; Campana 1990); although, this lethal method may be counterproductive for species that are depleted. Mark–recapture methods have also been used to assess growth, but these studies require large numbers of tagged individuals and a significant effort requiring considerable resources to recapture individuals (reviewed by Kohler and Turner 2001). Enzyme assays, RNA:DNA ratios, protein concentration, and lipid assessments have also been used to assess growth or condition of fish (Mathers et al. 1992; Guderley et al. 1996; Couture et al. 1998; Dutil et al. 1998; Majed et al. 2002); however, none of these methods are used routinely as a standard ecological metric directly related to body growth owing to varying technical, logistical, financial, and biological issues.

The endocrine system plays an integral role in regulating cell division and growth in all vertebrates (Oksbjerg et al. 2004; Wood et al. 2005; Reinecke et al. 2006), and thus researchers have turned to the endocrine system to develop new nonlethal approaches to measure growth. One of the principal hormones regulating growth is insulin-like growth factor 1 (IGF1). In the laboratory, positive relationships between the concentration of plasma IGF1 and growth rates are clearly established in Chinook salmon *Oncorhynchus tshawytscha* (Beckman et al. 1998), coho salmon *O. kisutch* (Pierce et al. 2001; Beckman et al. 2004a, 2004b), Atlantic salmon *Salmo salar* (Dyer et al. 2004), tilapia *Oreochromis mossambicus* (Uchida et al. 2003), gilthead seabream *Sparus aurata* (Perez-Sanchez et al. 1995; Mingarro et al. 2002), hybrid striped bass (white bass *Morone chrysops* × striped bass *M. saxatilis*; Picha et al. 2006), and Atlantic cod *Gadus morhua* (Davie et al. 2007). Review of the literature suggests these relationships are strongest when integrating growth over 2–4-week periods (Beckman 2010). The relationship between IGF1 levels and rates of body growth has not been directly tested in the field, but there is supporting evidence for a positive relationship between IGF1 and rates of body growth in wild fish populations. For example, IGF1 levels in lingcod *Ophiodon elongatus* are lowest in winter when growth is expected to be lowest because temperatures are coldest and food supply is lowest (Beaudreau et al. 2011). Moreover, IGF1 is positively correlated with the proportion of nonempty stomachs in lingcod (Beaudreau et al. 2011).

Levels of plasma IGF1 also show predictive capabilities at the population level, as we have seen strong relationships between IGF1 in Pacific salmon smolts and the subsequent rates of return of adults (Beckman et al. 1999). Beckman (2010) concluded, based on a review of the current literature on IGF1 and growth in fish, that IGF1 could provide a valid index of growth in fish. However, there are no data to suggest that IGF1 can provide an absolute measure of growth (i.e., g/d or mm/d); rather IGF1 provides a measure of relative growth—higher IGF1 levels are associated with higher growth rates, while lower IGF1 levels are related to lower growth rates.

A relative index of growth would provide researchers with a nonlethal method to estimate relative rates of body growth across sites differing in habitat quality and quantity or among populations that vary in density. Moreover, this tool would provide managers of commercially and recreationally important species with a process-based metric for evaluating the ecological response of individuals across management boundaries. The effectiveness of management strategies in achieving their goals has typically been evaluated with pattern-based metrics such as measurements of body size, density, biomass or biodiversity, or both, of taxa inside and outside management boundaries (e.g., Halpern 2003; Willis et al. 2003; Claudet et al. 2008; Lester et al. 2009). While these measurements are clearly useful, they do not measure differences in the underlying processes that may occur as a result of increases or decreases in the body size or density of fish in managed areas. Measurements of vital rates, such as body growth, provide a necessary link between pattern and process. In this study, we begin to evaluate whether IGF1 is useful for measuring spatial variation in body growth using lingcod as a model. First, we determine the relationship between IGF1 and growth rates of juvenile lingcod reared in the laboratory to confirm whether IGF1 acts as an index of relative growth in lingcod as it does in other fish. Next, we evaluate spatial variation in plasma IGF1 levels in lingcod among sites in the San Juan Islands archipelago. Last, we compare the spatial patterns of traditional biological measurements of lingcod with the spatial patterns of IGF1 levels of lingcod to determine whether IGF1 provides information that is different from that found when traditional measurements are used.

METHODS

Relationship between IGF1 Levels and Growth Rates in the Laboratory

Experimental design.—Lingcod were reared in laboratory aquaria at the National Oceanic and Atmospheric Administration (NOAA) field station in Manchester, Washington, from eggs collected in Puget Sound. At 5 months of age, lingcod were transported to a wet lab at the Northwest Fisheries Science Center (NWFSC) in Seattle. Fish were acclimated in 500-L aquaria containing flowing seawater with a salinity of 27‰ at

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12 ± 0.5°C. At 8 months old, we separated 15 larger individuals (218 ± 29 g [mean $\pm$ SD], 29.7 ± 1.2 cm total length [TL]) into one aquarium (tank A) and 23 smaller individuals (116 ± 32 g, 25.4 ± 1.5 cm TL) into each of two other aquaria (tanks B and C) to reduce opportunities for cannibalism ($n = 61$ fish total). At this time, we measured weight (g) and total length (cm) and inserted a passive integrated transponder (PIT) tag into the peritoneal cavity of each lingcod so we could identify individuals throughout the experiment. We fed lingcod in each aquarium to satiation every other day using dry fish pellets (BioOregon, Longview, Washington).

