Title:

Individual trophic specialisation in juvenile European seabass: Implications for the management of a commercially important species

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MRDC and AJ conceptualised the study, MRDC and WS collected and processed samples, MRDC conducted statistical analyses and wrote first manuscript draft, and all authors contributed equally to study development and manuscript review and editing.

Abstract:

The importance of individual trophic specialisation, where individuals use reduced and differing subsets of a population's overall resource base, has been increasingly recognised for its ecological implications, but has been little studied in a fisheries context. Stocks of the commercially important European seabass, *Dicentrarchus labrax,* have declined in recent years, and national and international policy has focused on increasing the minimum conservation reference size and restricting fishing effort in order to increase standing stock biomass. Inshore nursery grounds represent a critical habitat for this species in terms of recruitment to standing stocks, therefore additional management strategies at the local (and national) level, aimed at maximising survival and growth of juvenile seabass will complement recovery efforts. However a lack of understanding of the ecology of seabass at the level of the individual may limit the development of effective policy. To address this knowledge gap, we quantified levels of individual trophic specialisation in juvenile seabass from a common nursery area using stomach contents and stable isotope analyses applied to fish sampled at monthly resolution over an annual cycle. We found strong evidence for individual specialisation in stomach contents beyond seasonal and age effects on diet, and that the strength of specialisation exhibited seasonality, being absent in the spring. This was corroborated by stable isotope analyses, which showed significantly higher variance in seabass compared to two other concurrently sampled, sympatric bentho-pelagic predators. Our findings suggest that juvenile seabass form trophic-generalist populations composed of specialised individuals which may be driven by intraspecific competition within the nursery ground. This study emphasises the importance of incorporating individual specialisation into management strategies aimed at protecting the vulnerable life stages of this commercially important species.

Introduction:

The functional roles of different species within ecosystems are often quantified by parameters that capture typical or 'average' behaviours at the population level (Bolnick et al., 2003). However even when differences due to sex and ontogeny are accounted for, such descriptions miss a growing body of evidence showing that individuals within populations often exhibit differences in resource use, known as intraspecific niche variation or individual specialisation (reviewed by Araujo et al., 2011). For example, at a local scale a population observed to have a generalist diet may be composed of individuals consuming a similar, diverse suit of prey (cosmopolitan forgaing) or from individuals consuming different but limited subsets of prey drawn from the broader population prey-base i.e. individual trophic specialisation.

Individual specialisation may be response to density-dependent limitation of resources, or may arise due to variation in behavioural traits such as boldness, as differential behaviours expose individuals to different ecological opportunities (reviewed by Toscano *et al.,* 2016). Such specialisation is also a potential mechanism through which levels of intra- and interspecific competition, as well as predation, can be modulated (Araújo *et al.,* 2011). It is important to note however that the contributions of such mechanisms to individual specialisation are context dependent (Evangelista et al., 2014). Nevertheless, among other ecological implications, the degree of individual specialisation influences the stability of populations (Bolnick et al., 2011). Despite its potential importance for conservation and management (Bolnick et al., 2003; Hammaerschlag-Peyer & Layman 2010), there has been surprisingly limited appreciation of individual-level niche variation in commercially exploited species or in a fisheries context (but see Cucherousset et al., 2011).

The European seabass, *Dicentrarchus labrax* (Linnaeus, 1758, hereafter seabass) has been, until recently, an important resource for inshore recreational and commercial fisheries in the southern UK. DEFRA, the UK governmental department for environment, food and rural affairs, reports that 897t of seabass were landed into the UK in 2012 (mostly into England by the UK commercial fleet) with a first sale value of £5.6million (MMO, 2013). It is further estimated that an additional 230-440t of seabass were retained by recreational anglers in England in the same year (DEFRA, 2013) with an uncertain but likely significant economic benefit to local communities. However a large decline in seabass stocks has occurred since 2010 (*circa* 18kt in 2010 to below 7kt in 2017) and stocks are now identified as below B_{lim}, the limit reference point for spawning stock biomass (ICES, 2017). Since 2018, strict EU fishing regulations have come into force in an effort to improve seabass stock levels (MMO, 2018). Coupled with these EU-wide regulations, localised management strategies within England are currently being reviewed in conjunction with marine protected area (MPA) designation and the conservation of other species of interest. However it has been highlighted that uncertainties in seabass ecology, particularly at the individual level, are impeding policy development for the protection of this species (López *et al.,* 2015).

