

Growth and distributional correlates of behavior in three co-occurring juvenile flatfishes

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ABSTRACT: We explored whether anti-predator behavior and intrinsic growth are co-evolved traits in 3 co-occurring juvenile flatfish species: English sole *Pleuronectes vetulus*, Pacific halibut *Hippoglossus stenolepis* and northern rock sole *Lepidopsetta polyxystra*. English sole are risk prone, adopting behavior that renders them more vulnerable to predation, while northern rock sole are more risk averse. Pacific halibut are risk sensitive and modulate behavior to match perceived threats. We hypothesized that risk-taking behavior and intrinsic growth rate would be positively correlated in these species. We examined the willingness of each species to feed, both in the presence and absence of risk, and in separate experiments we measured their intrinsic growth rates under a range of temperatures. As predicted, risky behavior in English sole was accompanied by high intrinsic growth, while risk aversion in rock sole was accompanied by low growth. Pacific halibut confounded predictions, combining moderate risk-taking behavior with high growth. Lastly, we examined the depth distribution of each species. We expected English sole would be restricted to the shallows (<5 m), where predators are less common, while rock sole would have a deeper distribution, being better able to co-exist with predators. Halibut were expected to present an intermediate depth distribution. Again, English sole and rock sole conformed to predictions, while Pacific halibut confounded them by having a deeper depth distribution, comparable to that of rock sole. We suspect that the behavioral plasticity of Pacific halibut, combined with refuging behavior and well-developed escape capabilities, may allow them to have both high intrinsic growth as well as the ability to coexist with the predators. Thus, our results provide only partial support for our hypothesis that behavior and growth are co-evolved traits that together control the distribution of juvenile flatfishes across predation gradients.

KEY WORDS: Anti-predator behavior · Temperature-dependent growth · Foraging · Co-evolved traits · Flatfishes

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INTRODUCTION

Most animals engage in trade-offs by balancing the costs and benefits of various activities against one another. Whether the trade-off occurs through optimization (MacArthur & Pianka 1966), where the animal has near-perfect knowledge of costs, benefits and currencies, or whether simple 'rules of thumb'

(Wetterer & Bishop 1985) are followed as a means of approximating optimization, the concept of the trade-off as a means of improving fitness is at the heart of ecological and evolutionary theory. Perhaps the most commonly studied trade-off involves the conflict between feeding and anti-predator behavior. When feeding, animals often must leave refuges or social groups, which increases their vulnerability

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(Newman & Caraco 1987). In addition, the very act of feeding compromises vigilance (Pulliam & Caraco 1984). Yet, avoiding predators can decrease foraging intake and inhibit growth (Ryer & Hurst 2008). Complicating the matter is the fact that the consequences of altered foraging and anti-predator regimes often have very different time scales. Eating less to reduce predation risk may lower growth rate and have fitness consequences later on, such as reduced fecundity. Maximizing growth by ignoring predation risk can lead to a sudden truncation of fitness, i.e. death.

Studies examining the co-evolution of anti-predator behavior, growth potential and habitat use have often focused upon single species that occur in isolated habitats or across broad latitudinal gradients, where environmental and predation regimes differ markedly. Extensive studies with guppies *Poecilia reticulata* demonstrate that populations can evolve rapidly in both behavior and growth in response to selective pressures (Arendt & Reznick 2005). In our study we took an alternative approach and examined aspects of behavior, intrinsic growth rate and habitat/depth distribution of the juveniles of 3 closely related flounder species that co-occur in coastal nursery embayments in the North Pacific Ocean. English sole *Pleuronectes vetulus*, Pacific halibut *Hippoglossus stenolepis* and northern rock sole *Lepidopsetta polyxystra* are all right-eyed flounders of the family Pleuronectidae. Northern rock sole in the Gulf of Alaska spawn from February through April, whereas both halibut and English sole have more protracted spawning, extending from November to March and from December to April, respectively (Love 1996). Judging by the relative size of these species when they co-occur on the summer nursery grounds, English sole recruit somewhat earlier than the May to July recruitment characteristics of northern rock sole and halibut (Norcross et al. 1995, Matarese et al. 2003, Hurst et al. 2007). In Oregon and Washington, USA, where English sole have been more thoroughly studied, juveniles recruit from March to May, as evidenced by the peak abundance of metamorphosing larvae (Krygier & Pearcy 1986). In the Gulf of Alaska coastal embayments, the depth distributions of Age-0 northern rock sole and Pacific halibut have been well studied (Norcross et al. 1995, 1999, Abookire 1998, 2000). After settlement, both species occur on sandy substrates, where northern rock sole are most abundant at depths of <40 m and halibut at <30 m. The aforementioned studies have not clearly documented the depth distribution of English sole; however, one study conducted over a single 24 h period (Hurst et al. 2007) suggested English sole occur principally in water of <5 m depth. This

is consistent with data from Washington and Oregon, where Age-0 English sole occur principally in water that is <3 m deep in estuaries (Rooper et al. 2003), but is somewhat deeper than the depth of <16 m found along the open coast (Krygier & Pearcy 1986). We are unaware of any salinity tolerance studies for these 3 species, but by virtue of where they occur as juveniles, all 3 species experience seasonal variability in salinity.