On June 11 and July 10, 2007, we removed lingcod from aquaria, sedated them for 3–5 min with 0.05% tricaine methanesulfonate (MS-222), measured weight and TL, and withdrew 0.5 mL of blood from the caudal vein using a heparinized syringe. We returned lingcod to their respective aquaria after a 3–5-min recovery period.

We spun blood samples in a Sorvall Legend RT centrifuge (Kendro Laboratory Products, Asheville, North Carolina) for 20 min at 2,500 rpm, at 5°C to separate the plasma from the other components of the blood. The blood plasma was frozen and stored at −80°C. Plasma IGF1 concentration was quantified by means of the radioimmunoassay developed by Shimizu et al. (2000) with barramundi *Lates calcarifer* antibody and recombinant salmon IGF1. The assay was validated for lingcod by running a series of plasma dilutions and assessing parallelism of the lingcod plasma by comparison with to standards (Figure 1).

Data analysis.—We tested the hypothesis that growth of juvenile lingcod is associated with IGF1 concentrations using a linear mixed model (PROC MIXED, SAS 2004) with IGF1 concentration as the dependent variable, and aquarium, growth, and aquarium × growth as fixed effects. Growth was estimated between June 11 and July 10, 2007 as

$$\text{Growth} = [\log_e(W_2 - W_1) \times \Delta D] \times 100,$$

where W_2 was the weight of each fish on July 10, W_1 was the weight of each fish on June 11, and ΔD was the number of days between sampling.

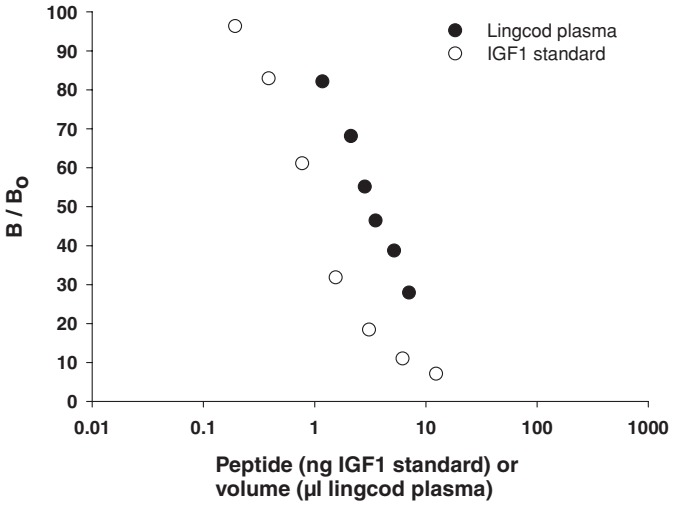


FIGURE 1. Displacement curves of radiolabeled recombinant salmon insulin-like growth factor 1 (IGF1) with either unlabeled recombinant salmon IGF1 or serially diluted lingcod plasma. B/B_0 = percent of label bound.

Spatial Patterns of IGF1 and Traditional Biological Metrics

Experimental design.—We collected lingcod from eight sites (four inside and four outside MPA boundaries) near Friday Harbor, Washington, in the San Juan archipelago during the summer of 2007 (Figure 2). Lingcod were collected at 4–50 m depth using the hook-and-line methods of Beaudreau and Essington (2007). Upon capture, fish were anesthetized with 0.05% MS-222 for 3–5 min. Weight (W) and TL were measured for each fish and the sex determined by examining the anal papillae (enlarged in males, Wilby 1937). We used Fulton's condition factor, K, to measure the overall "well-being" of each fish (Lambert and Dutil 1997) with the following equation:

$$K = 10^5 \times W\,(\text{g})/\text{TL}\,(\text{mm})^3.$$

We next extracted 1 mL of blood from the caudal vein with a heparinized syringe and immediately placed samples in a microcentrifuge tube on ice. After sampling, lingcod were placed in a recovery cooler for 5 min and then released alive into the water as close to the point of capture as feasible.

Upon returning to the laboratory (within 1–4 h), blood samples were spun in a Spectrafuge 16M microcentrifuge for 5 min at 5,000 rpm to separate the plasma from other blood components. Plasma was collected and stored, and the concentration of IGF1 was later quantified as described previously.

Catch per unit of effort (CPUE) was calculated individually for each sampling site as the number of lingcod caught per angler per hour fishing. To improve consistency in sampling effort across days and sites, angling was conducted from the same vessel throughout the study period with the same fishing gear. Effort was measured as time actively fishing (terminal tackle in the water) for each angler.

Data analyses.—In the analyses below, we included management status (MPA or non-MPA) and CPUE in the models to account for variation in these variables, but we were not explicitly testing hypotheses about whether IGF1 varied among management status or with density of conspecifics. Thus, we viewed "site" and "management status" as two different scales of spatial arrangement. We focused on measuring the magnitude of variation in IGF1 across individuals and space and whether there were similarities or differences between the spatial patterns of traditional biological metrics and IGF1 levels.