In light of this paucity of data and because of the migratory nature of the species, recent research efforts have focused on the individual movements of adult seabass using various tagging techniques (Doyle et al., 2017; de Pontual et al., 2018; O'Niell et al., 2018) and retrospective geochemical tracers (Cambrie et al., 2016) in order to better delineate stocks. Juvenile fish represent a vulnerable but also vital ontogenetic stage in terms of stock management as their successful recruitment directly increases standing stock biomass. Nursery grounds are therefore considered critical habitat and processes influencing juvenile survival rates, such as feeding behaviours, are important to consider within a management context (Le Pape & Bonhommeau, 2015). Current knowledge on the diet of seabass is focused towards young of the year (Aprahamian & Barr, 1985; Laffaille *et al.,* 2001; Cabral & Costa, 2001; Martinho *et al.,* 2008) and mature adults (Kelley, 1987; Spitz *et al.,* 2013). However the consensus is that seabass are typically opportunistic, generalist predators with diets reflecting the locally abundant prey that are available to the given life history stage and season (Pickett & Pawson, 1994; Rogdakis *et al.,* 2010). Despite the breadth of dietary studies, none to date have explored feeding behaviours at the individual level within seabass populations. Anecdotal evidence suggests that individual specialisation does occur in seabass populations: local differences in habitat preferences have been noted, with individuals occupying different microhabitats within estuaries (Kelley, 1986; O'Niell et al., 2018) and differential feeding patterns have been reported within young of the year cohorts (Fonseca *et al.,* 2011). Given its potential importance for the management of seabass, the lack of information on the dietary strategies at the individual-level for this commercially-relevant species including measures of individual specialisation should be addressed.

Here, we assess the level and nature of individual trophic specialisation of juvenile seabass, including young of the year, one year and two year aged cohorts across a seasonal cycle within an estuarine nursery ground. Individual specialisation in the diet can be quantified using stomach content data (Bolnick *et al.,* 2002; Araújo *et al.,* 2008; Zaccarelli *et al.,* 2013), stable isotope analyses (Layman *et al.,* 2007a; Dermond *et al.,* 2018) or a combination of both (Araújo *et al.,* 2009). Stomach content analyses offer high taxonomic resolution, however the information provided reflects a narrow time window of up to several hours prior to capture and may not record the true, time-averaged diet (Nielsen *et al.,* 2018), potentially biasing inferences towards higher levels of individual specialisation. Stable isotope analyses provide indirect information on the diet composition over a time frame of up to several weeks in the case of muscle tissue, as incorporation into the body occurs through tissue turnover and somatic growth (Fry & Arnold, 1982) but at the cost of reduced dietary resolution. High levels of individual specialisation in diet, where individuals utilise narrow subsets of the population's overall prey-base, increases dispersion of the population within isotopic space.

Providing that potential diet items have distinct isotopic compositions, relative levels of specialisation can be inferred from the isotopic variance, with higher variances being associated with higher levels of individual specialisation (Layman *et al.,* 2012). Using stomach content and stable isotope data, we test the hypothesis that the resident juvenile seabass population consists of specialised individuals rather than individuals with cosmopolitan foraging behaviours. We then explore whether levels of individual trophic specialisation, if any, vary on a seasonal basis and between age cohorts.

Materials and Methods:

Study Area, Sample Collection and Processing:

Sampling was conducted in Southampton Water; a partially mixed estuary located in southern England (50°52'N, 01°22'W). Southampton Water is 1.96km wide at its mouth and approximately 10km in length. It has an artificially deepened channel for much of its length, maintained by periodic dredging, and large areas have been extensively modified for industrial activity. The estuary is fed by three rivers, the Test, Itchen and Hamble, which have a catchment area of approximately 1500km^2, and is hypernutrified with relatively low turbidity: suspended particulates average 40mgl^{-1} at the mouth falling to 5-10mgl^{-1} at the head, making it a highly productive environment (Townend, 2008).

Physical sampling of seabass (and other fish species) was conducted opportunistically as part of an ongoing, licensed, environmental monitoring survey of Southampton Water. Individual fish were sampled via a fish-return system linked to a cooling-water intake pipe within Southampton Water. A 10mm mesh collection net was used on the fish-return system over a 24-hour period (one 18-hour overnight collection and six hourly collections) on a monthly basis from November 2015 through to January 2017. Catches were sorted, identified, counted and measured, and all available seabass collected. Samples were supplemented from quarterly trawls (part of the same survey), all of which fell within 3km of the intake pipe and within Southampton Water. A 10m-bottom otter trawl was used with a 10mm mesh cod end, trawled for 10 minutes with up to 10 trawls per quarter. As part of the survey's consent and/or exemption from the MMO (Marine Management Organisation) for scientific surveys, and with the cooperation of the Southampton harbour authority, all fish were treated as humanely as possible and only specimens deemed to stand no chance of survival were retained. Individual survivability within the nets is likely to be influenced by body condition, and therefore past feeding behaviour, potentially biasing results. However most individuals sampled came from the overnight net collection period, where prolonged capture resulted in limited viable live returns (approximately 90% retention of total seabass caught). All sampled fish were frozen post-collection until subsequent analysis.

For dietary analyses, seabass specimens were defrosted, standard length and wet-mass measured, and stomachs excised. Stomach contents were weighed separately, contents identified and sorted into 12 broad trophic categories under a binocular microscope (pelagic copepods, amphipods, isopods, mysids, shrimps, crabs, polychaetes, bivalves, gastropods, fish, algae and detritus). For each category, numeric counts were taken and volume estimated following the method described by Hellawall & Abel (1971).