As is characteristic of most flatfishes, these species employ a well-developed detection–minimization strategy, integrating co-evolved morphological and behavioral adaptations: a flattened body, cryptic coloration and specialized behavioral tactics (Gibson 2005, Ryer 2008a). Behavioral tactics include burial, lowered body posture (when not buried) and reduced movement (Ryer et al. 2004, Lemke & Ryer 2006a). Recent experiments with English sole, halibut and rock sole demonstrate variation in the value of these behavioral tactics between species. Northern rock sole have been described as adhering to a risk-averse strategy; they tend to remain buried and/or prone on the bottom when not feeding, minimize movement, especially when predators are about, and do not flee unless a predator gets very close (Ryer et al. 2004). In contrast, English sole are risk-prone; they are less inclined to bury, often adopt posture with their head and forward portion of the body elevated off the substrate, and more actively move about, increasing their conspicuousness to potential predators. Pacific halibut are risk sensitive, modifying their behavior to reflect the presence or absence of predators. In the absence of predation risk they behave like English sole. When faced with predation risk, they behave more like rock sole. Standardized predation trials indicated that English sole were the most vulnerable to predation, rock sole the least, and halibut were intermediate between the other 2 species (Lemke & Ryer 2006b, Ryer et al. 2008).

In the present study, we used these 3 species to evaluate the hypothesis that intrinsic growth and risk-taking behavior are co-evolved and together influence fish distribution along a depth/predation gradient. We used 3 separate approaches: (1) behavioral experiments, (2) laboratory growth trials and (3) field sampling of natural populations. First, we compared the willingness of all 3 species to feed, both in the presence and absence of perceived predation risk; most of the prior behavioral work with these species, with the exception of Boersma et al. (2008), has not explicitly involved a trade-off between feeding and predation avoidance (Lemke & Ryer 2006a,b, Ryer et al. 2008). We predicted that, as

per previous characterizations, English sole would be risk prone and willing to feed under risk of predation, whereas rock sole would be risk averse, and halibut would be risk sensitive. Second, we conducted a growth experiment, predicting that the intrinsic growth of English sole would be greater than that of either halibut or rock sole. Lastly, using 5 yr of field data, we examined the depth distribution of the 3 species at one of our study sites, Holiday Beach in Kodiak, Alaska, USA, where the 3 species co-occur as juveniles during the summer. Prior tethering studies demonstrate an increase in predation pressure, mostly from large flatfish, with depth at this site (Ryer et al. 2010a). Thus, juveniles should experience lower predation risk in the shallows. However, invertebrate biomass, and hence forage base for juvenile flatfish, increases with depth (Ryer et al. 2010b). Therefore, juveniles should be faced with a classic trade-off between foraging and predator risk. With a risk-prone behavioral strategy, we expected that English sole would be restricted to the shallows (<5 m). In contrast, we expected northern rock sole to be found deeper, where their cryptic behavior would allow them to avoid detection by predators and, because prey are more plentiful, minimize their time spent foraging. We expected Pacific halibut to exhibit depth distribution intermediate to these 2 strategies.

MATERIALS AND METHODS

Fish collection and maintenance

Age-0 Pacific halibut and northern rock sole for laboratory growth and behavior experiments were collected from Chiniak Bay, Kodiak, Alaska, with a beam trawl (2 m wide, 3 mm mesh) and transported by air to the National Marine Fisheries Service laboratory at the Hatfield Marine Science Center in Newport, Oregon, USA. In lieu of transporting Age-0 English sole from Kodiak, they were collected from Yaquina Bay in Newport. All fish were approximately 30 to 50 mm total length (TL) at the time of collection. Age-0 fish were maintained in 2 m diameter (3000 l) tanks and fed to satiation 3 times weekly on a gel food diet composed of squid, herring, krill, amino acid supplements and vitamins. All experiments were conducted in flow-through seawater tanks at salinities between 28 and 33. These salinities correspond to the typical salinities encountered by the 3 species on their summer nursery grounds in Kodiak, and Yaquina Bay (Rooper et al. 2003, Hurst et al. 2005, 2007).

Laboratory feeding and perceived risk

Groups of up to 30 conspecific fish were transferred from holding tanks to a 2.3 m diameter feeder-acclimation tank in which individuals acclimated for 1 wk to a food delivery system similar to that described below for the experimental tanks. Before being transferred to the experimental tanks, fish were briefly transferred to a 2.3 m predator-acclimation tank. Time in captivity for juvenile flatfish ranged from 3 wk to 3 mo; therefore, the predator acclimation was designed to reinforce the credibility of predation risk after variable periods of captivity. The predator tank contained a pair of 3 yr old halibut as predators (27 to 32 cm TL). Predators had been deprived of food for 48 h to achieve reliable feeding performance. To control mortality, juveniles remained in the predator tank for 2 h or until visual estimation indicated 50% mortality had been reached, whichever time was shorter. While it is likely that the predator acclimation period selected was for fish that had well-developed anti-predator defenses, it was necessary in order to ensure responsiveness to the predatory threat (see Lemke & Ryer 2006a for description of relative vulnerabilities of the 3 species). Of the surviving conspecifics, groups of 2 fish each were haphazardly selected and relocated to experimental tanks. Fish were allowed to acclimate to the experimental tanks for 1 wk, during which time they were fed every other day using the feeder system described below.

