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The food limitation hypothesis for juvenile marine fish

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Abstract:

Coastal zones are productive areas that serve as nursery grounds for a large number of marine species. However, the processes involved in survival success during the juvenile phase are not well-known. Some authors suggest that the availability of prey is important to support the production of pre-recruit fish whose fitness is enhanced through optimal feeding conditions. Accordingly, recruitment is limited by the carrying capacity of the nursery habitat. In contrast, other authors state that the carrying capacity of the nursery grounds is not fully exploited, suggesting that there is no effect of food limitation. This study combines an overview of the literature, focused on flatfish that are especially dependent on coastal and estuarine nursery grounds, an extension to other marine fishes and a modelling approach on growth and survival of juvenile fish to explore the controversy of food limitation in their nursery grounds. We demonstrate that the relative lack of growth limitation observed for young marine fishes at the individual scale is related to an observational bias: fish have been affected by size-selective mortality linked to food limitation, but only surviving individuals are observed. As the population is skewed towards the faster-growing juveniles, the growth of survivors remains close to optimal, even when food resources are limited. Food limitation is of major influence in determining the carrying capacity of the nursery habitat. To sustain marine fish populations and related fisheries, management action is needed to protect coastal and estuarine areas and maintain or restore nursery productivity.

Keywords: Estuaries and coasts ; food limitation ; habitat functionality ; juvenile fish growth ; size-dependent mortality ; trophic capacity of nursery habitat

Introduction

The life strategy of most marine teleost fish species is characterized by high fecundity, the production of large amounts of small pelagic eggs and the lack of parental care (Juanes 2007). This strategy leads to high mortality in early life stages (eggs, larvae and juveniles). Survival-to-maturity rates as low as 1:100,000 are common in many marine fish populations (Table 1). This low survival rate is specific to marine fish, as freshwater and anadromous species exhibit higher likelihood of surviving from egg to adult (e.g., 1% survival for Atlantic salmon (*Salmo salar, Salmonidae)* populations; Hutchings and Jones 1998). A life strategy with high and highly variable mortality makes the survival of eggs, larvae (Houde 1987, 2008, Cushing 1995, Bakun 1996) and juveniles (Sogard 1997) strongly dependent on abiotic and biotic environmental factors. This, in turn, results in high variability in the recruitment and mortality of early life stages with dramatic influence on the abundance of fish populations (Gallego et al. 2012). Most of the recruitment variability of marine fishes (10-fold interannually and 100-fold in overall variability; Houde 2008) is explained by larval and juvenile survival rates (Levin and Stunz 2005). These stages represent a bottleneck in the dynamics of fish populations and small changes in the survival rates of these stages can cause large differences in recruitment (Levin and Stunz, 2005; Daewel et al. 2011). Recruitment variability and the associated large fluctuations in fish populations have been a focus of marine and fisheries science since in the early 20th century (Hjort 1914) and continue to be important areas of research (Sinclair 1997, Houde 2008, Gallego et al. 2012).

The egg and larvae stage and the juvenile stage both exhibit low survival and contribute to the large recruitment variability:

- The variability-generating processes that occur at the egg and larval stages are of critical importance to population levels (Hjort 1914, van der Veer et al. 2000a, Rochette et al.

2012; Table 1). During these life stages, complex and varied mechanisms influence both growth and survival and are important determinants of recruitment success. These include the drift of eggs and larvae, temperature control over early life dynamics (i.e., life stage duration, growth and mortality), food availability for larvae and predation. These mechanisms interact to generate recruitment variability that can fluctuate by an order of magnitude (Houde 2008).

- Mortality rates of the juvenile stage are also high (Table 1), though significantly lower than the larval stage (van der Veer et al. 2000a). Processes occurring in the nursery habitat are important determinants of population density (Holbrook et al. 2000). Minto et al. (2008) investigated the link between survival variability and population density from stock recruitment relationships using both a modelling approach and a meta-analysis of wild fish populations. They show that the interannual variability of progeny survival increases at low adult abundance. This pattern is consistent with density-dependent mortality in the juvenile phase which follows stochastic density-independent mortality in the egg and larval stages. Thus, density-independent and -dependent effects on settlement, growth and mortality in the nursery habitat influence recruitment success and variability (van der Veer et al. 2000a, Peterson et al. 2000, Peterson 2003, Levin and Stunz 2005, Fodrie et al. 2009) and are important in regulating year-class strength (Scharf 2000, Stottrup and Sparrevohn 2007). As described in the concentration hypothesis, recruitment variability is lower in populations with large density-dependent effects (Iles and Beverton 2000) related to the capacity and features of the nursery habitat (Johnson 2007). This is especially verified for flatfishes (Iles and Beverton 2000, Le Pape et al. 2003c, Rooper et al. 2004). Thus, nursery habitats are particularly important for many marine fish species (Peterson et al, 2000, Beck et al. 2001 Fulford et al. 2011) and can act as habitat bottlenecks.

Though growth limitation and mortality on nursery grounds are thought to contribute to recruitment variability (Rauck and Zijlstra 1978, Karakiri et al. 1989, Cowan et al. 2000, Grover et al. 2002, Duncan and Holland 2006), survival processes of the juvenile phase are still not well known and remain controversial in regards to their contribution to recruitment variability.

- According to many analyses, prey availability is important to sustain production of pre-recruit fishes and juveniles. Coastal and estuarine (C&E) habitats (mudflats, salt marshes, kelp forests, seagrass beds, mangroves, coral reefs, upwelling regions, etc; Vasconcelos et al. in press), but also other productive habitats, serve as nursery grounds for many marine fish species (Able et al. 1999, Elliott and Dewailly 1995, Holbrook et al. 2000, Grover et al. 2002, Jones et al. 2002, Laegdsgaard and Johnson 2001, Peterson 2003, McLusky and Elliott 2004, Elliott et al. 2007, Franco et al. 2008, Selleslagh and Amara, 2008), and especially flatfishes (Gibson 1994, Meng et al. 2002, Le Pape et al. 2003b). Fishes aggregate in these productive areas where their fitness is enhanced through optimal growth from better feeding conditions (Blaber and Blaber 1980, Miller et al. 1984, Gibson 1994, Friedland et al. 1996, Beck et al. 2001, Houde 2008). The interannual distribution of food availability and juvenile fish biomass are synchronous (Fujii and Noguchi 1995, Walsh 1996, Vinagre et al. 2005, Wouters and Cabral 2009). Thus, food resources are often mentioned as a limiting factor in the capacity of nursery habitats (van der Veer and Witte 1993, Gibson 1994, Craig et al. 2007, Nash and Geffen 2000, Nash et al. 2007).

- Other studies show that juvenile growth is not affected by trophic conditions in nursery habitats, indicating that there is no effect of food limitation (Curran and Able 2002, Ross 2003, Hampel et al. 2005, Diaz et al. 2011; Selleslagh et al., 2012) and suggesting that the carrying capacity of nursery areas is not reached (Rogers 1994, Shi et al. 1997, van der Veer et al. 2000a, Vinagre and Cabral 2008). Van der Veer et al. (2000b) and Manderson et al. (2000) propose predation as the main factor in the variability of juvenile mortality and recruitment success, suggested for various species (McErlean et al. 1973, Blaber and Blaber

1980, Riley et al. 1981, Gibson 1994, Levin et al. 1997, Wennhage and Gibson 1998, Halpin 2000, Lewis 2001, Wennhage and Pihl 2001, Hixon and Jones 2005, Baker and Sheaves 2005, White and Caselles 2008, Sheaves 2009). Predators and their short-term response (Stier et al. 2013) to juvenile fish densities generate density dependent mortality (Johnson 2007, Juanes 2007), helping to explain why recruitment is dampened during the juvenile stage on nursery grounds.