To evaluate whether traditional biological measurements (TL, W, and K) and plasma IGF1 showed different spatial patterns we used a two-tiered analysis. First, we used permutational multivariable analysis of variance (ANOVA) (PERMANOVA,

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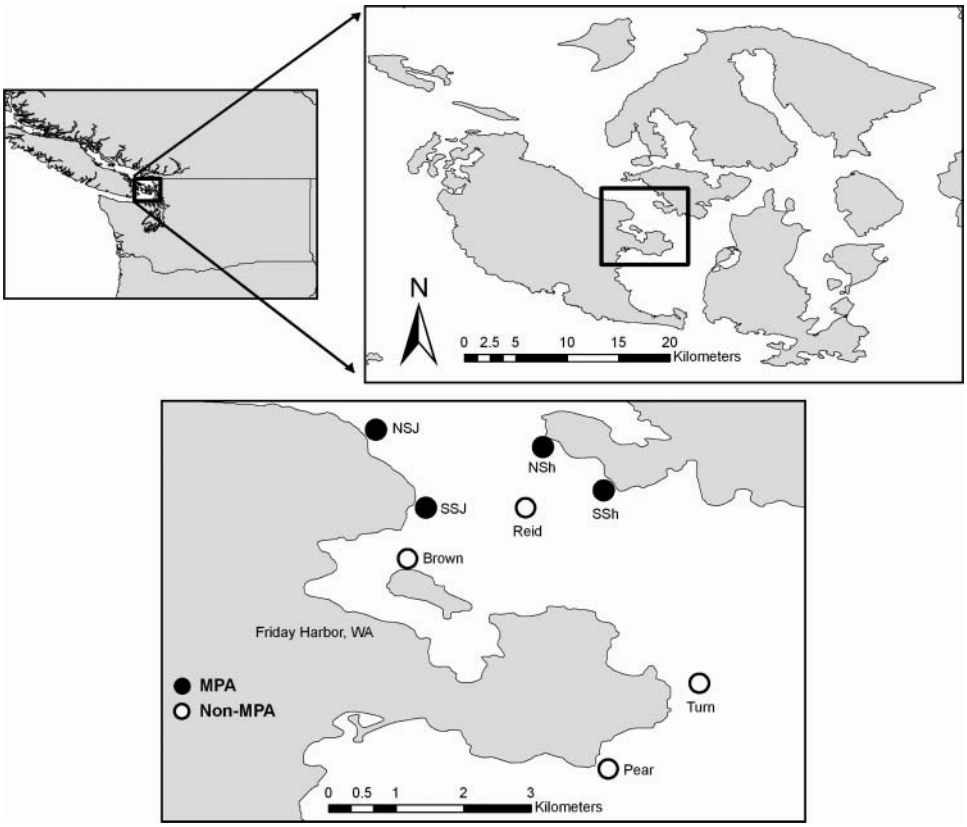


FIGURE 2. Location of lingcod collections near Friday Harbor inside and outside marine protected areas (MPAs). Area names are as follows: Brown = Brown Island, Pear = Pear Point, Reid = Reid Rocks, Turn = Turn Island, NSJ = North San Juan Island, SSJ = South San Juan Island, NSh = North Shaw Island, and SSh = South Shaw Island.

PRIMER 6; Anderson 2001) to determine whether lingcod differed across space based on measurements of size, condition, and growth (as measured by IGF1). Dependent variables were TL, W, K, and IGF1, and sex, status, site nested within status, sex × status, and sex × site(status) were fixed effects. The multivariate analysis was based on Euclidean distances of untransformed data and each term in the analysis was tested with 999 unique permutations. To visualize multivariate patterns of all four metrics, we used nonmetric multidimensional scaling (nMDS; PRIMER 6 2009) ordinations based on a Euclidean distance resemblance matrix calculated from untransformed data.

Secondly, we explored results of the PERMANOVA with univariate analyses of each dependent variable to determine which metrics were responsible for significant differences. Specifically, we used a linear mixed model (PROC MIXED, SAS 2004) with either TL, W, or K as the dependent variable, site nested within status and sex × site(status) as random effects, and status, sex, and status × sex as fixed effects. We evaluated whether the variance of each metric (TL, W, or K) differed between MPAs and non-MPAs using a residual log-likelihood test to determine whether model fit was improved when variance terms were estimated separately for each status group. If the residual log-likelihood test was significant ($P < 0.05$), the variance of the metric differed between MPAs and non-MPAs and we used the residual parameter estimates of each group to measure the relative difference (Wolfinger 1996; SAS 2004).

For IGF1, we analyzed each sex with separate linear mixed models (PROC MIXED, SAS 2004) to investigate variation across sites and management status. The IGF1 level was the dependent variable, site nested within status and TL × site(status) were random effects, and status, TL, CPUE, status × TL, status × CPUE, and TL × CPUE were fixed effects. The TL was included in the model to account for potential correlations between IGF1 and fish length as observed in lingcod by Beaudreau et al. (2011). Interaction terms were iteratively removed from the model if $P > 0.25$ (Underwood 1997). As described above, we also tested whether the variance of IGF1 differed between MPAs and non-MPAs. For female lingcod, we had to eliminate North San Juan Island and Turn Island from the analysis because of low sample sizes ($n = 1$ and $n = 2$, respectively).