The experimental tanks were cubic (0.5 m × 0.5 m × 0.5 m) glass tanks in which the bottoms were covered with sand to a depth of 2 cm: a 2:1 mixture of coarse (1 mm) to medium (0.5 mm) quartz particles. This sediment, while slightly coarser than the sediments where fish concentrate in the wild (Stoner & Abookire 2002, Stoner et al. 2007), still allows juveniles to bury, which is a critical factor in assuring nominal behavior and health (Stoner & Ottmar 2003). Tanks were kept on a 12 h light: 12 h dark photoperiod, with light at the water's surface being $\sim 10^{-1}$ $\mu\text{mol photons s}^{-1} \text{m}^{-2}$ during the daytime and $< 10^{-6}$ $\mu\text{mol photons s}^{-1} \text{m}^{-2}$ at night. Each experimental tank was equipped with a feeding apparatus, consisting of 2 food delivery systems going from the blind to the tanks, and 2 feeding stations on the tank bottom (for details see Boersma et al. 2008). Briefly, individual food pellets, entrained in a continuous water flow, were delivered by the 2 feeding tubes (the delivery systems) to positions just below the water's surface and directly above respective feeding stations located on the tank bottom. Pellets that appeared at the mouth of feeding tubes fell down through the

water column to their respective feeding stations: 10 cm diameter rings, with mesh grates, flush with the sand surface. Unconsumed pellets fell through the mesh grates and became unavailable, thus restricting the time period during which each pellet was accessible to the fish to 3 to 5 s (the duration of the fall).

Each experimental tank was positioned adjacent to an identically sized predator tank, separated by 6 cm to ensure visual contact (visual only) between experimental fish and the predator stimulus while allowing enough space for a 4 cm black foam divider between tanks. Each experimental–predator pair of tanks was separated from other pairs by an opaque black vinyl curtain to prevent transmission of visual cues between treatments. Additional visual barriers were employed to separate the observer from the tank. Video cameras were situated 0.91 m from experimental tanks and at a 20° angle above the level of the sand to provide an oblique camera view of each tank. Preliminary studies indicated that this view was most efficient at capturing juvenile fish behavior.

Fish were exposed to 2 risk treatments: predator absence (control) or predator presence (risk) for 2 min, followed by a longer behavioral observation period. The model predator was a weighted, 34.3 × 16.5 cm rubber flounder suspended by transparent line and made to undulate by an observer for the duration of the 2 min exposure period. Prior work has established that larger flatfish are dominant predators of juveniles at our Kodiak field sites (Ryer et al. 2010a). To initiate each risk exposure period, the opaque foam divider was raised remotely to allow juvenile fish visual contact only with the model predator (or empty predator tank). A model predator was used to ensure more consistent behavior than could be achieved with live predators. Preliminary trials indicated that juvenile flatfish responded to the model by exhibiting characteristic anti-predator behavior, and other laboratory experiments involving model predators support this observation (Ryer & Olla 1998). Additionally, pre-trial observations confirmed that fish did not respond to the movement of the foam divider alone.

Following the 2 min of predator exposure, or control exposure to an empty tank, the partition was lowered, and fish were observed during an 18 min focal period during which individual food pellets appeared from feeding tubes and fell to respective feeding stations at 1 min intervals. Randomization of where (which station) pellets dropped through the 18 min period helped assure that fish made deliberate moves to intercept pellets, thereby aiding in the identification of attempts to feed. The duration of this

focal period was chosen because preliminary observations indicated individuals of all 3 species would readily consume 18 pellets during this time period, provided they had not been fed during the previous 48 h. Thus, fish could be reasonably assumed to not lose interest in foraging during the focal period. Latency to the initial feeding attempt was recorded as seconds from the appearance of the first pellet at the mouth of the feeding tube until an individual's initial feeding strike. An attempt to feed, instead of successful food consumption, was used as the feeding metric because we assumed that the risk involved in a feeding attempt was equal to that of a successful consumption. In addition, fish frequently intercepted pellets immediately above the grating and it was sometimes difficult to determine whether a strike had been successful or not. We also recorded the cumulative time spent feeding by summing the total number of minutes that the fish fed (0 to 18 min). After the first predator exposure (Day 1), fish remained in their tanks and were fed 2 d later, then after an additional 2 d were subjected to the predation exposure and feeding sequence once more (Day 5). Five replicate trials were conducted for both predator and control treatments. After each trial fish were removed from experimental tanks and measured (TL). Fish ranged from 43 to 80 mm TL. Halibut (65.3 ± 2.34 mm [mean \pm SE]) were comparable in length to English sole (63.2 ± 2.04 mm), whereas both were longer than rock sole (55.5 ± 1.15 mm; $F_{2,45} = 9.35$, $p < 0.001$; Tukey's test, $p < 0.05$ for each).