This controversy is illustrated (Table 2) by several well-studied cases of numerous species of the juveniles of commercial flatfish off the Western coasts of Europe (Fig. 1) and other temperate and subarctic areas. In many studies, measures of growth, nutritional condition and body condition indicate almost no food limitation or links to prey availability of the juveniles collected on C&E nursery grounds during the summer growth period. Moreover, these juveniles appear to be protected from interspecific competition by the process of food partitioning. However, for the same species, study areas and periods, other studies indicate (i) nutritionally-limiting conditions during metamorphosis, (ii) a small decrease in growth, (iii) an overlap between the juvenile distribution of benthic species and their potential prey and synchronous spatio-temporal variations, (iv) a link between recruitment and food production and (v) density-dependent distribution of juveniles, with an increased range into the open sea for stronger year classes, related to the extension of enriched productive areas. As a consequence, the influence of food limitation on juvenile fishes in their C&E nursery grounds remains unanswered.

The primary aim of this synthesis is to shed light on this question by focusing on temperate and subarctic flatfish (Table 2) that are especially dependent on C&E nursery grounds (Iles and Beverton, 2000), and extending this focus to other marine fishes (pelagic, demersal and reef associated round fish and sharks, from tropical to subarctic ecoregions). We estimate the influence of trophic limitation on the density-dependent processes involved in year-class regulation during the juvenile stage of marine fishes in their nursery grounds. Solving this question has implications to understanding the main processes involved in the renewal of fish stocks during the juvenile stage. If food resources are an important regulating factor, the regulation of year-class strength during the juvenile stage depends, at least partly, on the productivity of consumable resources and the related capacity of nursery habitats (Hayes et al. 1996). In this case, maintaining the quality and productivity of essential nursery habitat is critical for the renewal of sustainable fish populations.

The question of food limitation in nursery grounds: the controversy from individual to population scale

Different and complementary approaches have been used to evaluate the impacts of food limitation on the survival of juvenile fish, from laboratory experiments and mesocosms to *in situ* gradients at different biological scales: individual (growth, condition), population size (density and distribution) and multispecific scales. Differing results are observed when comparing the different approaches used to analyze the effect of food limitation on nursery grounds.

Experimental approach in the laboratory

Laboratory experiments enables us to estimate the influence of abiotic factors (e.g., temperature and salinity; Fonds 1975) as well as biotic factors (e.g., the effect of food intake on the growth of young flatfishes). These experiments allow us to develop models (e.g., the metabolic scope for growth, Fonseca et al. 2010, or the Dynamic Energy Budget models, Kooijman 2000, van der Veer et al. 2003) to estimate juvenile flatfish growth with regard to the food supply (Table 2). These models are useful for further comparisons between *in situ* growth and estimates of growth based on controlled conditions. The experimental approach demonstrates that food quantity and quality affect juvenile flatfish growth. Limited food resources reduce growth, energy storage and the condition of juvenile flatfish after a few days, with important consequences on juvenile growth and survival, even for short-term events. Accordingly, a meta-analysis of starvation-induced changes in the early stages of fishes from laboratory-controlled experiments, including seven marine species (six round fishes, one flatfish) showed a general rapid exponential decrease of biogeochemical conditions with starvation, immediately followed by death (Meyer et al. 2012), thus extending previous mentioned results to round fishes.

Field experiments

Field experiments are less controlled experimental systems which provide favourable habitats in terms of the main factors governing juvenile fish growth, i.e., hydrodynamic exposure, food availability, predation and water temperature (Gibson 1994). They can serve to bridge the gap between field studies with the inherent difficulties of control, and laboratory experiments that can be standardized and replicated but suffer from a lack of environmental realism (Laffargue et al. 2007). Similarly, caging experiments that consist of stocking fishes in cages placed in the natural environment enables the comparison of growth rates in different habitats and living conditions (Able et al. 1999, Ciotti et al. 2010). However, growth rates of fishes in enclosures or from *in situ* experiments must be interpreted with caution, as fish movements and the threat of predation may be influential but are not realistically represented (Stunz et al. 2002).

Both types of field experiments demonstrate that patterns in food availability result in differences in growth rates for juvenile fish. They also show competition for food to be the underlying mechanism in determining juvenile growth and survival for various marine fish species (Sogard 1992, Craig et al. 2007). In accordance with laboratory studies, field experiments confirm that, in spite of a trade-off with other factors and especially the threat of predation (Sogard 1992, Halpin 2000), food availability on the nursery ground is a primary driver of habitat choice and juvenile fitness.

In situ *analysis, individual scale*

Many field studies have analyzed growth limitation for juvenile wild fishes from individual food intake, growth and individual condition with the primary objective to estimate habitat quality and the link between food availability and living conditions. At this individual scale, food limitation often appears to be of minimal importance for juvenile flatfishes (Table 2). Measures of growth, nutritional condition and body condition indicate neither significant food limitation, nor a link with prey availability or juvenile density. However, some limited signals of limitation can be observed from gut content, recent condition, body condition and lipid reserve, especially just after settlement, with advantages to the first-settled fishes. Juvenile flatfishes appear to be not food limited and comparisons between experimental models and *in situ* estimates show that coastal nurseries provide a maximal potential for food intake, without negative density-dependent growth. Food limitation in the sense of starvation, individual growth and consumption of the prey of juvenile flatfishes often suggests that the carrying capacity of nursery areas is not reached (van der Veer et al. 1994). Concerning other fish orders (i.e., round fishes), Diaz et al. (2011) provide evidence that the Argentinean anchovy (*Engraulls anchoita, Engraulidae)* may not be food limited in any of their nursery grounds; juvenile growth and condition do not differ between nursery habitats for two other round fish species (Ross 2003) and individual consumption indicates no effect of food limitation on European sea bass (*Dicentrarchus labrax, Moronidae*) (Hampel et al. 2005).

On the contrary, some authors reach opposite conclusions from *in situ* approaches at the individual scale on local habitat. Indeed, significant differences in condition are observed at small scales for juvenile plaice (Table 2). Concerning round fishes, Islam and Tanaka (2005) use RNA:DNA ratios, total protein and growth rates to estimate the proportion of starving juvenile Japanese sea bass (*Lateolabrax japonicas, Lateolabracidae)* and to show their dependency on prey availability. The condition of juvenile sea bass was not equal throughout the nursery grounds. Fishes in the upper river were in better condition than those in the lower estuary. Juvenile fishes living on prey-impoverished habitats have significantly higher metabolic costs, and thus higher foraging expenses (Goto and Wallace 2010). Lastly, when considering juvenile hammerhead shark (*Sphyrna lewini, Sphyrnidae)*, a non-teleost species with parental care and much larger juvenile individuals, the link between starvation and body condition, i.e., the effect of food limitation, is highly significant (Duncan and Holland 2006).

In situ *estimation, population scale*

Contrary to studies of individuals, population-scale *in situ* studies generally conclude that growth limitation and density-dependent effects on abundance and distribution are linked to competition and mortality related to food limitation. Firstly, limited effects are revealed when flatfish growth is analyzed from the size of individuals in the population (Table 2). With regard to model estimates based on laboratory experiments or to optimal conditions in mesocosms, *in situ* observations show smaller sizes of flatfish juvenile during part of the growing season in the nursery grounds, with a slight decrease in regards to optimal estimates. A synthesis of Table 2 suggests growth rates that were close to experimental values after settlement but food limitation in summer for large juveniles that had settled a few months previously. These lower growth rates and the related density-dependent regulation suggest competition for food during the summer growth period. Similarly, growth rates appear to be positively related to food quantity and quality in space and time. Estuarine habitats offer optimal opportunities for flatfish juvenile growth, at least partly due to higher food availability, as growth varies annually with the most important food source in the nursery ground. When considering juvenile round fishes, Phelan et al. (1999) demonstrated that the growth of juvenile tautogs (*Tautoga onitis, Labridae)* is faster where prey availability is higher. Moreover the average length of juvenile Atlantic cod (Lekve et al. 2002) and red drum (*Sciaenops ocellatus, Sciaenida)e* (Scharf 2000) decrease with increased density, indicating density-dependent effects. By coupling analyses of growth and density in different estuarine habitats, Sogard (1992) concludes that juvenile fishes of various species are most abundant in habitats that support faster growth.