RESULTS

Relationship between IGF1 Levels and Growth Rates in the Laboratory

Lingcod in two of the aquaria showed a positive association between IGF1 and growth (Figure 3; aquarium B: $n = 17$, adjusted $r^2 = 0.185$, $P = 0.048$; aquarium C: $n = 6$, adjusted

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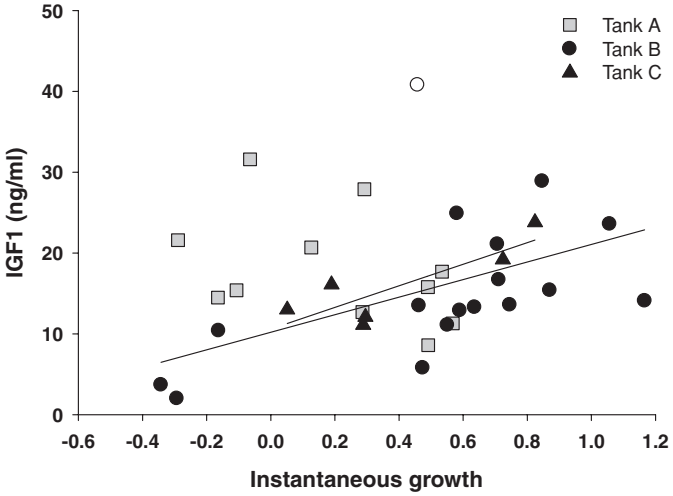


FIGURE 3. Relationship between instantaneous growth and insulin-like growth factor 1 (IGF1) in juvenile lingcod. The significant relationships found in tanks B and C are drawn. The outlier in tank B is shown as an open circle, but it is included in the regression line.

$r^2 = 0.634$, $P = 0.036$), while in aquarium A, we did not detect a significant association between IGF1 and growth ($n = 11$, adjusted $r^2 = 0.077$, $P = 0.209$). While the slopes and strength of the relationships between IGF1 and growth were qualitatively different in tank A versus tanks B and C, the interaction between aquarium and growth was not statistically significant ($F_{2, 28} = 2.83$, $P = 0.076$). The analysis identified one individual as an outlier in aquarium B (IGF1 = 40.8 ng/mL; Studentized residual = 4.64). If removed, we detected a significant interaction between aquarium and growth ($F_{2, 27} = 5.18$, $P = 0.012$) and the relationship between IGF1 and growth for aquarium B was stronger (adjusted $r^2 = 0.438$, $P = 0.003$). There was no relationship between TL or W and IGF1 among all individuals (TL: adjusted $r^2 = 0.008$, $P = 0.268$; W: adjusted $r^2 = 0.015$, $P = 0.227$). We did not include gender as a covariate because we were unable to visually differentiate between genders at this age. The number of individuals in the analysis differed from the number stocked at the beginning of the experiment owing to mortality.

Variation in IGF1 in Wild Lingcod

We collected 146 lingcod (97 males and 49 females) across all sites encompassing a wide range of sizes (32–114 cm). Plasma IGF1 levels varied by nearly an order of magnitude in both males (3.8–34.7 ng/mL) and females (3.8–35.3 ng/mL). Across all sites, the coefficient of variation (CV = SD/mean) in IGF1 was 0.50 for males and 0.43 for females. Within sites, the CV in IGF1 ranged between 0.30 at North San Juan Island to 0.67 at Turn Island.

TABLE 1. Results from permutational multivariable analysis of variance using the following lingcod characteristics as dependent variables: total length, weight, condition factor, and IGF1. Sex, management status (marine protected area [MPA] or non-MPA), site nested within status (site [status]), and sex × site (status) were the fixed effects. Abbreviations are as follows: SS = sum of squares; MS = mean square.

Source	df	SS	MS	Pseudo-F	P
Sex	1	13.84	13.84	4.27	0.074
Status	1	39.90	39.90	8.16	0.023
Site (status)	6	33.70	5.62	1.72	0.067
Sex × status	1	9.93	9.93	3.07	0.101
Sex × site (status)	6	19.36	3.23	0.99	0.452
Residual	130	424.94	3.27		
Total	145	580.00			

Spatial Patterns of IGF1 Levels and Traditional Biological Metrics

Multivariate analysis showed that lingcod differed between MPAs and non-MPAs, while there were no significant differences (at $\alpha = 0.05$ level) between gender or sites based on the measured biological characteristics of TL, W, K, and IGF1 (Table 1). Using nMDS plots to investigate these results more closely, we found that TL, W, and K covary with each other, while IGF1 did not (Figure 4). Distances between points on the nMDS plots represent how similar (points close together) or different (points far apart) lingcod are from one another based on the four measured characteristics (TL, W, K, and IGF1). All three traditional measurements separated lingcod along nearly the same axis ($\sim x$-axis), while IGF1 tended to separate lingcod along the y-axis. Traditional measurements clearly explained the differences between lingcod in MPAs from lingcod in non-MPAs; most of the non-MPA individuals are clustered on the right side of the graph, while MPA individuals extend far to the left side of the graph (Figure 4b). In contrast, there is no separation of lingcod in MPAs from lingcod in non-MPAs along the IGF1 axis (in the y-axis direction) (Figure 4b).