Our response variables, i.e. feeding latency and time spent feeding, were averaged across each pair of fish. Preliminary analysis for both feeding latency and time spent feeding were conducted using repeated measures ANOVA, with day as the repeated measures variable. In this preliminary analysis, we did not concern ourselves with whether data conformed to the assumptions of homogeneity of variance normality. This analysis suggested a consistent effect of day, with latency decreasing and time spent feeding increasing from Day 1 to Day 5. Day did not interact significantly with either species or predator presence/absence to influence of latency or time spent feeding. Consequently, since exposure-dependent acclimation in risk sensitivity was not a principal goal of our experimentation, we decided to take the average of Day 1 and Day 5 for each dependent variable to simplify analysis and graphical representation of results. In the resultant data, feeding latency did not conform to assumptions of homogeneity of variance; for halibut in the 'no predator' treatment, all fish commenced feeding immediately,

i.e. responded to the first pellet, resulting in zero variance in this cell. Although ANOVA is robust relative to heterogeneity of variance (Lindman 1974), we considered this deviation severe enough to preclude use of standard ANOVA. Accordingly, we adopted a randomization (permutation) approach. Briefly, an ANOVA was conducted to obtain F -values for independent and interactive effects. Subsequently, the observed data were randomly reassigned to cells in the factorial design and the F -values recalculated. This was done 5000 times. To determine the significance of both independent and interactive effects, we calculated the proportion of F -values that were as extreme as or more so than the original F values. In our results, we present the original F -values, but the associated probability values are denoted as p_{rand} to alert the reader that this probability was calculated, not from an F -statistic table, but via randomization. Data for time spent feeding met basic ANOVA assumptions, as residuals were both homoscedastic (Bartlett's $\chi^2_5 = 5.04$, $p = 0.411$) and normally distributed (Shapiro-Wilk $W = 0.960$, $p = 0.185$).

Intrinsic growth

Growth experiments were conducted in 1 m diameter circular tanks provided with flow-through seawater. Sand covered the tank bottoms to a depth of 1 cm. Lighting was provided by overhead fluorescent lamps, on a 12 h light: 12 h dark photoperiod, producing illumination at the sediment surface of approximately $0.1 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. Seven fish were introduced to each of 12 tanks held at a temperature of $9 \pm 1^\circ\text{C}$. During the next 7 d, temperatures in tanks were gradually adjusted until they reached their final experimental temperatures of 5, 9, 13 and 16°C ($\pm 0.5^\circ\text{C}$). Fish were allowed another week of acclimation. During acclimation and the subsequent growth experiments, fish received a single daily ad libitum ration of gel food, and all uneaten food was removed after 2 h. The growth experiment commenced when fish were removed from tanks, measured (TL, mm) and weighed (g) and then returned to their respective tanks. Fish were measured and weighed twice more at 2 wk intervals. Care was taken to avoid damaging or stressing fish during handling, and observation indicated fish had generally resumed feeding 1 d afterwards.

Experiments were conducted first with English sole, then Pacific halibut and finally northern rock sole, with 84 individuals of each species (7 fish per tank, 3 tanks per temperature, 4 temperatures).

Although collected at approximately 30 to 50 mm TL, fish continued to grow during the 6 to 8 wk period during which they were initially held and subsequently acclimated to experimental tanks. Thus, when the growth experiment commenced, fish ranged from 42 to 82 mm TL and from 0.66 to 6.34 g wet weight. Nonetheless, we make the explicit assumption that relative differences in growth rate at this size can be used to characterize differences between species when they coexist in the nursery. Halibut (69.3 ± 0.73 mm) were longer than English sole (62.3 ± 0.80 mm), which in turn were longer than rock sole (50.8 ± 0.55 mm), with comparable species ordering for initial wet weights (length: $F_{2,249} = 180.0$, $p < 0.001$; weight: $F_{2,249} = 81.7$, $p < 0.001$; Tukey's test, $p < 0.05$ for each).

In lieu of individual markings, and by following the methods of Hurst & Abookire (2006), the fish in each tank were assumed to have maintained a rank order in body weight throughout the experiment. Mass specific growth rates were calculated as $100 \{[\ln(w_2 - w_1)]/t\}$, where w_2 and w_1 are fish wet weights on the second and first measurement days, respectively, and t is the number of days between measurements. Length-growth rates were calculated as the change in total length, divided by the number of days between measurements. Growth rates were calculated for each fish for each 2 wk growth period, as well as for the entire 4 wk period, then averaged by tank. Data were analyzed using analysis of covariance (ANCOVA, Sokal & Rohlf 1969) with temperature and species as independent variables, and either mean (by tank) initial fish weights or lengths as covariates. Initial analysis revealed that growth patterns during each 2 wk period were similar, so we focused upon growth over the entire 4 wk period. Residuals for weight-specific growth data were homoscedastic (Bartlett's $\chi^2_{11} = 9.28$, $p = 0.597$) and normally distributed (Shapiro-Wilk $W = 0.949$, $p = 0.100$). Similarly, when they were natural log transformed, residuals of length-growth data were also homoscedastic (Bartlett's $\chi^2_{11} = 17.8$, $p = 0.086$) and normally distributed (Shapiro-Wilk $W = 0.981$, $p = 0.783$). Where significant effects were detected ($p < 0.05$), differences in treatment means were examined using Tukey's multiple range test (Sokal & Rohlf 1969).