Alternatively, studies which focus on spatial distribution and recruitment success also point out a clear influence of bottom-up food limitation on juvenile flatfishes (Table 2). Especially, a significant relationship is found between fluvial discharge and the abundance of high densities of flatfish juveniles in ecosystems of freshwater influence. This indicates that the freshwater supply helps sustain the ability of estuarine nurseries to support juveniles. The freshwater particulate organic matter propagates up the food web to juvenile flatfish, showing the role of river discharge and terrigeneous subsidy input in the function of nurseries. Richness in organic matter impacts the settling of benthic communities preyed upon by juvenile flatfishes. The influence of terrestrial discharge on juvenile flatfish differs in intensity and spatial extent between years with relation to river inputs and is correlated to the seaward extent of high densities of these juveniles. High land-based run-off is favorable to the productivity of invertebrate prey and consequently to the productivity of flatfish species. Trophic enhancement related to river inputs at least partly influences recruitment. The influence of estuarine organic matter supply for the development of a community that is tolerant to low salinity and can provide suitable food for juvenile fish were confirmed for round fish species (Costa and Bruxelas 1989, Pasquaud et al. 2008). Similarly, the density dependent distribution of juvenile, from estuaries to open waters, was also verified for round fishes (Bacheler et al. 2012). For instance, juveniles of filter-feeding Atlantic menhaden (*Brevoortia tyrannus, Clupeidae*) are found to be associated with gradients of phytoplankton biomass in their estuarine nurseries along the Eastern coast of the USA (Friedland et al. 1996). When densities of juveniles are pooled for all marine species, the maximum juvenile density is observed in the middle mesohaline region of estuaries (Nicolas et al. 2010). The amount of organic matter is the highest in these areas and conditions are particularly suitable for the development of benthic invertebrate prey (Moore 1978, Elliott and Taylor 1989). This high abundance of benthic prey leads to high fish density, especially of juvenile marine species (Courrat et al. 2009). Accordingly, a human-induced limitation of the river flow that lowered the primary production of the adjacent shelf is found to negatively impact the recruitment of the European anchovy population in the Gulf of Cadiz (Ruiz et al. 2009). Likewise, severe droughts can reduce primary productivity in estuaries, with cascading effects on higher trophic levels, food availability and juvenile survival for various fish species (Wetz et al. 2010).

The relationship between food availability and juvenile flatfish abundance (Table 2) and distribution are also confirmed outside regions of freshwater influence. In coastal areas, the migrations of juvenile flatfish demonstrate the influence of foraging opportunities on daily movements. At larger (i.e., seasonal to annual) time scales, their distribution match the distribution of their prey. Similarly, the interannual variation of abundance and distribution of juvenile flatfish are synchronous with those of the macrobenthos (Table 2). The density-dependent distribution of juveniles that extends to deeper water when abundance increases in their C&E nurseries is also verified for Atlantic cod on North West Atlantic coast (Swain 1993).

For flatfishes, local population density is a trade-off between larval supply and high mortality rates (Nash et al. 2007). Accordingly, competition for a limited food resource is one of the main causes of restocking failure in coastal stock enhancement programs (Stottrup and Sparrevohn 2007). The survival rate of hatchery-reared fish is first related to the number of larvae released and then to the total (wild and hatchery-reared) recruitment intensity, indicating that there are limits in the carrying capacity of nursery grounds (Goto 2006). White and Cazelles (2008) examine the effect of density-dependent processes linked to larval supply and habitat capacity on post-settlement interactions in juvenile reef fish. They estimate that the abundance of juvenile fish is not limited by the larval supply at low densities of recruits, but by density-dependent competition for food resources and shelter at high densities of recruits. However, other studies that estimate total consumption in C&E nursery grounds using growth, daily food consumption and density find that food is abundant enough to sustain juvenile growth for flatfish (Table 2), suggesting that the carrying capacity of nursery areas is not reached.

Thus, using population approaches, even if opposite conclusions are sometimes reached, density-dependent growth and mortality related to food availability appear to be major factors controlling recruitment success of juvenile stages (Juanes 2007).

In situ, *interspecific competition*

Many studies of C&E flatfish nurseries demonstrate that if numerous species use the same nursery area, they develop strategies of resource partitioning to avoid food limitation and niche overlap. Species, but also different cohorts or age groups of a given species, had specialized their feeding behavior, with only a moderate niche overlap. Differences in feeding rhythms, habitat use, and food preference reduce food competition (Table 2). More generally, when all fish species are considered, niche overlaps vary: they are higher between species of the same family but remain limited (Pasquaud et al. 2010b). Juvenile fish of different species avoid competing for food resources even if competition is observed between resident species (Lafaille et al. 2000).

Resource partitioning, indicative of competition (Nunn et al. 2012), is a strategy to optimize food availability and appears as an adaptation to limited food resources that allows coexistence of species within the nursery zone. Such partitioning results from the long term natural selection of a trophic strategy. Indeed, there is no need to avoid niche overlap if food supply exceeds the need of the different species. This conclusion is reinforced by ontogenic shifts from higher overlap in diets of larval fish, to lower overlap in diets of juvenile fish, enabling competition avoidance between different size and age classes of the same species (Nunn et al. 2012). Geange and Stier (2009) analyze the timing of settlement on coral reef systems and find that species survive best in the absence of competitors and that survival declines when species enter the community later than their competitors. These interspecific effects related to settlement time provide additional evidence of the importance of competition in nursery areas.

In spite of some intra-scale discrepancies, different approaches that measure common parameters such as growth, condition, density or distribution allow us to draw different conclusions about food limitation. Laboratory and field experiments, *in situ* studies at population scales and interspecific competition show a significant influence of food limitation on juvenile fish growth and survival. *In situ* studies that focus on individuals lead mainly to opposite conclusions; growth of juvenile fishes, especially small juvenile fishes, on the nursery grounds does not appear to be food limited. These opposing conclusions are obvious for populations of juvenile flatfishes on C&E areas (Table 2). However, they are verified elsewhere for other fish species in different types of nursery habitats, from tropical to subarctic ecoregions.

Bridging the gap between the different approaches and scales and their opposing conclusions

Size-selective mortality in juvenile stages of teleost fish is critical (Sogard 1997). If direct evidence of density-dependent competition for food is weak (Cowan et al. 2000), especially on an individual scale, the influence of food limitation on juvenile fish growth and survival becomes obvious when changes in the size distribution associated with mortality are distinguished from changes due to individual growth.

Size-dependent mortality during juvenile life stages

A range of daily mortality as high as 5-40%, with a mean of 18% (Selleslagh 2008), is observed for the Eastern Channel plaice during the highly sensitive post-settlement period (Geffen et al. 2007, Nash and Geffen, 2012). The same level of mortality is estimated for tropical reef fishes (9-20%; Juanes 2007). Such high mortality rates for newly-settled larvae are far from specific to flatfishes and reef fishes, i.e., Atlantic cod shows even higher mortality rates at the juvenile stage (Houde 2002; Table 1).

These high mortality rates during the juvenile stages appear to select the faster growing individuals (Hovenkamp 1992, Houde 1997, Marchand et al. 2003, Craig et al. 2007, Juanes 2007, Selleslagh 2008). Natural mortality rates decline dramatically with increasing body size (Houde 1987, Miller et al. 1988, Conover 2007), leading to size-selective processes: as individuals grow rapidly, they spend less time in the smallest size classes that are most vulnerable to predation (Sogard 1997). For example, growth of anchovies in the Bay of

Biscay was investigated using the otolith growth data collected during repeated larval and juvenile surveys on spawning and nursery grounds (Allain et al. 2003). The surviving juveniles show much faster growth rates during their larval period than the pool of larvae from which they originate, indicating dramatic growth-selective survival. Similarly, Atlantic cod have a high potential for growth- and starvation-induced mortality (Daewell et al. 2011). Lekve et al. (2002) demonstrate that the size distribution of juvenile Atlantic cod is skewed to the larger size classes on nursery grounds, indicating size-selective mortality. This skewness increases with increased density in relation to density-dependent processes. More generally, size distribution of juvenile fish within a cohort is strongly influenced by intraspecific competition for resources, often leading to skewed frequency distributions (Ohlberger et al. 2012). The aforementioned studies and numerous others mentioned in Sogard (1997) provide evidence that body size during the juvenile stages is a major determinant of survival. Thus, the disproportionate removal of small fish causes an overestimation of growth rates if it is based only on survivors (Sogard 1997).