Univariate analyses for TL showed a significant sex × site(status) interaction (Table 2) because females were larger than males at five sites, while males were larger than females at three sites (Figure 5a). Lingcod were significantly larger in MPAs than in non-MPAs (64 and 46 cm, respectively) and the variance in TL was 2.7 times greater in MPAs than in non-MPAs (residual estimates in Table 2). For W, we found a significant interaction between status and sex (Table 2), in which females were twice as heavy as males in MPAs (averaging 4.2 and 2.0 kg, respectively) but weighed the same as males in non-MPAs (averaging 1.0 and 0.9 kg, respectively) (Figure 5b). The variance in weight was 6.7 times greater in MPAs than in non-MPAs (residual estimates in Table 2). We found no significant differences in K among the explanatory variables (Table 2; Figure 5c).

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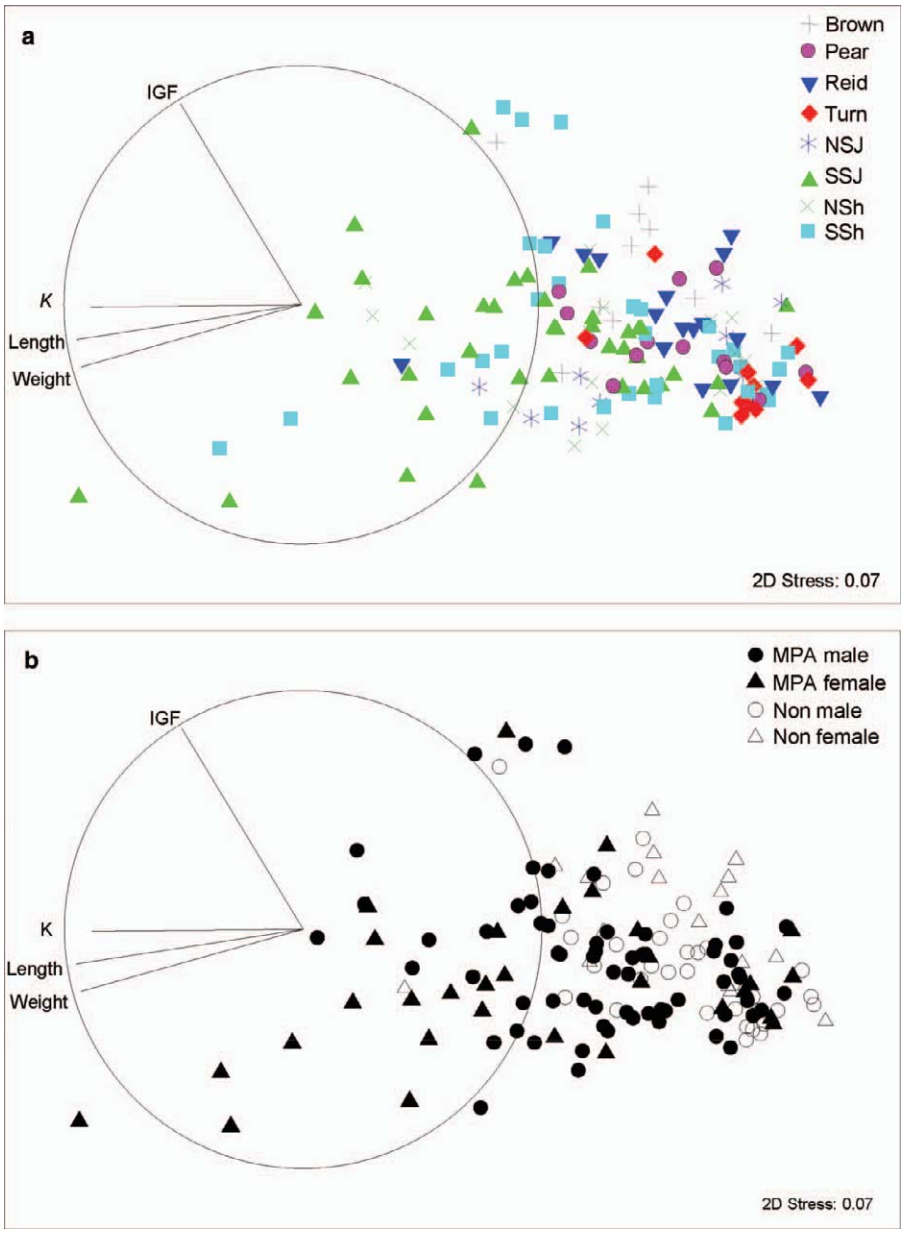


FIGURE 4. Nonmetric multidimensional scaling plot of lingcod ($n = 146$) by **(a)** site and **(b)** management status. The distances between points indicate how similar (points close together) or different (points far apart) lingcod are from one another based on four measured characteristics (total length, weight, Fulton's condition factor [K], and IGF1). The solid lines within the circles show the dimensional directions in which the different characteristics act upon lingcod during ordination. Abbreviations are given in the caption to Figure 2.

For IGF1, we did not find any differences among sites or management status in females, but there was a significant difference in IGF1 levels among sites in males (Table 2; Figure 5d). While there was no difference in mean IGF1 level between MPAs and non-MPAs, the variance of IGF1 was 2.5 times greater in MPAs than in non-MPAs for males (residual estimates in Table 2).

Estimates of CPUE (one-way ANOVA: $F_{1,6} = 7.9$, $P = 0.031$) and biomass ($F_{1,6} = 14.34$, $P = 0.009$) were significantly higher in MPAs than in non-MPAs (Figure 6). We collected 55% more individuals and nearly five times as much biomass per angler-hour in MPAs than in non-MPAs.