For stable isotope analyses, small plugs of muscle (*circa* 0.5cm^3) were taken from below the second dorsal fin, with skin removed, and stored in eppendorf tubes and refrozen. For small individuals, whole fillets were taken, with skin, bone and spines removed to avoid isotopic disparity between tissue types. Samples were freeze-dried at -55°c for 24 hours (Heto Power dry LL3000) then stored in sealed containers at room temperature. Dehydrated tissue samples were homogenised and weighed using a Sartorius microbalance with a precision of 0.001mg. Samples of 1.9mg ± 0.1mg were weighed out into tin capsules and were analysed at NERC Life Sciences Mass Spectrometry Facility, SUERC, using an Elementar vario Pyrocube (Hanau, Germany) coupled to an IsoPrime (now Elementar) VisION Mass Spectrometer (Cheadle, UK). All isotopic values are reported relative to their respective international standards: Pee Dee Belemnite (PBD) for carbon, atmospheric air for nitrogen and Cañon Diablo Troilite (CDT) for sulphur. Isotopic compositions are expressed as delta (δ) per mille (‰) notation, given by:

$$\delta X = \left[\frac{R_{sample}}{R_{standard}} - 1\right] \times 1000$$

where X is either ^{13}C, ^{15}N or ^{34}S and R is the ratio of ^{13}C:^{12}C, ^{15}N:^{14}N or ^{34}S:^{32}S. Equipment calibration and compensation for drift over time was corrected for by internal standards run between every 10 samples, with analytical measurement errors (s.d.) of 0.1‰, 0.2‰ and 0.6‰ for $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ respectively. As sample C:N ratios were relatively low and similar across all samples and species (mean of 3.22 ranging from 3.08 to 3.51), lipid correction was not deemed necessary and raw $\delta^{13}C$ values were used throughout the study (Skinner *et al.,* 2016).

Dietary Analyses:

Seabass were assigned an age class determined by size cohorts of standard length and month of capture following Claridge and Potter (1983). Two dietary indices were calculated to describe trophic behaviour for each seasonal age class following Rosecchi *et al.* (1988):

$$I_{RI} = p_F \times (p_N + p_V)$$

$$I_{MF} = \sqrt{\left\{\frac{p_V \times (p_N + p_F)}{2}\right\}}$$

where p_F is the proportional frequency of occurrence of prey categories across stomachs containing food, p_N is the proportional numerical abundance of prey categories and p_V is the proportional volume of each prey category. The index of relative importance, I_{RI}, was first described by Pinease *et al.* (1971) whereas the main food item index, I_{MF}, was described by Zander (1982). While Zander (1982) originally used percentage dry weight, we used percentage wet volume (following Rosecchi *et al.,* 1988) and normalised each index to its total sum within each seasonal age group to allow comparisons between different age classes and seasons. The vacuity index, I_V, was also recorded as the proportion of empty stomachs for each group.

Statistical Analyses of Individual Trophic Specialisation:

Since individual-level diet variation can be confounded with other sources of intra-population diet variation (Araújo et al., 2011), we first tested for differences in diet associated with ontogeny and season. We utilised the proportional similarity index, *PS*, (Schoener, 1968):

$$PS_{ij} = 1 - \frac{1}{2}\sum_{k}\left|p_{ik} - p_{jk}\right|$$

where p_{ik} and p_{jk} are the proportions of prey category k (by numerical abundance) in the diets i and j respectively. PS_{ij} is a measure of the overlap in the diets i and j, ranging from 0 (no overlap) to 1 (complete overlap). We calculated PS between each individual and the average diet of the whole population, age class, season, and age class by season (average diet taken as the mean of individual proportional diets for a grouping). Increasing mean PS values within group comparisons compared to the whole population suggests that the grouping explains some of the variation in individual diet. To test whether any explained diet variation was due to a random grouping effect, we randomly permutated across age classes and seasons and compared observed values to those from 10,000 draws to obtain approximate p-values. Results indicated that the increase in average proportional similarity from 0.287 for the whole population to 0.439 for age class by season was not due to a random grouping effect ($p \approx 0.0049$). Seabass were therefore grouped in age classes by season for subsequent analyses (average proportional similarity for age class and season were 0.360 and 0.349 respectively). Seasons were defined as November to January, February to April, May to July and August to October for winter, spring, summer and autumn respectively.

To quantify the strength of individual specialisation based on stomach content data we calculated the E index, which is based on average pair-wise individual overlap (Araújo *et al.,* 2008) given by:

$$E = 1 - \frac{2 \times \sum_{pairs} PS_{ij}}{n(n-1)}$$

where diets i and j are those of two individuals from a group of size n and where E ranges from 0 (no individual specialisation) to 1 (maximum individual specialisation). $\sum_{pairs} PS_{ij}$ is the sum across all possible *ij* pairs, the number of which is equal to $n(n-1)/2$. The E index may be biased towards higher values when individuals consume low numbers of prey items, therefore the observed index (E_{obs}) is adjusted based on a null value calculated from Monte Carlo resampling methods to allow direct comparison between groups (Zaccarelli *et al.,* 2013):

$$E_{adj} = \frac{E_{obs} - E_{null}}{1 - E_{null}}$$

where E_{null} is the mean value from the null distribution.