Two explanations have been proposed to explain this size-selective mortality.

- Firstly, survival of larger fish is enhanced because larger members of a cohort can better tolerate physical extremes and endure longer periods without food (Sogard 1997). A lack of food affects energetic reserves of individuals and makes them more sensitive to other sources of mortality (Nash et al. 2007). Faster growing juveniles gain survival advantages via resistance to starvation and also through the ability of larger individuals to ingest a wider variety of prey (Salgado et al. 2004; Nunn et al. 2012). Rapid growth provides a size advantage in which larger fish have stronger competitive effects (Geange and Stier 2009).

- Secondly, predation is a significant size-selective process, especially for early stages, as predation mortality is directly determined by fish size, with decreasing mortality rates with the increasing size (van der Veer et al. 1994). Slow-growing and small fish remain vulnerable to predation for a longer period (i.e., the stage duration hypothesis; Sheperd and Cushing 1980, Houde 1987; Anderson 1988). For example, individuals of newly metamorphosed demersal fish, e.g., plaice (Gibson et al. 1995, Gibson and Robb 1996), are subject to strong size-selective predation by crangonid shrimp (*Crangon crangon, Crangonidae)* (Burrows et al. 2001), which primarily consume fish < 30 mm (van der Veer et al. 1997). Accordingly, Ellis and Gibson (1995) estimate that flatfish reaching 45 mm are at much lower risk from predators. More generally, after the dramatic decline in natural mortality with increasing size in early life stages, a lower but steadier density level is maintained for large juveniles of marine fish species (Conover 2007, Dingsor et al. 2007). Thus, growth limitation influences body size and affects resistance to unfavorable environment factors and to food limitation. It also affects foraging ability and vulnerability to predation, which in turn influence individual fitness (Ohlberger et al. 2012) and recruitment.

The link between size-dependent mortality and growth explains the hidden effect of food limitation at individual scales

Average growth rates of fish larvae and juveniles are lower under food-limited conditions (Houde 2008). As demonstrated for larvae in the stage duration hypothesis (Sheperd and Cushing 1980, Houde 1987), mortality rates of juvenile fish are inversely related to size and linked to growth. According to the “bigger is better hypothesis”, mortality and predation during young fish stages are related to nutritional deficiencies (Miller et al. 1988, Sogard 1997, Suthers 1998).

This link could explain why food limitation effects are not obvious for very young fishes. If there is high mortality of starving juveniles, a disproportionate removal of small fish causes an overestimation of the population mean growth rate from the size of survivors, which could be misleading (Houde 2008). As the population is skewed toward faster growing juveniles, the growth of survivors could be close to experimental values under optimal conditions (Table 2), even when food limitation is important. The relationship between food availability and size-dependent mortality hinders variability in growth by selecting faster-growing individuals and dampening recruitment variability. This also helps explain why the relationship between the mean length of a cohort and the year class strength appears to be relatively weak (van der Veer et al. 1994), even if food limitation alters growth performance (dynamic self-thinning, Nash et al. 2007). Similarly, this could explain why estimates of the total food consumption by juvenile fish over the summer period suggest that food is abundant enough to sustain juvenile growth (Table 2). The juvenile population size, in abundance, is adapted to the available food after the high mortality period during the first post-settlement stages. Growth limitation is more obvious for larger fish with lower mortality rates, e.g., 1 year old juvenile common sole (Le Pape et al. 2003a) or sharks (Duncan and Holland 2006).

Testing the food limitation hypothesis using simulations

Using a simulation framework, we test if, in conditions of limited food, the growth curve that is observed at the population scale during the first months of juvenile growth differs from the theoretical optimal growth curve. For illustrative purposes, we choose the life history traits of common sole and simulate a population of one million larvae.

Model

Individuals of the population grow according to a von Bertalanffy equation:

$$L_{i,a} = L_{inf} . \varepsilon_1(a) - \left(L_{inf} . \varepsilon_1(a) - L_0\right) . e^{\left(-k . t . \varepsilon_2(a)\right)}$$

where t is the time (in months), $L_{i,a}$ is the length (in cm) of the individual i at age a (in months since metamorphosis), L_{inf} is the maximal length (i.e., 54 cm; Fishbase.org), L_0 is the length at metamorphosis (0.5 cm; Fonds 1979), k is the growth rate (0.26; Fishbase.org). $\varepsilon_1(a)$ and $\varepsilon_2(a)$

are random noise that have a normal distribution with a mean equal to 1 and a standard deviation equal to 0.1 (i.e., 10% noise). This random noise is added to k and L_{inf} to account for inter-individual variability. The growth of one million fish over their first year (from metamorphosis in the spring to the end of the year) is described in the size-at-age matrix ($L_{i,a}$). Two scenarios are developed: (S1) there is no food limitation and the growth is simulated as in Eq. 1. Ten thousand individuals are then randomly sampled in the population to simulate a survey. (S2) Food limitation is simulated. As food limitation is shown to decrease the maximal length (e.g., Kooijman 2010), a negative offset is subtracted from the infinite length. This offset corresponds to 20% of the maximal length ($L_{inf,} = 43.2$). Individuals die following a size-related natural mortality as defined by Gislason et al. (2010). This mortality is defined for each individual for each age in a mortality-at-age matrix ($M_{i,a}$):

$$M_{i,a} = 0.55 - 1.61 . \log\left(L_{i,,a}\right) + 1.44 . \log\left(L_{inf}\right) + \log\left(k\right)$$

where $M_{i,a}$ is the instantaneous mortality rate per year of the individual i at age a (in months) and for its size, $L_{i,a}$.

The probability of survival of each individual per month is directly calculated from the mortality-at-age matrix with the equation $S_{i,a} = e^{-M_{i,a}}$. Over the first six months of the juvenile stage, the estimate of survival is about 10%, which is in accordance with estimates for the common sole (Rochette et al. 2013). The survival probability, $S_{i,a,}$ is then used to define the probability that an observer would sample the larva i at age a in the wild. Ten thousand fish were sampled within the whole population using the survival probability as a weighting.

Results

For the two scenarios, the sampled population has an estimated mean length within the same range as the theoretical growth curve (Fig. 2). If sampling occurs over the whole population without accounting for the individual mortality (S1), the length of individuals is randomly distributed over the theoretical growth curve. As only survivors are observed or sampled in S2 (food limitation scenario; Fig. 2b), individuals having a slower growth rate due to food limiting conditions are not sampled or are sampled less often. The mean length of sampled individuals in S2 is very similar to the theoretical growth curve but the distribution is less variable and skewed, with lower a longer tail towards higher lengths, corresponding to the observation made for Atlantic cod by Lekve et al. (2002). This simulation demonstrates the bias of *in situ* sampling; as only survivors are observed, i.e., juveniles with the fastest growth; thus, the sampling is biased towards fast-growing individuals (Fig. 2b). This shows that even in food-limited conditions, one observes individuals close to the theoretical growth curve.

Thus, the synthesis of different approaches and scales demonstrates both the trophic limitation in C&E nursery areas and the lack of an obvious signal when food limitation is observed on survivors at the individual scale. Though the present approach is at first focused on temperate and subarctic flatfish, further extension to other marine fishes (pelagic, demersal and reef associated round fish, from tropical to subarctic ecoregions) allows us to broaden these conclusions. As hypothesized by Gibson (1994), food appeared to be the main factor affecting juvenile fish concentration in nursery grounds. Juvenile fish growth is related to food availability, and its limitation interacts with other factors, such as size- (growth) dependent predation (Wennhage 2000) and mortality (Sogard 1997) to determine survival rates. Moreover, the negative relationship between growth and the duration of life stages increases the period when mortality and predation are higher for food limited juveniles. Thus, food limitation affects both the duration of the juvenile stage and the survival during this stage (Sheperd and Cushing 1980, Houde 1987, van der Veer et al. 1994).