Depth distribution in the field

The depth distributions of English sole, Pacific halibut and northern rock sole were quantified using a

beam trawl with 2 m plumb-staff and 3 mm cod end mesh at Holiday Beach, a juvenile flatfish nursery embayment at Kodiak Island (Ryer et al. 2010a). A total of 52 tows were made during the months of July and August from 2005 to 2009. Trawls were made parallel to shore at depths ranging from 3 to 25 m. Tows were approximately 5 min in duration and GPS positions at the beginning and end of each tow allowed us to correct catches to a standard catch per unit effort for a 200 m distance. Trawls were grouped into 5 m depth bins. Where multiple trawls were made in a bin for a month/year combination, the mean number of Age-0 fish of each species was calculated. We then calculated the total number of individuals for each species captured from trawls for a given month/year combination. Lastly, the number of individuals of each species from each depth bin was divided by the respective species totals and multiplied by 100 to produce independent proportional abundance values for each species. This minimized variance associated with differences in abundance between years and months, as well as differences in sampling effort, and allowed us to more effectively examine the relative abundance of each species across depth. We conducted an ANOVA that compared the proportion of each species that were found in the shallowest, 0 to 5 m, depth bin. Residuals were both homoscedastic (Bartlett's $\chi^2_2 = 1.52$, $p = 0.469$) and normally distributed (Shapiro-Wilk $W = 0.964$, $p = 0.626$).

RESULTS

Behavior

Both species and predator presence/absence had an influence upon juvenile flatfish feeding behavior. When presented with food, the rapidity with which fish commenced feeding differed between species, as indicated by feeding latencies ($F_{2,24} = 4.45$, $p_{\text{rand}} = 0.023$; Fig. 1A). English sole generally began feeding sooner; northern rock sole took longer, while Pacific halibut were intermediate between them. Similarly, English sole tended to feed longer (Fig. 1B) than the other 2 species, although this was not statistically significant ($F_{2,24} = 2.65$, $p = 0.091$). The presence/absence of a model predator in the adjacent tank influenced behavior. Juvenile flatfish were slower to start feeding ($F_{1,24} = 23.33$, $p_{\text{rand}} < 0.001$) and spent less time feeding ($F_{1,24} = 11.15$, $p = 0.003$) when they had been exposed to the model predator prior to food introduction. Although visual examination of Fig. 1

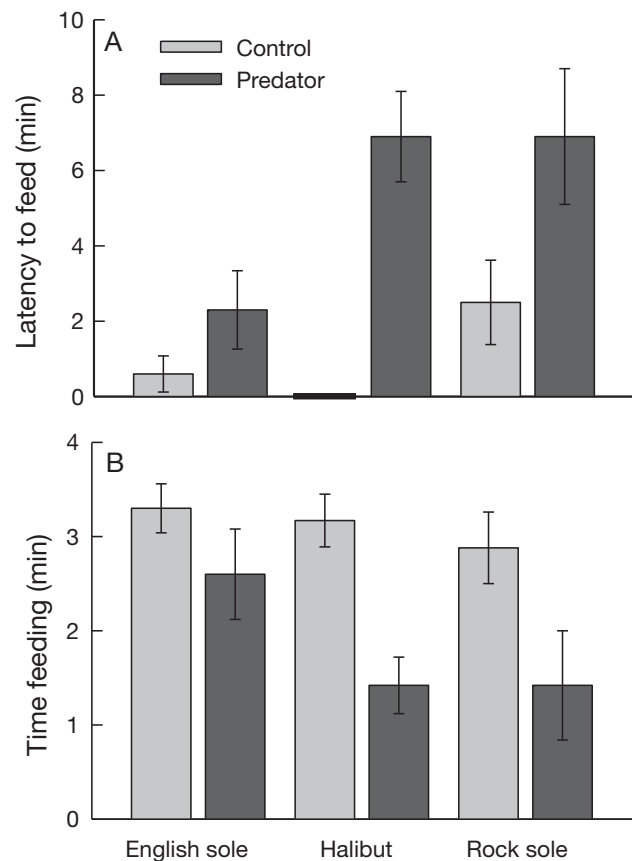


Fig. 1. Feeding behavior (mean \pm SE) of English sole, Pacific halibut and northern rock sole, as measured by (A) feeding latency (time till first feeding) and (B) cumulative time spent feeding, both in the absence (control) and presence of a model predator. Five replicate trials were conducted for each combination of treatments. For the halibut control trials, the mean latency was 0 with SE of 0

suggested that halibut were most likely to alter their behavior in the presence of a predator, and English sole the least likely, there were no statistically significant interactions between predator presence/absence and species for either feeding latency ($F_{2,24} = 2.80$, $p_{\text{rand}} = 0.086$) or time spent feeding ($F_{2,24} = 0.84$, $p = 0.443$).