The statistical significance of E was tested and the value of E_{null} derived using a Monte Carlo approach to generate a null diet distribution (n=9999), based on creating datasets were individuals sample stochastically from a shared prey distribution (the average diet by numerical abundance of the group). For each simulation, individuals draw prey items equal to the number that each individual was observed to contain within their stomachs. This approach assumes that each prey item within a stomach represents an independent feeding event which may not hold if prey are patchily distributed. Further, the null model does not incorporate stomach fullness or differences in prey contributions to satiation and therefore assumes relatively equal sized prey items. We limited the calculation of the E index to those groups with $n \geq 5$ (individuals with empty stomachs were excluded from analyses). In addition to the seasonal age groups, we calculated E for the combined 2+ cohort from winters 2015 and 2016 (n = 5 and 7 respectively) to make sample sizes comparable to other groups for which it was calculated (n ranging from 10 to 13). Mean proportional diets are taken as the average proportional diet of individuals (i.e. not the proportional diet of summed prey items across all individuals).

For populations feeding across the same isotopic baseline, higher levels of individual specialisation can be inferred from increasing isotopic variance as the tissues of individuals equilibrate to different, isotopically distinct subsets of the population's overall prey base (Layman *et al.,* 2012). Suitable sampling of the seasonally varying isotopic baseline represents a considerable logistical effort that was beyond the scope of this study. We therefore instead calculated the dispersion of individual seabass in isotopic space compared to two sympatric, concurrently sampled, generalist bentho-pelagic fish predators: pout, *Trisopterus luscus* (Linnaeus, 1758), and whiting, *Merlangus merlangus* (Linnaeus 1758) in order to gage levels of relative individual trophic specialisation among these three species. Juvenile pout and whiting occur within estuaries, exhibit limited movements and predate on a variety of invertebrate and fish prey (Heessen *et al.,* 2015) making them suitable candidates for comparison.

Due to logistical constraints, subsamples of seabass, pout and whiting that were representative of the size and temporal distribution within Southampton Water were selected for isotopic analysis by random draws from monthly size-frequency averages (using seven years of survey abundance data). The size ranges of pout and whiting represent a similar range of ontogenetic stages to those of sampled seabass (see Fig. 1). Pout are a fast growing gadoid that typically attain lengths of up to 18cm after their first year and up to 27cm after their second year at which point they mature (Heessen *et al.,* 2015). Therefore data represented here encompass a majority of 0-group and a smaller proportion of 1-group juveniles. The growth of whiting is variable across their distribution (Heessen *et al.,* 2015) however data from southern England suggest that whiting typically attain lengths of 17cm after their first year of growth, up to 25cm during their second and approximately 32cm after their third (Potter *et al.,* 1988). As a majority of whiting typically mature after their second year of growth (Heessen *et al.,* 2015), data here likely represent a mix of 0 and 1-group juveniles and recently matured adults (~2). Note that for seabass, the age of 50% maturity varies from 4-7 years across their distribution, with an increasing trend with decreasing water temperature (Heessen et al., 2015).

Isotopic variance was compared graphically by constructing standard ellipses, a two dimensional equivalent of standard deviation containing approximately 40% of the data, and differences in dispersion tested for using Euclidean distances of individuals from the population centroids following Anderson (2006). Prior to analyses, isotope values were normalised to their observed range across all species so that distances in each isotope dimension were weighted equally. Post-hoc pair-wise comparisons using a Tukey test followed significant differences in dispersion.

All statistical analyses were conducted in R 3.3.2 (R Core Team, 2016) with individual specialisation metrics calculated using the package "RInSp" v1.2 (Zaccarelli *et al.,* 2013), dispersion tests using the package "vegan" v2.4-5 (Oksanen *et al.,* 2017) and Bayesian standard ellipses constructed using the package "SIBER" v2.1.1 (Jackson *et al.,* 2011). Priors used to calculate the posterior distribution of standard ellipse areas were the inverse Wishart distribution with 2 degrees of freedom and a normal prior around the mean with a precision of 10^{-3}. Two chains of 10,000 iterations were run with a burn in of 1000 and thinned by a factor of 10.

Results:

Dietary Analyses:

The number of individual seabass collected are summarised in table 1, totalling 115 individuals over the whole period. As only one individual was collected during the summer of 2016, this period was excluded from further analyses. The age class 2+ includes all individuals estimated to be 2 years or older: only two individuals were estimated to be 3 years of age and one individual as 4.

Although there were moderate levels of stomach vacuity, there was generally broad agreement between I_{RI} and I_{MF}, table 1. Briefly, polychaetes appear to be a highly important food source for seabass across all age classes and seasons. Amphipods were a key resource for young of the year throughout the entire seasonal cycle, however they were only important for the year 1 cohort in winter 2015 and absent in all but one individual from the 2+ age class. Copepods were only present in the diet of the young of the year in the autumn, where they were the dominant food source, but absent in all other seasons and age classes. Prey fish showed a similar pattern for age class 2+, being the main food source in autumn but only making minor contributions to the diet during other seasons and practically absent in other age classes. Shrimp and crabs contributed to the diet of all age classes, although more so for the 2+ seabass, with contributions shifting over seasons. Over the winter period, bivalves were a considerable component of the diets of the young of the year and the 2+ age class. Other prey categories made only minor contributions to the diet of seabass.