The influence on fish populations of trophic limitation and habitat capacity in C&E nursery grounds

An obvious but variable dependency of juvenile fish on the productivity of C&E essential habitats

Juvenile fish of many species aggregate in productive C&E nursery areas in order to enhance their fitness (Blaber and Blaber 1980, Miller et al. 1984, Gibson 1994, Beck et al. 2001). Habitat suitability, which is linked to production and food quality and availability, is highly influential on the spatio-temporal patterns of juvenile fish (Holbrook et al. 2000, Nicolas et al. 2007). Though trophic limitation is a primary factor in determining the suitability of nursery habitat, juvenile fish-habitat interactions are complex (Fulford et al. 2011). Habitat suitability is a trade-off between habitat selection, foraging quality and predator avoidance (Sogard 1992, Wennhage and Gibson 1998, Laegdsgaard and Johnson 2001, Able 2005, Sheaves 2009). The level of juvenile dependence on trophic limitation varies with time, among cohorts (i.e., density-dependent variations related to interannual variations in settled larvae; Fig. 3) and even among subcohorts during the settlement period (Fonseca et al. 2006, Geange and Stier 2009, Nash and Geffen 2012, Geffen et al. 2011). This dependence varies at small spatial scales and between different nursery habitats of the same population (Nash et al. 2007, de Raedemaecker et al. 2011), with relations to juvenile density and food availability. It also varies between different populations of the same species, e.g., the influence of food limitation appears significantly higher for plaice in the Irish Sea (Nash and Geffen 2000) relative to those in the North Sea (van der Veer et al. 1986) or in the Wadden Sea (van der Veer et al. 2000a). Finally, it varies from one species to another, even in the same area, e.g., in the North Sea, trophic dependence is important for common sole (van der Veer et al. 2001) but limited for plaice (van der Veer et al. 1986).

An influence on marine fish population renewal

For a fish population to persist, habitat must be available to sustain all periods of development (Nunn et al. 2012). As such, the capacity of nursery habitats is a key contributor to the overall population fitness (Fodrie et al. 2009), stability and extinction risk (Ohlberger et al. 2012). Nash et al. (2007) provide evidence of self-thinning for plaice at the local population scale: when juvenile population density is high, food limitation depends on the number of individuals that settle relative to the productivity of the nursery ground. Populations that strictly depend on limited nursery habitats approach the carrying capacity of the habitat, at least when settlement is high. Post-settlement survival depends on nursery habitat size and productivity, in relation to the amount of larval settlement (Rooper et al. 2004, Johnson 2007, Nash et al. 2007). Thus, fish populations are limited by the quantity and quality of habitat and food available for juvenile fishes (Nunn et al. 2012). Food dependent size-selective mortality dampens the variability in size distribution and reduces among-year variability in recruitment strength (van der Veer et al. 1994, Le Pape et al. 2003b, Minto et al. 2008). Accordingly, habitat bottlenecks have been identified for juvenile fish stages of species or populations for which the variation in habitat quality has a disproportionate effect on renewal (Fulford et al. 2011). This dependence appears especially important for C&E nursery dependent flatfish species (Iles, 1994), but is also of important concern for many other fishes. Iles and Beverton (2000) demonstrate that nursery-dependent species at high spawning stock biomass have asymptotic stock recruitment relationships, with a maximum recruitment level hiding a linear relationship to spawning biomass (i.e., the concentration hypothesis). These species depend on the capacity of nursery habitats for their recruitment (Fig. 3): density-dependent processes are at least partly linked to prey resources that regulate recruitment strength and dampen recruitment variability (Cowan et al. 2000, van der Veer et al. 2000a, Le Pape et al. 2003c, Houde 2008, Minto et al. 2008).

Thus, if variability-generating processes operating at the egg and larval stages are of major importance, processes occurring during the juvenile stage are also important in determining recruitment strength (van der Veer et al. 2000a) and variability (Iles and Beverton 2000, Minto et al. 2008). Among these juvenile processes, density-dependent effects related to food limitation appear to be a main governing factor (Cowan et al. 2000). Nevertheless, food limitation influence differs for different species, populations, cohorts, nursery habitats, and years in relation to the balance between juvenile density and food availability (van der Veer et al. 2000a, Nash and Geffen 2000, Nash et al. 2007).

The critical first juvenile stages

The present synthesis provides evidence of trophic limitation on juvenile marine fishes in their C&E nursery grounds but the question remains for which juvenile stage(s) this limitation constrains the recruitment strength.

The transition phase, after the last larval metamorphosis (Geffen et al. 2007), is demonstrated to be a critical stage (Juanes 2007), and thus demands thorough attention (Nash and Geffen 2012). Indeed, for the juvenile stages, density-dependent processes in young fish survival decline as they grow (Dingsor et al. 2007), with an especially dramatic decline of mortality with increasing body size (Houde 1987, Miller et al. 1988). Size-selective mortality appears to be mainly restricted to the first year of life (van der Veer et al 1994) and is especially high during the first juvenile stages. Indeed, during ontogeny at young stages, both improvements in vision and swimming performances and increases in gape size lead to shifts in diet composition and a larger choice of prey (Nunn et al. 2012). The density-dependent regulation of a cohort derived from a reduction in prey resources is hypothesized to occur at a critical size and/or weight following the larval settlement (van der Veer 1986, Houde 1997, Cowan et al. 2000; Nash and Geffen 2012). Fish are most vulnerable in the period following the larval settlement, as the lack suitable prey due to their limited predation abilities, potentially leading to either reduced growth or starvation, reduce survival (Nunn et al. 2012). This limitation occurs when densities of fish populations and consumption of resources remain high relative to the prey density and the replenishment rate (Cowan et al. 2000, Nash et al. 2007), and before the shift in resource use (Nunn et al, 2012) and the drop in vulnerability. At young stages, the decline in prey density by juvenile consumption is large enough to result in density-dependent effects, as is demonstrated in several cases studies (Cowan et al. 2000).

In summary, after an exponential decrease in mortality with body size/weight (Conover 2007), fish reach a body size related both to lower predation and to an increase in prey size, energy content and availability (i.e., a larger choice of species item and size spectra, Nunn et al. 2012), and mortality is dramatically reduced (Ellis and Gibson 1995, Gibson et al. 1995). Thus, a dramatic regulation of the size of a population occurs for the lowest juvenile size (Dingsor et al. 2007) during the critical period (Houde, 2008) when mortality is high enough to sharply modulate the population via limited food resources (Fig. 3). Indeed, density-dependent processes influence year-class strength mainly during the first weeks after settlement in the nurseries (van der Veer 1986, Rijnsdorp et al. 1992).

Implication of food limitation for management of essential nursery habitats

The need to preserve the functionality of C&E nursery habitats for marine fish population renewal

The present synthesis focuses on the important influence of the biotic habitat capacity, i.e., food availability, on the early life stages of fish (Rijndorp et al. 1992, Schmitt and Holbrook 2000, Johnson 2007, Nash et al. 2007, Hayes et al. 2009). Recruitment strength and population dynamics are strongly determined by the productivity and food resources in C&E nursery habitats. Maintaining large and high quality nursery habitats should be a primary focus to preserve fish species whose population range depends on the trophic capacity of their habitat at the juvenile stage (Hodgson et al. 2011, van de Wolfshaar et al. 2011). There is a need for protection of the quality and productivity of nursery habitats to maintain fish stock renewal. The nutrient supply from C&E areas stimulates primary production, which supplies food sources for larvae and juveniles, consequently, sustains the related fisheries (Beck et al. 2001, Lamberth et al. 2009, Sheaves et al. 2009). Quantitative and qualitative factors related to anthropogenic disturbances influence the capacity of C&E nurseries and, thus, the recruitment and the renewal of populations (Cowan et al. 2000, Meng et al. 2000, Peterson et al. 2000, Peterson 2003, Phelan et al. 2000, Scharf 2000, Rochette et al. 2010). It is important to maintain a high ecological quality of essential nursery habitat in C&E areas in order to sustain marine populations and fisheries. Measures aiming at improving or preserving the capacity of juvenile habitat are the most effective for improving adult biomass of populations regulated by density dependence during the juvenile phases (van de Wolfshaar et al. 2011). Preservation and rehabilitation measures should be designed to provide nursery habitats for fishes and enhance their food base (Nunn et al. 2012). Nursery function must be accounted for in monitoring systems of C&E waters to maintain high ecological status (Beck et al. 2001) and especially for the establishment of MPAs to provide and export juveniles, to enhance fishing yields (Pelletier and Magal 1996, Gell and Roberts 2003, Kaplan 2009) and benefit the fisheries (Mesnildrey et al. 2013).