DISCUSSION

Plasma IGF1 levels are positively related to rates of body growth in a number of teleost species (Perez-Sanchez et al. 1995; Beckman et al. 1998; Pierce et al. 2001; Mingarro et al. 2002; reviewed by Beckman 2010). This study is an initial step

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TABLE 2. Univariate linear mixed model results in which each traditional metric or IGF1 is the dependent variable.

Metric	Parameter	Estimate	SE	Z	P
Length ($n = 146$)	Site (status)	0			
	Sex × site (status)	34.14	23.34	1.46	0.036
	Residual non-MPA	112.48	24.19	4.65	<0.001
	Residual MPA	307.70	46.07	6.68	<0.001
	Fixed effects:				
	Status	$F_{1, 6} = 20.42$			0.004
	Sex	$F_{1, 6} = 3.74$			0.101
	Status × sex	$F_{1, 6} = 2.46$			0.168
Weight ($n = 146$)	Site (status)	0			
	Sex × site (status)	0.19	0.20	0.95	0.085
	Residual non-MPA	0.94	0.20	4.73	<0.001
	Residual MPA	6.33	0.95	6.63	<0.001
	Fixed effects:				
	Status	$F_{1, 6} = 30.38$			0.002
	Sex	$F_{1, 6} = 9.36$			0.022
	Status × sex	$F_{1, 6} = 6.86$			0.040
K ($n = 146$)	Site (status)	0.001	0.001	1.04	0.074
	Sex × site (status)	0			
	Residual	0.006	0.001	8.26	<0.001
	Fixed effects:				
	Status	$F_{1, 6} = 5.49$		0.058	
	Sex	$F_{1, 6} = 0.02$		0.889	
	Status × sex	$F_{1, 6} = 2.18$		0.191	
IGF1					
Females ($n = 46$)	Site (status)	0			
	TL × site (status)	0			
	Residual	40.92	9.15	4.47	<0.001
	Fixed effects:				
	Status	$F_{1, 3} = 2.22$			0.233
	CPUE	$F_{1, 34} = 2.93$			0.096
	TL	$F_{1, 3} = 1.61$			0.294
	CPUE × TL	$F_{1, 34} = 2.78$			0.105
	TL × status	$F_{1, 3} = 2.71$			0.198
Males ($n = 97$)	Site (status)	14.74	11.65	1.27	0.050
	TL × site (status)	0			
	Residual non-MPA	15.35	4.17	3.68	<0.001
	Residual MPA	39.64	7.27	5.45	<0.001
	Fixed effects:				
	Status	$F_{1,5} = 0.02$			0.888
	CPUE	$F_{1, 80} = 2.21$			0.141
	TL	$F_{1, 7} = 0.84$			0.391
	CPUE × TL	$F_{1, 80} = 4.34$			0.040

to understand the relationship between IGF1 and growth rates in lingcod and to quantify the spatial variation of IGF1 in wild lingcod populations. Our results provide preliminary evidence that IGF1 is positively related to body growth of lingcod and that IGF1 may be useful for detecting spatial differences in growth rates of lingcod.

In the laboratory, we found consistent relationships between IGF1 and growth in two of the three groups of juvenile fish assessed. Experiments conducted with juvenile coho salmon have produced cleaner, more distinct, and more consistent relationships (Beckman et al. 2004a, 2004b, 2004c) than observed in lingcod, but differences between the two species may, in large