Individual Trophic Specialisation:

For the six age class by season groups tested, four showed significant levels of individual specialisation as determined by E_{adj}, see table 2 (null distributions are provided in the supplementary materials). Through time, significant individual trophic specialisation was expressed in juvenile seabass during the autumn and winter seasons, however was absent in the diet during the spring. Results also indicate that the degree of individual trophic specialisation differed between age groups, with the 2+ cohort consisting of more specialised individuals, as expressed by larger E_{adj} values, compared to the young of the year during the winter.

A total of 42, 53 and 44 individual bass, pout and whiting respectively were analysed for their stable isotope compositions. The individual size distributions are shown in Fig. 1 and are relatively similar across species, although whiting were larger on average (mean length of 127mm, 121mm and 215mm for seabass, pout and whiting respectively). The three isotope biplots for carbon, nitrogen and sulphur are shown in Fig. 2. Seabass show greater variance in isotopic space compared to pout and whiting, indicated by the large standard ellipses whose posterior distributions were greater across all three stable isotope biplots, Fig. 2. This was confirmed by significant differences in dispersion distances ($F_{2,135} = 14.5$, $p < 0.001$), with post-hoc testing indicating that seabass were more dispersed compared to pout (difference in mean distance from centroid of 0.929, $p < 0.001$) and whiting (difference of 1.091, $p < 0.001$). Pout and whiting showed no significant difference in dispersion (difference of 0.161, $p = 0.719$).

Discussion:

The research presented here, to the best of our knowledge, is the first quantitative study on the extent of individual dietary behaviour of juvenile seabass. We hypothesised that seabass within Southampton Water, an important nursery ground for this species, exhibited individual trophic specialisation and this hypothesis was confirmed using two complementary sources of evidence: stomach content data and stable isotope analyses, which capture short and longer term dietary behaviours respectively. The *E* index of individual trophic specialisation from stomach content data yielded significant results for the majority of cohorts after accounting for seasonal and ontogenetic changes in diet. Similarly, stable isotopes analyses revealed that seabass had greater isotopic variation compared to pout and whiting, suggesting comparatively higher levels of individual trophic specialisation compared to two sympatric species with similar population-level feeding behaviours. Previous dietary studies have concluded that seabass exhibit opportunistic feeding behaviours based on the observation that the diet typically varies in relational to regional differences in the availability of potential prey (Pickett & Pawson, 1994). For example, seabass in south east England predominantly feed on the readily available Nereididae spp., amphipods and *Carcinus maenas* (Fonseca et al., 2011), whereas in the Wadden Sea the abundant brown shrimp, *Crangon crangon,* dominates the diet (Cardoso et al., 2015). However here we explicitly tested for the presence of individual specialisation within a single locality, Southampton Water, within which juvenile seabass are presumably exposed to the same potential prey base, and found that the population consists of specialised individuals.

Individual specialisation has been documented in a variety of other species (e.g. Tinker et al., 2012; Rosenblatt et al., 2015), but most notably fishes, although it is unclear whether this is a true reflection of prevalence across taxa or due to research bias (Araújo et al., 2011). Multiple mechanisms may give rise to individual specialisation, however increasing density levels, a proxy for intraspecific competition, has been shown to be a key driver of specialisation in fishes both in the field (Svanbäck & Persson, 2009; Frédérich et al., 2010; Evangelist et al., 2014) and through mesocosm experiments (Huss et al., 2008). As the system carrying capacity for a population is approached and individuals readily compete for finite resources, dietary specialisation may confer increased fitness due to increased profitability from different prey (Newsome et al., 2015). For example, a study on individual specialisation within a population of European eels found increased body condition in individuals that specialised on either invertebrate or fish prey compared to individuals that consumed both (Cucherousset et al., 2011). While estuarine and coastal nursery grounds are highly productive, they typically represent food-limited environments for juvenile fish due to high population densities (Le Pape & Bonhommeau, 2015). Although abundances of juvenile seabass where not explicitly estimated in this study, an ongoing regional seabass survey of Southampton Water and the surrounding areas suggests that recruitment into the nursery was particularly strong in 2016 compared to the preceding 20 years (Brown, 2017). High densities may therefore explain the observed incidence of individual trophic specialisation in seabass during this study, but whether individual trophic specialisation is consistently expressed on an interannual basis as the abundance of juvenile fish fluctuates remains unclear.

Variability in the local environment has also been suggested as a potential mechanism giving rise to individual specialisation: brown trout, *Salmo trutta,* have been shown to express higher levels of individual specialisation in hydrographically-stable rivers compared to less stable rivers (Dermond *et al.,* 2018). The reasoning is that environmental variability imparts variability in available resources and therefore increased specialisation on a small subset of resources becomes a less favourable trade off as resource abundance is less predictable (Dermond et al., 2018). In this study, we compared dietary specialisation through the use of stable isotopes between populations of sympatric predators exposed to the same environmental dynamics over the course of a year, and therefore environmental variability alone cannot explain the differences in specialisation observed among seabass, and pout and whiting.