Estimating habitat suitability from large juvenile fish growth and density: an appropriate tool

The density, growth and condition of juvenile fishes are relevant indicators to estimate the ecological quality of nursery habitats (e.g., Guindon and Miller 1995, Suthers 1998, Able et al. 1999, Duffy-Anderson and Able 1999, Phelan et al. 2000; Selleslagh and Amara, 2013). However, as starving and newly-settled juveniles are removed from the population by high mortality rates, growth rates are overestimated for very young stages and cannot be used as indicators of the nursery function. With regards to high mortality rates of post-settlement juvenile fishes in relation to the nutritional deficiencies of their nursery grounds (i.e., the food limitation hypothesis, Fig. 3), it could be misleading to determine essential nursery habitats and estimate their quality from the density and growth of newly post-settled fish.

In contrast, large juveniles experience dramatically lower mortality and it is more reliable to collect data on larger juvenile fish to identify nursery habitat and estimate its ecological status. Indeed, density is less variable, food limitation is more obvious (Duncan and Holland 2006), and growth is less biased due to size-dependent selection (Meng et al. 2000, Le Pape et al. 2003a, Gilliers et al. 2006, Amara et al. 2007, Amara et al., 2009; Selleslagh and Amara, 2013). Nevertheless, biased and incorrect decisions regarding habitat quality can still be made when using a growth-based assessment without identifying factors, such as temperature and density, that may underlie differences in growth rates (Searcy et al. 2007).

A given habitat is considered a nursery if it contributes disproportionately to the size and number of adults relative to other juvenile habitats (Beck et al. 2001). The most environmentally-sensitive fish populations are those whose nursery areas are restricted to a few coastal sites (Parrish et al. 1997). The identification of these sites is an important consideration for coastal management (Cogan et al. 2009, Vasconcelos et al. 2011, Vasconcelos et al. in press). During the settlement period, the high spatiotemporal variability in juvenile abundance linked to both the pulses of larval supply and high mortality rates (Nash et al. 2007) leads to spurious estimates of juvenile abundance and habitat capacity. On the contrary, the abundance of juvenile fish is dramatically less variable after larval settlement and the huge decline in mortality caused by the dampening effects of density-dependent processes (Iles and Beverton 2000, Rooper et al. 2004, Johnson 2007). At this older juvenile stage, the habitat contribution to the population, i.e., the total biomass of individuals added to adult populations (Beck et al. 2001) from a given habitat, can be estimated from juvenile abundance. It is possible to quantify essential and effective juvenile habitats (i.e., the overall contribution from specific habitats to the adult population; Dahlgren et al. 2006), from habitat suitability models (Norcross et al. 1997, 1999, Guisan and Zimmermann 2000, Beck et al. 2001, Le Pape et al. 2007, Stoner et al. 2007, Dahlgren et al. 2006) and related mapping approaches (Le Pape et al. 2003b, Fodrie and Mendoza 2006, Rotenberry et al. 2006, Trimoreau et al. in press). Such procedures can be based on populations but can also be estimated from a multimetric index for a more general definition of the essential fish habitats of C&E ecosystems (Courrat et al. 2009, Delpech et al. 2010). Policy objectives, such as the sustainability of fish resources, ecosystem health or the design of MPAs, should be based on quantitative maps of essential fish habitats (Cogan et al. 2009; Johnson et al; 2012). Furthermore, quantitative indices of habitat suitability can be useful tools to assess the vulnerability of fishes to various anthropogenic disturbances (Steizenmuller et al. 2010), such as habitat loss and degradation linked to xenobiotics (Rochette et al. 2010) or invasive species (Kostecki et al. 2011).

Conclusion and suggestions for future research

The aim of the present synthesis is to shed light on the controversy of food limitation for juvenile fishes in their C&E nursery grounds and to analyze the related consequences for survival and future recruitment. We demonstrate that the relative lack of observed growth limitation for young fishes at the individual scale in their nursery grounds is at least partly related to size-selective mortality affecting food-limited and newly-settled fishes (Sogard 1992). This synthesis confirms the conclusions of studies that use different approaches (i.e., experiments on individual juvenile fishes and *in situ* observations at the population scale) and enhances the understanding of the strategy of food partitioning developed between age groups and between species to limit competition for food resources. Though the present approach focuses on temperate and subarctic flatfish for illustration purposes, a large amount of references to other marine fishes allows us to extend these conclusions to other fish species, and especially to the large proportion of C&E nursery dependent fishes (Beck et al. 2001).

The food limitation hypothesis is such: juveniles aggregate in C&E productive areas where their fitness is enhanced through better feeding conditions and optimal growth (Beck et al. 2001). Food limitation is of major importance in determining the nursery habitat capacity (Nash et al. 2007). Nevertheless, this influence can vary between species, populations, cohorts (and even subcohorts), locations and years (van der Veer et al. 2000a). Habitat structure, refuge opportunities and connectivity between habitats modulate this ecological function (Able 2005, Sheaves 2009).

This synthesis provides enough information to demonstrate the influence of the productivity of C&E nursery habitats on the recruitment of fish populations (Rijnsdorp et al. 1992, Gibson 1994, Iles and Beverton 2000). After the nursery stage, juvenile fish move out of C&E ecosystems to join and sustain fish populations on the continental shelf (Beck et al. 2001, Sheaves 2009). Breaking closure of life history cycle causes severe problems and C&E habitat degradation is one of the most serious threats to the recovery of fish stocks. There is a need to maintain and restore the ecological function of C&E nursery grounds to sustain marine fish populations and related fisheries (Hall 1998, Elliott et al. 2007). Spatial and temporal relationships between fisheries species and habitats must be included in fisheries management plans (Peterson 2003). In this context, an important challenge is to account for nursery function in MPA designs to protect juvenile fish from various anthropogenic pressures. To that aim, observations of *in situ* density and growth of relatively large and old juvenile fish could provide useful tools when density estimates become reliable and size-selective mortality is not hindered by food limitation. Data on these large juveniles could be used to develop habitat suitability models to identify and map essential nursery habitats and to estimate indicators of ecological status for these essential fish habitats.

Nevertheless, the underlying ecological processes are still unknown and further studies are needed for young juvenile stages when food limitation is mostly influential (Cowan et al. 2000, Juanes 2007, Vasconcelos et al. in press; Fig. 3). It is critical to investigate the dependence level of recruitment on food availability and the variability of this dependence (e.g., interannual or interspecific). In forthcoming research, there is a need to focus on the young post-settlement stage to understand the trophic dependence of juvenile fish on their nursery grounds (Able 2005), as this is one life stage that has not received enough study (Nash and Geffen 2012, Vasconcelos et al. in press). However, the study of food availability for these very young fish remains a challenge and requires a fine analysis of biological and ecological processes to determine the critical stage and to understand the trophic limitation. The uncertainty of the precise life stage on which to focus, the high spatiotemporal variability in both larval supply and mortality (and, thus, density) and the high turnover rate of fish and small invertebrate prey during the first juvenile stages requires data with small time steps (Fonseca et al. 2006, Geange and Stier 2009, Nash and Geffen 2012) and fine spatial scales (de Raedemaecker et al. 2011; Johnson et al. 2012). Moreover, as the main governing process varies among species and even among populations (Van der Veer et al. 2000a), solving the problem with a general explanation may be an unrealistic goal. Numerous specific case studies are necessary before drawing generic conclusions on the trophic limitations of fish populations.