Growth

As expected, temperature strongly influenced growth. Rock sole exhibited lower growth rates at high temperatures and a less pronounced dependence of growth on temperature, compared with English sole and halibut. Supporting this interpretation, ANCOVA detected significant species by temperature interactions in both average daily length

increments and average daily mass-specific growth increments (length: $F_{6,23} = 8.07$, $p < 0.001$; mass: $F_{6,23} = 3.21$, $p = 0.019$). Initial length did not significantly influence growth as measured by length increment (covariate coefficient < -0.01 , $F_{1,23} = 0.56$, $p = 0.463$). However, initial wet weight did significantly influence mass-specific growth (covariate coefficient $= -0.75$, $F_{1,23} = 0.56$, $p = 0.463$), with growth decreasing as initial wet weight increased. Within the overall pattern of increasing growth with temperature, daily length increments (Fig. 2A) were similar between species at both 5 and 9°C, but at 13 and 16°C, increments were greater for English sole and halibut than for rock sole (Tukey's comparison, $p < 0.05$). Rock sole daily length increments, and to a lesser extent those of the other species, decreased as temperature increased from 13 to 16°C; however, these decreases were not significant (Tukey's comparison, $p > 0.05$). Mass-specific growth (Fig. 2B)

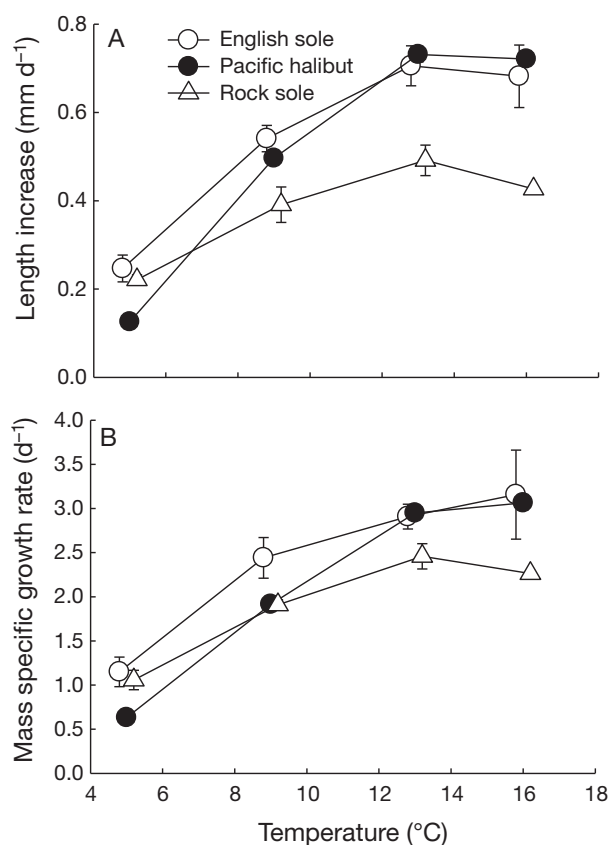


Fig. 2. Growth rates (mean \pm SE) of English sole, Pacific halibut and northern rock sole, in terms of (A) daily length increase and (B) daily mass-specific growth, at temperatures of 5, 9, 13 and 16°C. There were 3 tanks for each temperature, with the average growth calculated for each tank. Figure depicts the mean growth for tanks by species and temperature

demonstrated a similar pattern of difference between means as that seen for growth in fish length (Tukey's comparison, $p < 0.05$).

Field depth distribution

Of the 3 species, English sole were most clearly associated with shallow water, being most abundant at 0 to 5 m (Fig. 3). In contrast, both halibut and rock sole were more uniformly distributed. A significantly greater proportion of the total catch occurred in shallow water (< 5 m) for English sole, compared with halibut and rock sole ($F_{2,17} = 7.40$, $p = 0.005$).

DISCUSSION

Results of this study were partially consistent with our hypothesis that risky behavior and growth are positively correlated. Maximum growth rates of northern rock sole were the lowest of the 3 species, and they were the most behaviorally conservative when feeding. English sole had a higher growth rate and was the most unaffected by predator presence in the behavior trials. These 2 species also exhibited depth distributions in accordance with our predictions: English sole inhabited shallow, mostly predator-free waters, while rock sole were found in deeper waters. However, Pacific halibut did not match our predictions in any of the 3 experiments. We think that a broader understanding of the ecology of these 3 species may help explain this apparent anomaly.

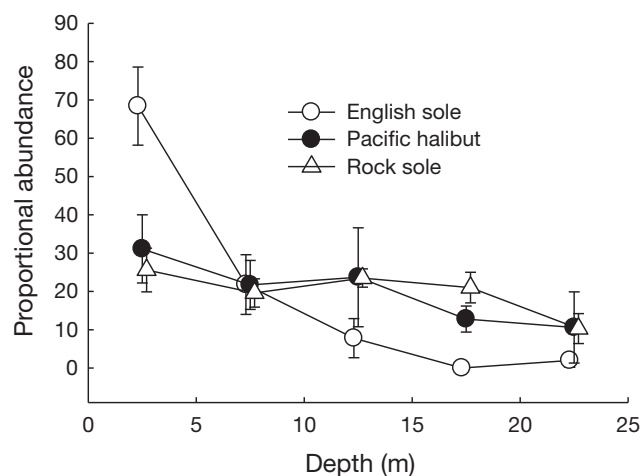


Fig. 3. Proportional abundance (mean \pm SE) for English sole, Pacific halibut and northern rock sole by depth at Holiday Beach, Kodiak, Alaska, during July and August from 2005 to 2009

Rapid growth can only occur when animals maximize foraging, which increases their vulnerability to predation (Metcalf et al. 1987). As visually oriented foragers, flatfish typically make short movements along the substrate, interspersed with sometimes lengthy pauses, as they search for prey (Gibson 2005). Such movements make juveniles more conspicuous to predators. Further, the visual and locomotor coordination involved in approaching and maneuvering to strike a prey item will almost certainly divert attention from vigilance. Additionally, the metabolic requirements of rapid growth may actually lead to physiological impairment of anti-predator capabilities such as swimming (Munch & Conover 2003). Thus, a trade-off between anti-predator behavior and growth clearly exists.