Although variable across the year, changes in prey abundance express strong but predictable seasonality in temperate systems. Despite this, stomach data showed seasonal differences in the level of individual trophic specialisation in seabass, with the *E* index only being significant during the autumn and winter. The role of seasonality in individual-level specialisation, or indeed of temporal trends in general, has so far received relatively little attention in the literature (but see Hammerschlag et al., 2010), but could potentially help in identifying key drivers. This study was conducted towards the northern limits of known seabass nursery grounds, making the winter and associated cold temperatures a critical period for juvenile survival. Loss rates can be high for seabass in nursery areas in southern England, with near total juvenile mortality during notable cold spells (Kelley, 2002), although the deeper channel within Southampton Water likely offers refugia from such extremes. The abundance and population density of juvenile seabass is therefore expected to be relatively low emerging from winter into spring, and coupled with increasing levels of productivity within the estuary, would result in reduced levels of intraspecific competition, potentially explaining the relative lack of individual specialisation during spring. It is interesting to note that during the spring, polychaetes dominated the diets of these two cohorts (I_{RI} = 0.60 and 0.93 for young of the year and age 1 respectively, see table 1) compared to other groups for which individual specialisation was quantified, suggesting that polychaetes are a preferred prey. While reduced prey diversity, and therefore reduced ecological opportunity, is also known to reduce individual specialisation in predatory fish (Layman et al., 2007b), this appears not to be this case here as the number of prey categories present in the stomachs of different groups is similar across ages and seasons (tables 1 and 2).

It is important to note that, compared to other dietary studies on seabass, the total number of seabass sampled here is relatively low (e.g. 404 in Spitz *et al.,* 2013 and 570 in Rogdakis *et al.,* 2010) and that suitable sample sizes were not available to test across all combinations of age class and season. For statistical analyses, we used null models based on Monte Carlo resampling that maintain data structure and therefore incorporate small sample sizes when testing for significance (Zaccarelli *et al.,* 2013). For stable isotope analyses, we included as balanced a design as possible, given the available samples. Considering the agreement between stomach content data and stable isotope analyses, we have confidence in the results presented and the conclusions that are drawn despite the limited sampling,.

The presence of individual trophic specialisation in juvenile seabass has implications for management as it implies behavioural differences among individuals that may influence the stability of the population (Bolnick et al., 2011; Toscano *et al.,* 2016). This is corroborated by behavioural observations in seabass showing phenotypic differences in risk aversion (Millot *et al.,* 2009; Killen *et al.,* 2011), shoaling (Boulineau-Coatanea, 1969), and segregation along temperature and salinity gradients (López *et al.,* 2015). Spatially, seabass have recently been shown to exhibit high but differing site fidelities within an estuarine system (Doyle et al., 2017). In terms of fisheries management, this is important because (1) conservation actions should capture the range of individual behaviours in order to best protect the population and its inherent diversity (Bolnick et al., 2003), and (2) such information is required to produce realistic species or ecosystem models that are used to inform policy decisions (López *et al.,* 2015). For juvenile seabass in particular, the expression of individual trophic specialisation appears related to levels of intraspecific competition, although it is appreciated that only one location was included in this study and therefore the regional extent of specialisation is unclear. Management measures designed to maintain diverse habitats facilitating individual specialisation and reducing levels of intraspecific competition will therefore promote survival and population growth in juvenile seabass during early, vulnerable life stages that are more susceptible to climatic fluctuations (Kelley, 2002; Le Pape & Bonhommeau, 2015; Bento *et al.,* 2016) (Araújo et al., 2011). Enhanced juvenile survival will contribute to increasing standing stock biomass at a time when efforts are required at multiple levels to the recovery of this commercially important species (ICES, 2017; MMO, 2018).

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Figure and Table Legends:

Fig. 1: Length-frequency distributions of seabass (top left, n = 42), pout (top right, n = 53), and whiting (bottom left, n = 44), for which stable isotopic signatures were measured.