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Table 1: Mortality during the pre-adult life phases in some marine fish populations

Species	**Populations**	**Overall pre-adult survival***	**Eggs & larvae surv.***	**Juvenile surv.***	**Reference**
Northern anchovy *(Engraulis mordax, Engraulidae)*	All or whole	10^{-5}	10^{-3}	10^{-2}	Peterman et al. 1988
European anchovy *(Engraulis encrasicolus, Engraulidae)*	Bay of Biscay	10^{-5}	10^{-3}	10^{-2}	Calculated from Allain et al. 2003 and Allain 2004
Altantic cod *(Gadus morhua, Gadidae)*	North Sea	10^{-7}– 10^{-8}	10^{-5}– 10^{-6}	10^{-2}	Houde 2002
Common sole *(Solea solea, Soleidae)*	Bay of Biscay	10^{-5}	10^{-3}	10^{-2}	calculated from Koutsikopoulos et al. 1989 & 1991
	Eastern Channel	10^{-5}	10^{-3}	10^{-2}	Rochette et al. 2013.
Plaice *(Pleuronectes platessa, Pleuronectidae)*	North Sea	10^{-5} – 10^{-6}	10^{-3} - 10^{-4}	10^{-2}	Geffen et al. 2007
	Irish Sea	10^{-5}	10^{-3}	10^{-2}	Calculated from Harding and Talbot 1973 and Talbot 1977
	English Channel	10^{-5}	10^{-3}	10^{-2}	
Winter flounder *(Pseudopleuronectes americanus, Pleuronectidae)*	All or whole	10^{-5} – 10^{-6}	10^{-3} - 10^{-4}	10^{-2}	Rose et al. 1996
Atlantic eel *(Anguilla Anguilla, Anguillidae)*	All or whole	10^{-4}	3.10^{-4}	0.3	Bonhommeau et al. 2009
Atlantic bluefin tuna *(Thunnus thynnus, Scombridae)*	All or whole	10^{-4}	4.10^{-4}	0.3	Simon et al. 2012
Pacific bluefin tuna *(Thunnus orientalis, Scombridae)*	All or whole	$6\text{-}8.10^{-5}$	4.10^{-4}	0.1-0.2	Iwata et al. 2012, Polacheck et al. 1997,Whitlock et al (2012)
Southern bluefin tuna *(Thunnus macoyii, Scombridae)*	All or whole	2.10^{-5}	4.10^{-4}	0.06	Tsuji (1998)

* Survival rates are estimated with important associated variability and estimation error.

Table 2: Analysis of food limitation in temperate and subarctic juvenile flatfish: species, location, methods and conclusions

Species	**Area**	**Approach**	**Conclusion**	**Reference**
Common sole		Experimental	Food limitation	Fonds and Saksena 1977
Common sole		Experimental	Food limitation	Fonds et al. 1989
Plaice, European Flounder *(Platichthys flesus, pleuronectidae)*		Experimental	Food limitation	Fonds et al. 1992
Stone flounder *(Kareius bicoloratus, Pleuronectidae)*		Experimental	Food limitation	Malloy et al. 1996
California flounder *(Paralichthys californicus, Pleuronectidae)*		Experimental	Food limitation	López-Rasgado and Herzka 2009
Plaice		Experimental	Food limitation	Ciotti et al. 2010
Plaice		Experimental	Link to prey availability	Selleslagh and Amara 2013
Plaice		Experimental	Link to prey availability	Wennhage and Gibson 1998
Winter flounder		Experimental	Link to prey availability	Phelan et al. 2001
Senegalese sole *(Solea senegalensis,Soleidae),* Common sole	Iberian shelf	Field, individual	No food limitation	Fonseca et al. 2006
Winter flounder	New Jersey, USA	Field, individual	No food limitation	Curran and Able 2000
Common sole, Plaice, Dab *(Limanda limanda, Pleuronectidae)*	English Channel	Field, individual	No food limitation	Gilliers et al. 2004
Plaice	English Channel	Field, individual	No food limitation	Selleslagh and Amara 2013
Common sole	French coasts	Field, individual	No food limitation	Gilliers et al. 2006
Common sole, Plaice, Dab	English Channel	Field, population	No food limitation	Amara 2004
Senegalese sole, Common sole	Iberian shelf	Field, population	No food limitation	Vinagre and Cabral 2008
Common sole	Bay of Biscay	Field, population	No link to prey availability	Amara et al. 2000
American plaice *(Hippoglossoides platessoides, , Pleuronectidae)*	Gulf of St Lawrence	Field, population	No link to prey availability	Swain and Morin 1996
Common sole	North Sea	Field, population	No link to prey availability	Rogers, 1994
Plaice	North Sea	Field, population	No link to prey availability	Van der Veer et al. 2000b
Senegalese sole, Common sole	Iberian shelf	Field, population	No link to prey availability	Fonseca et al. 2010
English sole *(Parophrys vetulus, Pleuronectidae)*	Washington, USA	Field, population	No link to prey availability	Shi et al. 1997
English sole	Washington, USA	Field, population	No link to prey availability	Chittaro et al. 2009
Common sole	Bay of Biscay	Field, individual	Partial food limitation	Amara and Galois 2004
Plaice	Wadden Sea	Field, individual	Food limitation	Karakiri et al. 1989
Plaice	North Sea	Field, individual	Food limitation	Van der Veer et al. 2001
Plaice	Irish Sea	Field, individual	Food limitation	Ciotti et al. 2013
Common sole	Bay of Biscay	Field, population	Food limitation	Laffargue et al 2007
Common sole, Plaice; European flounder	Western Europe	Field, population	Food limitation	Freitas et al. 2012
Plaice	North Sea	Field, population	Food limitation	Teal et al. 2008

Plaice	North Sea	Field, population	Food limitation	Van der Veer et al. 2010
Plaice	Baltic Sea	Field, population	Food limitation	Pihl et al. 2000
Plaice	North Sea	Field, population	Food limitation	Ciotti et al., 2013
Plaice	Irish Sea	Field, population	Food limitation	de Raedemacker et al., 2011
Plaice	Wadden Sea	Field, population	Food limitation	van der Veer and Witte 1993
Plaice	Irish Sea	Field, population	Food limitation	Nash and Geffen 2000
Plaice	Irish Sea	Field, population	Food limitation	Nash et al. 2007
Common sole	Bay of Biscay	Field, population	Link to prey availability	Le Pape et al. 2003c
Common sole	Bay of Biscay	Field, population	Link to prey availability	Marchand and Masson, 1989
Winter flounder	Connecticut, USA	Field, population	Link to prey availability	Howell et al. 1999
Pleuronectiforms	Eastern Bering Sea	Field, population	Link to prey availability	McConnaughey and Smith, 2000
American plaice	Bering Sea	Field, population	Link to prey availability	Walsh 1996
Common sole, Plaice	English Channel	Field, population	Link to prey availability	Riou et al. 2001
Common sole	Bay of Biscay	Field, population	Link to prey availability	Le Pape et al 2007
Common sole	Bay of Biscay	Field, population	Link to prey availability	Nicolas et al. 2007
Common sole, European flounder	Iberian shelf	Field, population	Link to prey availability	Costa and Bruxelas 1989
Common sole, European flounder	Iberian shelf	Field, population	Link to prey availability	Vinagre et al. 2005
Senegalese sole, Common sole	Iberian shelf	Field, population	Link to prey availability	Vinagre et al. 2006
Bastard halibut *(Paralichthys olivaceus, , Pleuronectidae)*	Northwestern Japan	Field, population	Link to prey availability	Fujii and Noguchi 1995
Common sole	North Sea	Field, population	Link recruitment / food	Leakey et al. 2008
Common sole	Bay of Biscay	Field, population	Link recruitment / food	Le Pape et al. 2003a
Common sole	Bay of Biscay	Field, population	Link recruitment / food	Le Pape et al. 2003b
Common sole	Bay of Biscay	Field, population	Link recruitment / food	Le Pape et al. 2003d
Common sole	Western Europe	Field, population	Link recruitment / food	Le Pape et al. 2013
Common sole	Bay of Biscay	Field, population	Link recruitment / food	Kostecki et al. 2010
Common sole	Gulf of Lions	Field, population	Link recruitment / food	Salen Picard et al. 2002
Common sole	Gulf of Lions	Field, population	Link recruitment / food	Darnaude et al. 2004
Pleuronectiforms	Gulf of Lions	Field, population	Link recruitment / food	Darnaude et al. 2005
Senegalese sole, Common sole	Iberian shelf	Field, population	Link recruitment / food	Vinagre et al. 2008
Pleuronectiforms	Iberian shelf	Field, interspecific	Link to prey availability	Wouters and Cabral 2009
Pleuronectiforms	Iberian shelf	Field, interspecific	Food partitioning	Cabral et al. 2007
Senegalese sole, Common sole	Iberian shelf	Field, interspecific	Food partitioning	Cabral and Costa 1999
Senegalese sole, Common sole	Iberian shelf	Field, interspecific	Food partitioning	Cabral 2000
Common sole, Plaice, Dab	English Channel	Field, interspecific	Food partitioning	Amara et al. 2001
Pleuronectiforms	Gulf of Lions	Field, interspecific	Food partitioning	Darnaude et al. 2001
Common sole, Plaice	English Channel	Field, interspecific	Food partitioning	Kostecki et al. 2012
Flounder, Common sole	Iberian shelf	Field, interspecific	Food partitioning	Vinagre et al. 2005,

Figure legends

Fig. 1: Location of the regional seas in Western Europe where many of the studies in this review have taken place.