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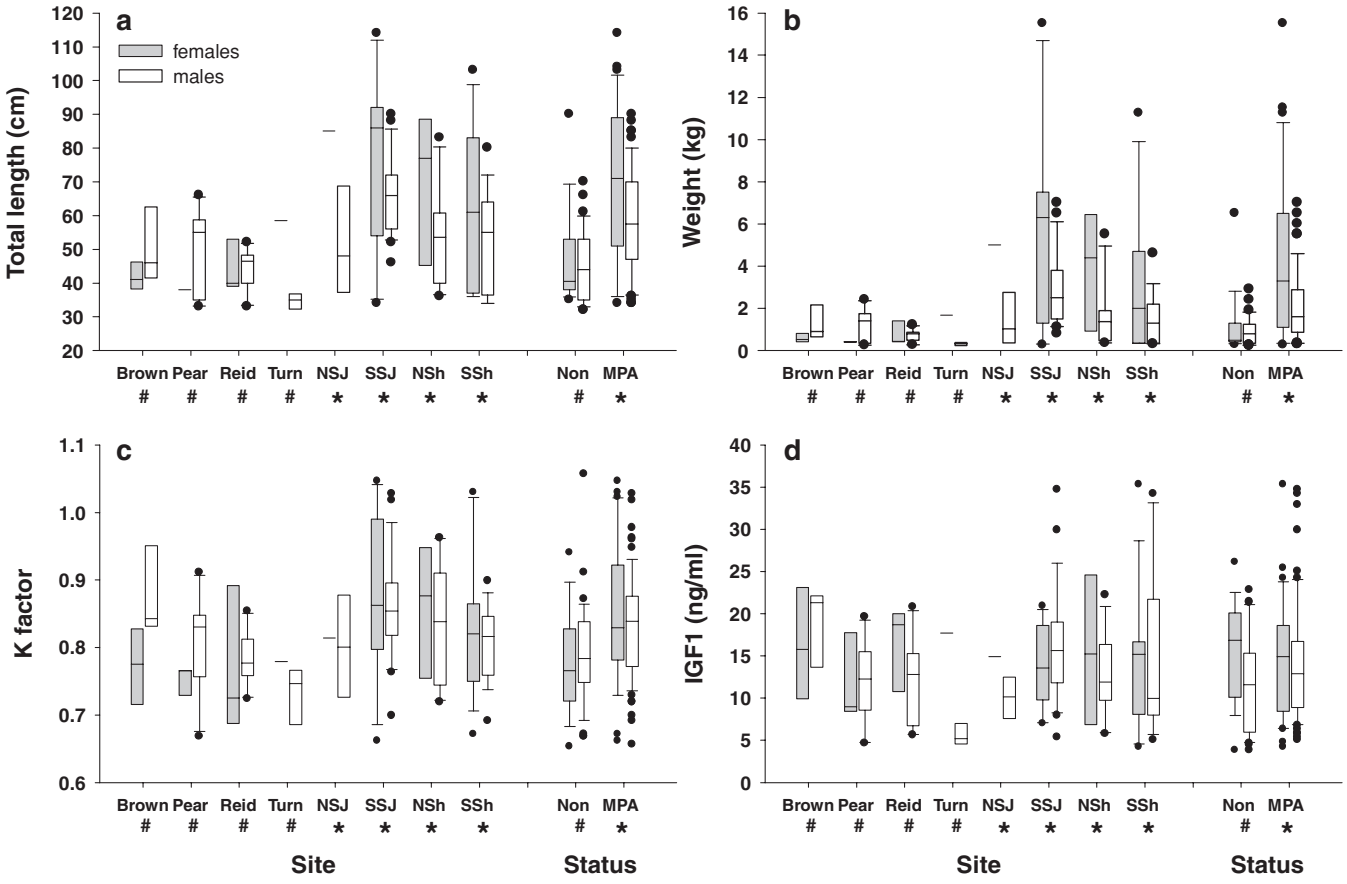


FIGURE 5. Comparison of traditional biological measurements and plasma levels of IGF1 of lingcod from eight sites inside and outside marine protected areas near Friday Harbor. Abbreviations are given in the caption to Figure 2. Horitzontal lines = medians, box dimensions = 25th through 75th percentiles, whiskers = 5th and 95th percentiles, and dots = all outliers.

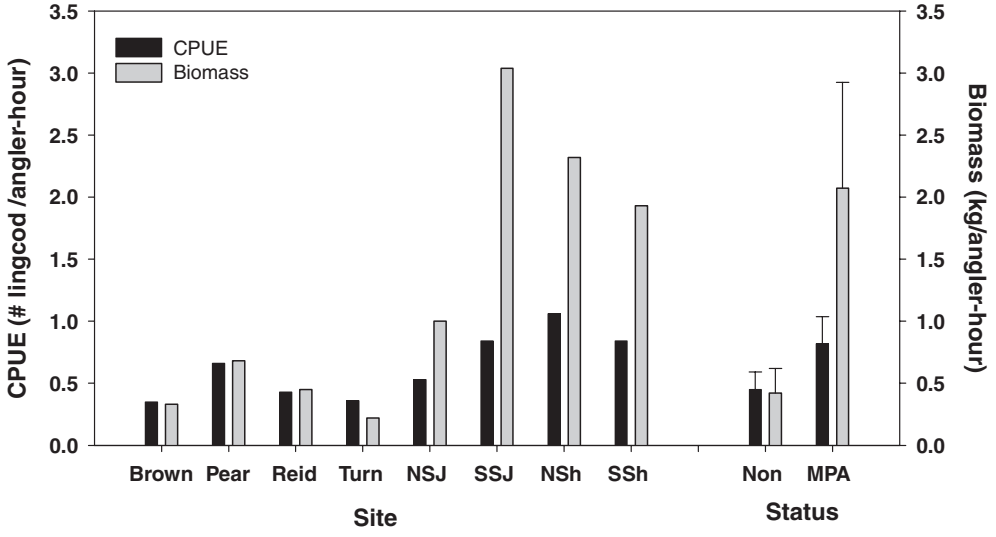


FIGURE 6. Catch per unit effort (CPUE) and biomass of lingcod from eight sites inside and outside marine protected areas near Friday Harbor. Error bars represent SDs. Abbreviations are given in the caption to Figure 2.

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part, be related to practical experience in fish culture and juvenile rearing. There is a long history of salmonid culture and we have conducted several laboratory-style experiments with juvenile salmon. Commercial lingcod culture does not exist and there have been relatively few laboratory experiments reported with lingcod older than a few months (but see Beaudreau and Essington 2009). We were fortunate to obtain a group of juvenile lingcod that had been trained to eat artificial feeds. Unfortunately, these particular fish did not thrive on the artificial feeds provided and grew poorly compared with our experience with salmonids. This could be due to either the culture conditions (tank size, tank depth, fish density, lack of structure, manner of feed presentation) or the feed composition itself (commercial salmon feed).