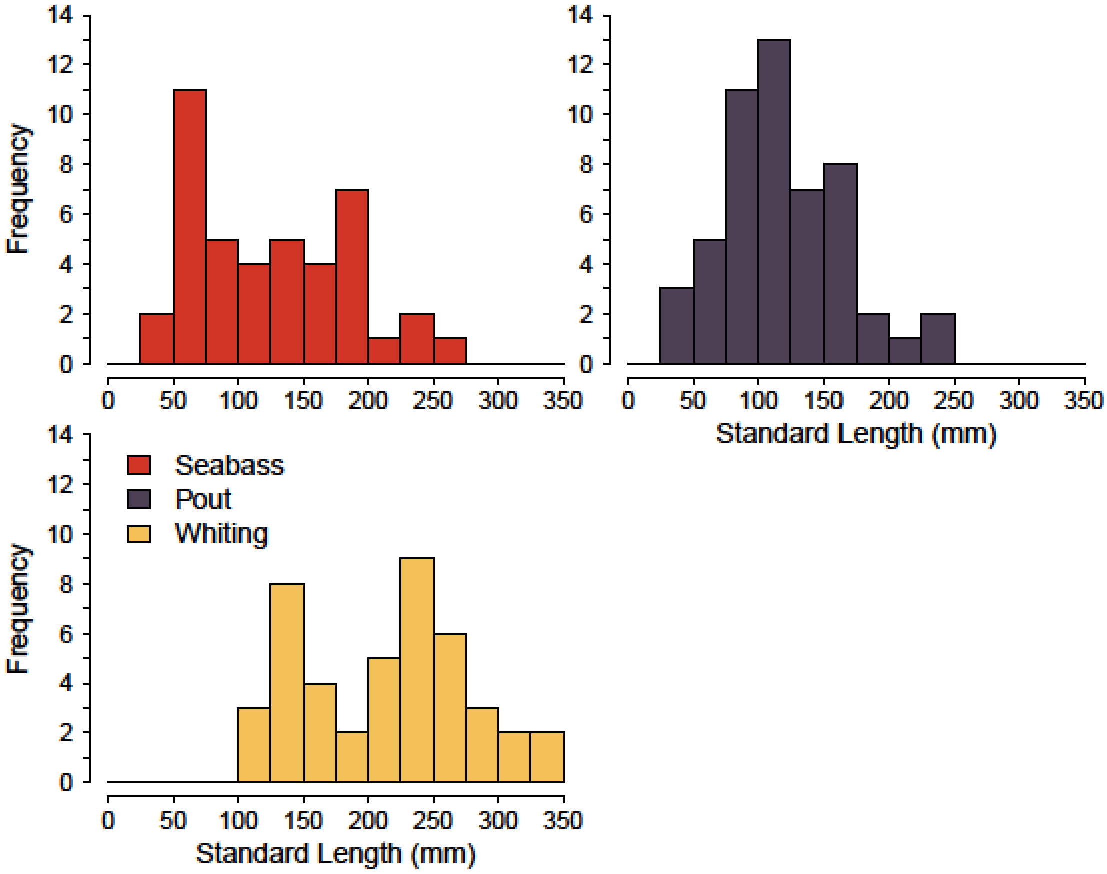
Fig. 2: Stable isotope biplots of individual sea bass, pout and whiting, with standard ellipses plotted for each species. Bottom-right panel shows the Bayesian posterior

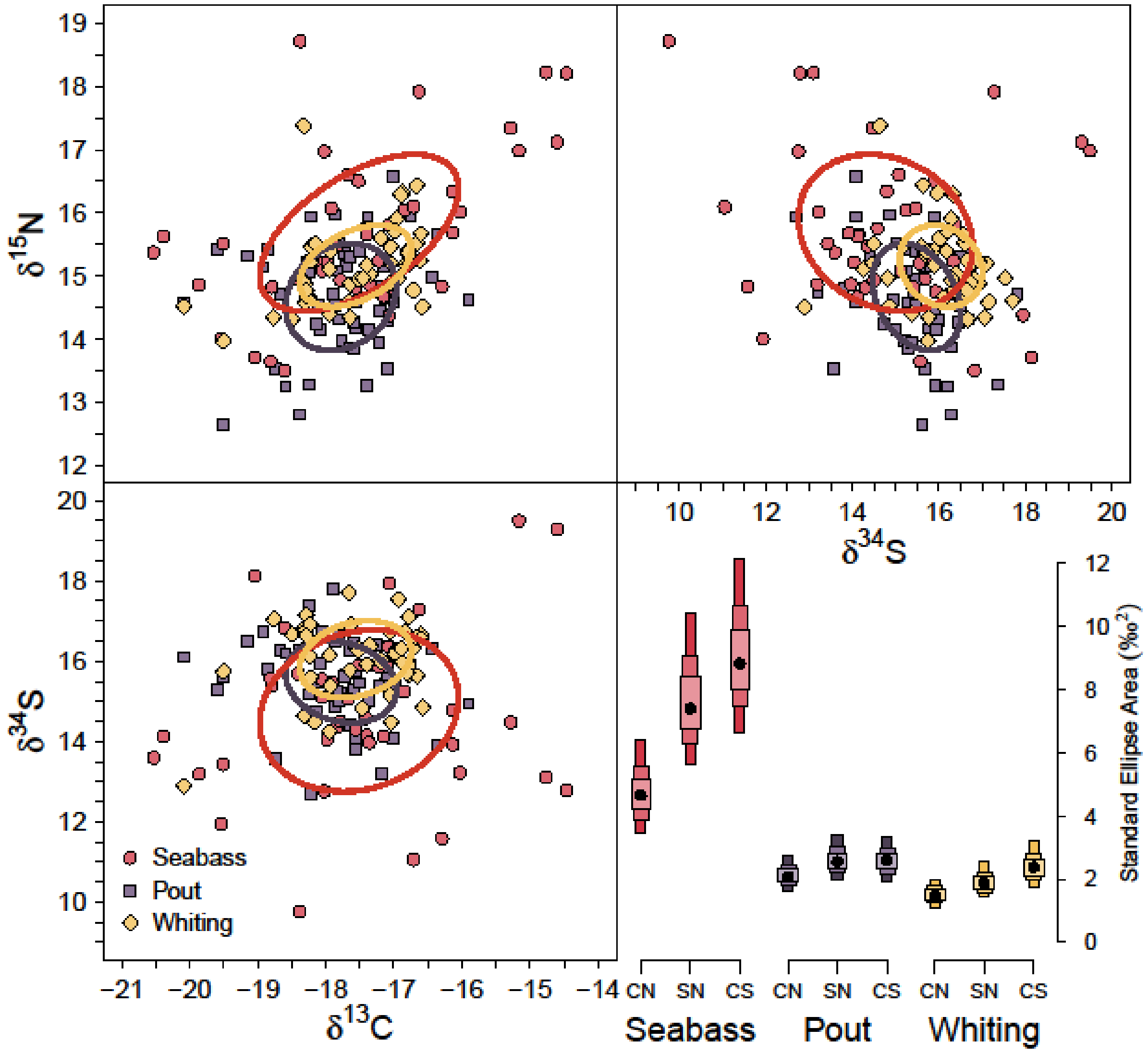
distributions of the standard ellipse areas for each species for each biplot, where CN is carbon-nitrogen (top-left), SN is sulphur-nitrogen (top-right) and CS is carbon-sulfur (bottom-left). Credible intervals are 50%, 75% and 95% with the mode of each distribution indicated by a black circle.