Fig. 2: Comparison of the theoretical growth curve of the common sole after settlement during their first year (grey line) and simulations of sampling carried out each month for 10,000 (out of 1,000,000) juvenile common sole that experienced a) no food limitation and b) food-limited conditions (i.e., maximal length reduced by 20% in the model).

Fig. 3: Processes involved in the food limitation hypothesis: consequences of the limited trophic capacity of nursery habitats during the settlement and post-settlement period on the recruitment variability of marine fishes (pluriannual variability in cohort abundance is represented for two different life stages, larval / large juveniles, before and after the stage of food limitation).

1 Figure 1


Irish Sea
North Sea
Wadden Sea
English Channel
Bay of Biscay
Gulf of Lions
Iberian
Shelf

2

Figure 2

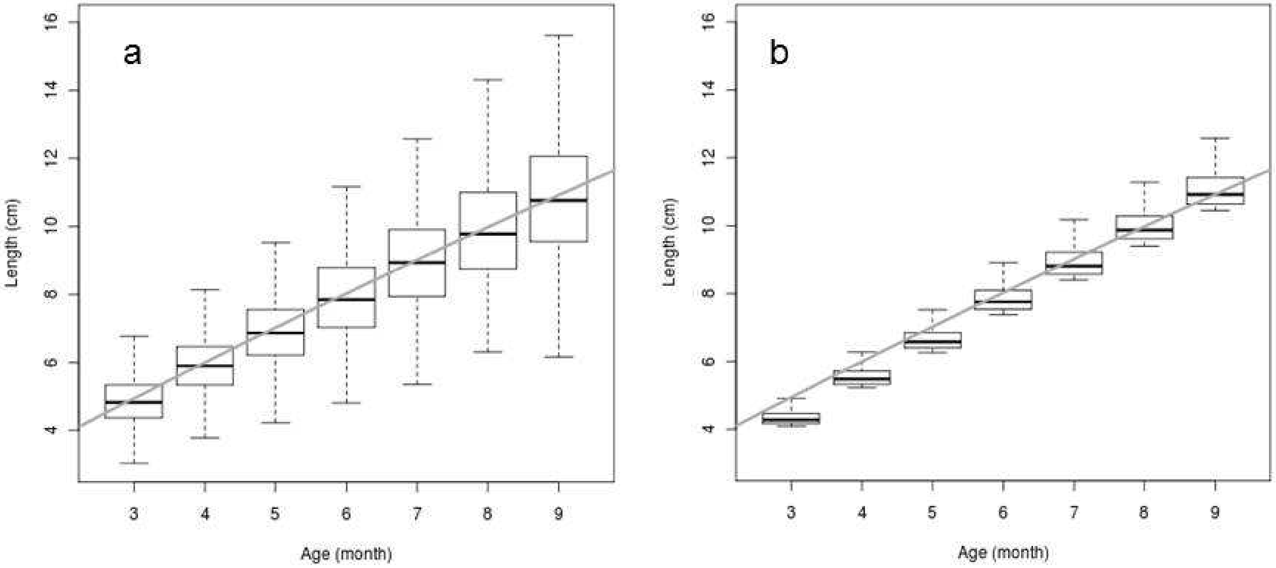
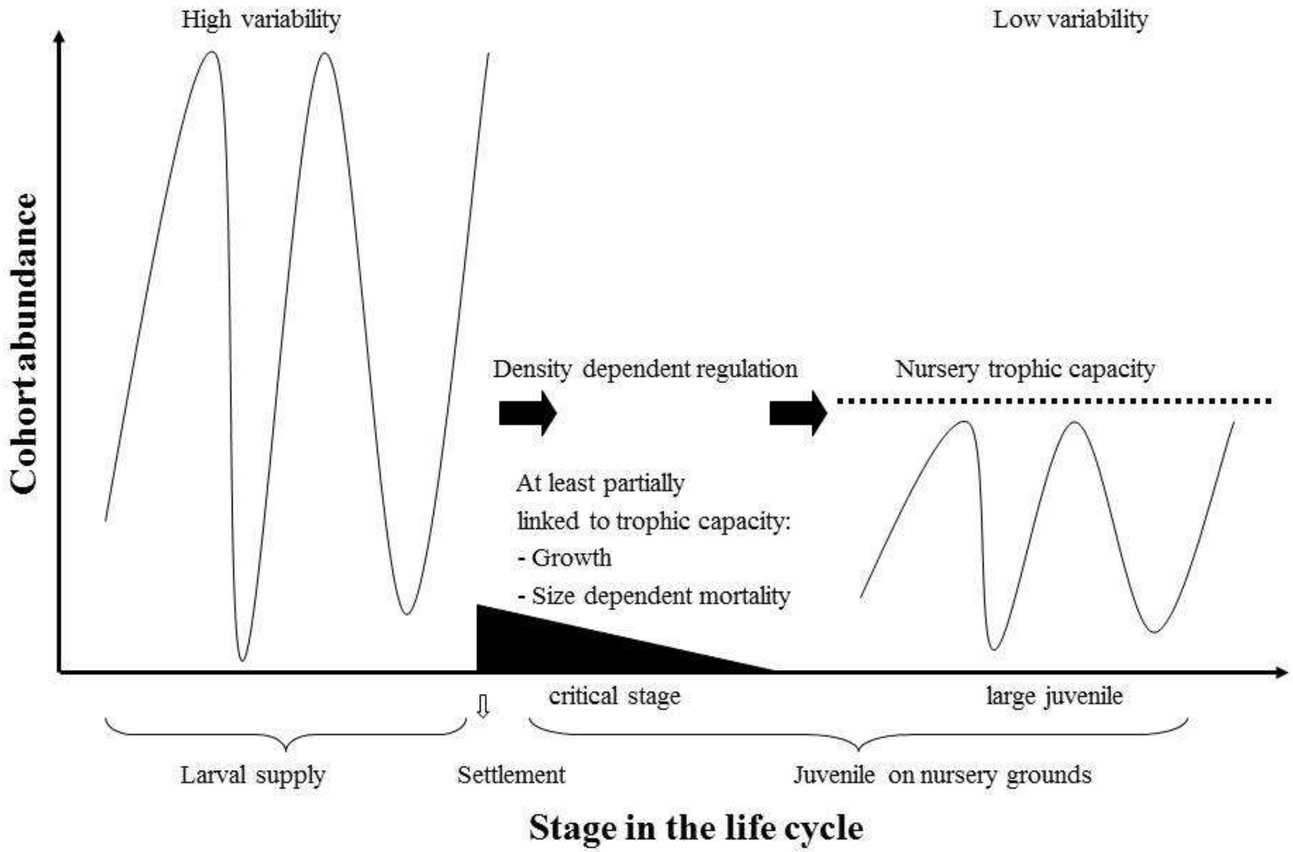


Figure 3


High variability
Low variability
Cohort abundance
Density dependent regulation
Nursery trophic capacity
At least partially
linked to trophic capacity:
- Growth
- Size dependent mortality
critical stage
large juvenile
Larval supply
Settlement
Juvenile on nursery grounds
Stage in the life cycle