The relatively small range in growth rates results in reduced power to discern significant relationships between IGF1 and growth, particularly at small sample sizes ($n = 11$, 17, and 6 in tanks A, B, and C, respectively). In addition, there was little if any growth in length over the course of the experimental period (0–1.7 cm in 4 weeks). Beckman (2010) demonstrated that there is a stronger relationship between IGF1 level and growth in length than IGF1 level and growth in weight (which was used in our analysis). Despite the overall low growth rate and small sample size of experimental fish, the relationships between IGF1 and growth in two of the three groups of lingcod were consistent with the relationships demonstrated for other fish (e.g., salmonids, Atlantic cod, and striped bass). Thus, we consider the positive and significant relationships we found to be similar enough to those found in other species to suggest that IGF1 may be useful as a relative index of growth in lingcod and that further work in the laboratory and in the field is warranted.

The in situ measurements of IGF1 we made are one of the first evaluations of spatial variation in IGF1 in wild fish populations. Plasma levels of IGF1 varied substantially among lingcod, with a CV of 0.48 across all individuals. This level of difference among individuals implies that ecologically significant differences may be present. Other studies investigating the utility of IGF1 as an index of growth observed CVs in IGF1 of 0.15 for Chinook salmon in laboratory studies (Beckman et al. 1998) and 0.14 and 0.06 for ocean-caught coho salmon in Puget Sound, Washington, and the Strait of Georgia, British Columbia, respectively (Beckman et al. 2004a). These salmon studies only examined juvenile fish; in contrast, the lingcod examined in this study included both juvenile and adult fish. Several fieldwork studies have shown that factors related to season, size of individual, and stage of maturity (Onuma et al. 2010; Beaudreau et al. 2011) explain some of the variation in IGF1 in wild fish. Further work to determine how lingcod IGF1 levels vary with these factors may be necessary to judge when it is appropriate to directly compare IGF1 values between groups of fish in the field to infer differences in growth rate (i.e., Can males and females or individuals in different stages of maturity be considered together?).

Despite multiple potential sources of variation, we detected spatial differences in IGF1 across sites in male lingcod. Because of the relatively close proximity of our sites, this result suggests there may be localized differences in growth conditions across small spatial scales for males. Lingcod occupy relatively small core areas in both the summer (<500 m^2) and winter (<250 m^2) on reefs in Puget Sound (Tolimieri et al. 2009). It also appears common for males to establish and guard nests within the same territory, even under the same boulder or in the same crevice, year after year (King and Withler 2005). Thus, male lingcod display high levels of site fidelity year round and from year to year, and their rates of growth are likely to vary with differences in local habitat conditions and prey resources. Levels of IGF1 did not vary across sites in females, but this may be due to overall small sample sizes (only 49 females compared with 97 males) and the lack of females collected in some sites, rather than a comment on lack of spatial variation.

In addition to examining spatial variation of IGF1, we wanted to determine whether IGF1 provides novel information not provided by traditional metrics. Multivariate analyses clearly showed that spatial patterns of IGF1 and traditional biological measurements are different. In our data, it appears that traditional measurements explain more of the variation *between* management status (MPA or non-MPA), while IGF1 levels explain more of the variation *within* management status. This distinction may be particularly important for species, such as lingcod, with high site fidelity (Tolimieri et al. 2009) living in patchy reef habitats. These patterns are also evident in the univariate analyses, which showed that the mean and variance of traditional biological measurements were higher in MPAs than in non-MPAs, whereas IGF1 levels were also more variable in MPAs than in non-MPAs but mean levels were not different between MPA and non-MPA sites.

These data are consistent with many other studies and review articles that show MPAs have more and larger individuals than do non-MPAs (e.g., Halpern 2003; Willis et al. 2003; Lester et al. 2009); however, we are not aware of other studies that compare the variance of metrics among management areas. Higher variance of IGF1 in MPAs may indicate disproportionate access to a heterogeneously distributed resource. For instance, Fretwell (1972) proposed the ideal despotic distribution (IDD) for territorial species, in which the suitability of a habitat patch for an individual declines as density increases. The IDD predicts that early settlers will occupy high quality territories, and over time new settlers will be forced into lower quality patches. Importantly, the presence of new individuals does not reduce patch quality for early settlers (Sutherland 1996). Thus, for territorial species of fish, such as lingcod, the IDD predicts that as fish densities increase in MPAs, there should be an increase in the among-individual variance in IGF1 (growth rates) in heterogeneous landscapes. Alternatively, higher variance in IGF1 could simply be due to larger or older individuals surviving in MPAs, whereas larger or older individuals have been removed from the non-MPA populations, creating a truncated distribution.

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Distinguishing between these alternative hypotheses requires fine-scale movement and demographic data for lingcod inside and outside MPAs.

Measuring rates of growth in situ of marine fishes has been a difficult task, but novel nonlethal tools such as IGF1 may help overcome these challenges. This research provides a first step towards using IGF1 as an ecological indicator rather than just a physiological one. Having tools to measure growth synoptically at large spatial scales would augment traditional biological measurements to provide much-needed information about the processes underlying observed patterns. Moving from pattern-based information to a process-based understanding of the ecological consequences of management strategies would significantly improve our abilities to forecast and evaluate the results of management actions. While further work is needed, the results presented here suggest that IGF1 analysis can be a useful tool in this regard.

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