Table 1: Dietary indices based on stomach content analyses of sea bass in age class by season groups, see Materials and Methods for description of indices. Values of 0.1 or greater (major components) highlighted in bold. N denotes the total number of individuals sampled.

Table 2: Metrics of individual specialisations for groups with 5 or more individuals with non-empty stomachs, including age class 2+ pooled across both winters. Significance levels denoted by asterisks (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Figures and Tables:


Frequency
14
12
10
8
6
4
2
0
0
50
100
150
200
250
300
350
Standard Length (mm)
Seabass
Pout
Whiting


δ15N
19
18
17
16
15
14
13
12
δ34S
10
12
14
16
18
20
δ34S
20
18
16
14
12
10
Seabass
Pout
Whiting
−21
−20
−19
−18
−17
−16
−15
−14
δ13C
CN
SN
CS
CN
SN
CS
CN
SN
CS
Seabass
Pout
Whiting
Standard Ellipse Area (‰2)
12
10
8
6
4
2
0

	Age Class 0				**Age Class 1**				**Age Class 2+**			
	Winter 2015	Spring 2016	Autumn 2016	Winter 2016	Winter 2015	Spring 2016	Autumn 2016	Winter 2016	Winter 2015	Spring 2016	Autumn 2016	Winter 2016
N	7	14	17	19	7	15	0	7	9	5	4	10
I_V	0.57	0.29	0.29	0.42	0.43	0.13	-	0.86	0.44	0.4	0	0.3
Prey	**I_{RI} (I_{MF})**											
Amphipods	**0.53(0.38)**	**0.35(0.26)**	**0.22(0.22)**	**0.50(0.27)**	**0.51(0.54)**	0.01(0.01)	-	0 (0)	0 (0)	0 (0)	0.01(0.01)	0 (0)
Copepods	0 (0)	0 (0)	**0.68(0.39)**	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Isopods	0 (0)	0.04**(0.12)**	0.01(0.02)	0.03(0.07)	0 (0)	0.02(0.08)	-	0 (0)	0 (0)	0 (0)	0 (0)	0.01(0.03)
Mysids	0 (0)	0 (0)	0 (0)	**0.11(0.13)**	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Crabs	0 (0)	0 (0)	0.03**(0.10)**	0.03**(0.10)**	0.04(0.09)	0.01(0.04)	-	0 (0)	**0.47(0.46)**	0.01(0.03)	0.05**(0.10)**	**0.55(0.40)**
Shrimp	**0.20(0.24)**	0.01(0.05)	0.02(0.08)	0.05**(0.11)**	0 (0)	0.02(0.07)	-	0 (0)	0.03(0.07)	0.04(0.09)	**0.20(0.22)**	**0.26(0.17)**
Polychaetes	**0.15(0.20)**	**0.60(0.51)**	0.04**(0.11)**	**0.28(0.30)**	**0.44(0.33)**	**0.93(0.70)**	-	**1.00(1.00)**	**0.40(0.28)**	**0.94(0.82)**	**0.16(0.14)**	0.04(0.08)
Fish	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.02(0.08)	-	0 (0)	0.07**(0.15)**	0 (0)	**0.53(0.43)**	0.07**(0.14)**
Bivalve	**0.12(0.17)**	0 (0)	0.01(0.04)	0 (0)	0 (0)	0 (0)	-	0 (0)	0.03(0.05)	0.02(0.06)	0.05**(0.11)**	0.06**(0.14)**
Gastropod	0 (0)	0.01(0.04)	0.01(0.04)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Algae	0 (0)	0 (0)	0 (0)	0.01(0.03)	0.01(0.05)	0.01(0.02)	-	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Detritus	0 (0)	0.01(0.02)	0 (0)	0 (0)	0 (0)	0.01(0.01)	-	0 (0)	0 (0)	0 (0)	0 (0)	0.02(0.06)

Age Class	Season	E_{adj}	Non-Empty Stomachs	Total number of prey categories present	Stomachs with only one prey type
0	Spring 2016	0.245	10	6	7
0	Autumn 2016	0.324**	12	8	6
0	Winter 2016	0.334*	11	7	5
1	Spring 2016	0.123	13	8	4
2+	Winter 2015	0.505*	5	5	2
2+	Winter 2016	0.664***	7	7	4
2+	Winter 2015/16	0.446***	12	7	6