A number of published studies on fish have identified the relationship between high intrinsic growth rate and risky behavior and/or diminished anti-predator capabilities. For example, in aquaculture, where rapid growth is valued, domestication typically results in suppression of anti-predator behavior (Kohane & Parsons 1988). Presumably, selection for faster-growing animals also involves selection for increased secretion of growth hormone. Treatment of both wild and hatchery brown trout *Salmo trutta* with growth hormone, which increases energy demand and the motivation to feed, also increases risky behavior, such as feeding in close proximity to a predator (Johnsson et al. 1996). Similarly, in comparing low versus high intrinsic growth populations of Atlantic silverside *Menidia menidia*, it was demonstrated that individuals of the high growth populations were more vulnerable to predation by juvenile bluefish *Pomatomus saltatrix* (Munch & Conover 2003), owing to decreased swimming performance (Billerbeck et al. 2001).

However, this linkage between intrinsic growth rate and anti-predator behavior was not observed for halibut in our study. Previous studies have found halibut behavior to be more plastic than that of either English sole or rock sole; a result repeated in this study (Lemke & Ryer 2006a,b, Boersma et al. 2008). Both halibut and rock sole exhibited significant latencies to feed in the presence of the predator. Yet, like English sole, the halibut exhibited a high intrinsic growth rate, at least at the higher temperatures (10 to 12°C) characteristic of summer nurseries (Hurst & Abookire 2006). This could mean that our hypothesis that risky behavior and growth are positively correlated is not supported in this species and that overarching models to predict behavior and growth differences between species may be inherently

intractable. Alternatively, we may have been overly simplistic, because we did not acknowledge that growth, like behavior, is flexible and conforms to environmental influences, such as predation.

In the present study fish were reared with no predation risk. Would halibut exhibit lower growth when subjected to chronic risk? In the behavior trials, halibut tended to exhibit greater responsiveness to predation risk, suggesting that the risk sensitivity observed in burial behavior and activity (Lemke & Ryer 2006a,b) extends to foraging activity (Boersma et al. 2008). This raises the possibility that the high intrinsic growth rate exhibited by halibut may be suppressed under conditions of chronic predation risk. Predator-induced growth suppression has been documented for a number of fish species (Pratt & Fox 2002, Harter & Heck 2006), including juvenile northern rock sole (Ryer & Hurst 2008). In that experiment, actual predation was infrequent, probably owing to the cryptic behavior of rock sole; however, the presence of predators suppressed growth. We attempted to replicate this experiment with English sole, expecting that their risk-prone nature would result in negligible growth suppression. Despite identical protocols as in Ryer & Hurst (2008), nearly all the English sole were consumed, making it impossible to accurately estimate growth rates (authors' unpubl. data). While not the result we anticipated, it does attest to the inability of English sole to adopt more conservative behavior, suggesting they would be unlikely to exhibit predator-induced growth suppression in the presence of a potential predator. Further experimentation will be needed to determine whether behavioral plasticity in Pacific halibut also confers plasticity in growth. Lastly, we should acknowledge that we compared behavioral traits (as well as growth) of fish collected from Oregon (English sole) with those of fish collected from Kodiak (northern rock sole and Pacific halibut), making the explicit assumption that these individuals were representative of their respective species throughout their ranges. While we deem this a reasonable assumption, geographic variation in species behavior could conceivably be present.

As expected, English sole were largely restricted to the shallowest depths at Holiday Beach. This finding is consistent with depth distribution reported by Hurst et al. (2007) at the same site. Farther south, in Oregon, Washington and California, Age-0 English sole are broadly distributed in nearshore coastal waters (Krygier & Pearcy 1986, Rooper et al. 2003), but appear dependent upon estuaries (Brown 2006). Estuaries are important nursery areas for many juvenile fishes because of these habitats' higher tempera-

tures and abundant food resources that promote rapid growth, while low predator densities, structural refuges (e.g. eelgrass *Zostera marina*), and/or high turbidity enhance survival (Heck & Orth 1980, Boesch & Turner 1984, DeRobertis et al. 2003). This is precisely the type of habitat where one may expect to find a species that grows rapidly and has poorly developed anti-predator capabilities. In many respects, the shallows at Holiday Beach have characteristics similar to estuaries. Water < 5 m deep at Holiday Beach is typically 2°C warmer than at 15 m and more turbid owing to wave action (C. H. Ryer pers. obs.). Tethering studies also reveal that predation is markedly lower at 5 m than at 15 m depth (Ryer et al. 2010a). We consider it likely that English sole occur predominantly in this habitat because it offers the greatest survival potential, given their other life-history traits.

Unlike English sole, rock sole were more uniformly distributed across depth. With a behavioral repertoire that reduces their conspicuousness, rock sole can more successfully coexist with predators. Further, with a lower intrinsic growth rate, rock sole may adopt more of a time minimization foraging strategy (Schoener 1971), concentrating their foraging during dusk hours (Hurst et al. 2007), when they are less vulnerable to piscivores (De Robertis et al. 2003). Although Pacific halibut grew like English sole, their depth distribution was comparable with that of rock sole. If we had extended our sampling to greater depths, we may have seen that halibut occur at a somewhat shallower depth than rock sole (Norcross et al. 1995). Yet, halibut may have a different set of behavioral and morphological capabilities to mitigate predation risk, thereby allowing them to co-occupy much of the depth range utilized by rock sole. While both species occur predominantly on sandy sediments (Norcross et al. 1999, Stoner & Abookire 2002), halibut have a greater affinity for biogenic and physical habitat structure. In laboratory experiments, Stoner & Titgen (2003) found that halibut strongly preferred sediment with emergent structural features, such as sponge, bryozoans, shells and sand waves, whereas rock sole demonstrated a weaker preference for such emergent structure. Other juvenile flatfishes prefer habitat with emergent structure (e.g. winter flounder *Pseudopleuronectes americanus*, Pappal et al. 2009). Occupancy of structured habitats in a laboratory experiment mitigated predation for halibut to a greater extent than for rock sole (Ryer et al. 2004). In addition, halibut have more robust escape capabilities than rock sole, owing to narrower and thicker bodies, as well as a narrower

caudal peduncle; both attributes are associated with fast swimming (Stoner & Ottmar 2003). Halibut are more likely to flee an approaching predator, whereas rock sole tend to remain motionless and let the predator pass, regardless of habitat. This behavioral disparity reflects the consequences of flight; once flushed, there was a greater likelihood that halibut would escape, compared with rock sole (Ryer et al. 2004). The combination of affinity for structural refuge, behavioral plasticity and greater escape capacity may enable halibut to occupy much of the rock sole's broad depth range, while simultaneously maintaining a high realized growth rate.

On a more applied level, our results expand knowledge of intrinsic growth rates for species of ecological and commercial importance in the North Pacific Ocean. Like other ectotherms, temperature strongly influences growth in juvenile flatfish. Temperature growth data for rock sole are consistent with those measured for Age-0 juveniles by Hurst & Abookire (2006). Prior growth estimates for Age-0 halibut were available for 2 and 10°C (Hurst et al. 2005), and these estimates were generally consistent with our results. However, our temperature growth estimates for English sole were very different than those reported by Williams & Caldwell (1978), where growth decreased above 9.5°C. Our results indicate increased growth from 9 to 13°C, which would allow English sole to maximize their growth in shallow waters that frequently reach summer temperatures of 13°C at our Kodiak site and 16°C in Oregon and Washington estuaries (authors' pers. obs.). We can only assume that some factor associated with feeding or husbandry of their Age-0 English sole repressed the expression of intrinsic growth potential in the Williams & Caldwell (1978) study.

We consider it logical that species-specific temperature-growth relationships will influence seasonal patterns of growth in these species. While each species demonstrated a positive correlation between growth and temperature, the magnitude of the temperature response differed. Halibut were the most temperature dependent, while rock sole were the least. Halibut growth (in terms of length) was 5.8 times greater at 13°C than at 5°C. For English sole and rock sole growth was 2.7 and 2.3 times greater, respectively, at the higher temperature. Being more influenced by temperature, halibut are probably highly dependent upon maximizing growth during the summer, when temperature in the nearshore is high. In contrast, the lower summer growth rates of rock sole may be compensated for by continued modest growth during the rest of the year. Naturally,

this speculation rests upon the assumption that species-specific temperature dependence of growth we observed persists during the entire first year, rather than changing along differing ontogenetic trajectories.

In this work we have attempted to elucidate the relationships between anti-predator behavior, intrinsic growth rate and depth distribution in 3 juvenile flatfish species that co-occur in nursery areas around Kodiak during the summer months. We had predicted that 'relaxed' anti-predator behavior (English sole) would be associated with a shallow depth distribution and high intrinsic growth rate. In contrast, we predicted that 'more conservative' anti-predator behavior (northern rock sole) would be associated with slower growth and a deeper depth distribution. These predictions were largely borne out by our experiments and fish distributional data. Yet a third species (Pacific halibut), characterized by a more flexible anti-predator strategy, defied our predictions and demonstrated a high intrinsic growth rate, like English sole, but a deeper depth distribution, like rock sole. In formulating hypotheses, we had focused upon the pre-encounter predator avoidance tactics inherent in the flatfish detection minimization strategy. In retrospect, we may have overlooked the importance of affinity for refuge, post-encounter escape behaviors and behavioral plasticity, which also determine the realization of intrinsic growth and distribution along predation gradients. However, we feel that our approach of more holistically considering co-evolved behavior, growth and patterns of habitat use, provides a useful construct for understanding juvenile fish ecology.

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