Latitudinal and taxonomic patterns in the feeding ecologies of fish larvae: a literature synthesis

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1   *Abstract.* The longtime focus on factors that influence the survival of marine fish larvae has

2   yielded an extensive number of studies on larval fish diets and feeding success. In light of a

3   recent increase in such studies within lower latitudes, results from the peer-reviewed literature

4   were synthesized to examine both latitudinal and taxonomic differences in several trophic-related

5   categories, including feeding incidence, trophic niche breadth, ontogenetic diet shifts, dominant

6   prey types, diet broadness, and larval piscivory. A total of 204 investigations (taxon-article

7   combinations) contained suitable results for at least one of these categories. Feeding incidences

8   (proportions of larvae containing food) were significantly higher in lower latitudes with all taxa

9   combined, as well as only within the order Perciformes. Feeding incidences also differed among

10   orders, with Perciformes and Scorpaeniformes having the highest values. The number of larval

11   taxa exhibiting a significantly increasing niche breadth (SD of the log of prey sizes) with larval

12   size decreased toward lower latitudes, with some taxa in lower latitudes exhibiting a decrease in

13   niche breadth with size. The frequency of exhibiting ontogenetic diets shifts decreased with

14   decreasing latitude, as did relative diet broadness (a function of prey types). The most common

15   dominant prey types in the diets of higher latitude larvae were nauplii and calanoid copepods,

16   with cyclopoids being rare in higher latitudes. Dominant prey types in lower latitudes were more

17   diverse, with nauplii, calanoids, and cyclopoids being equally important. Appendicularians

18   increased in importance with decreasing latitude, and one of the clearest latitudinal distinctions

19   was the display of larval piscivory (almost exclusively by scombroid taxa), which was highly

20   concentrated in lower latitudes. Overall, the latitudinal differences observed for multiple trophic-

21   related factors highlight inherent distinctions in larval fish feeding ecologies, likely reflecting

22   differences in the overall structure of planktonic food webs over large latitudinal gradients.

23

1. Introduction

Studying the diets and feeding success of planktonic marine fish larvae has a long history (e.g. Hjort, 1914; Hunter, 1981). The impetus for such work has largely been the desire to gain a better understanding of why economically important adult fish populations can suddenly and often inexplicably display large fluctuations. The link between millimeter-scale planktonic larvae and multi-billion-dollar fishing industries lies in the potential for minor changes in larval fish survival, due to the initially high numbers of hatching larvae, to have a substantial influence on the number of individuals surviving to later stages (Cushing, 1975; Houde, 1987)..

Because the world's important fisheries are more concentrated in higher latitudes (Watson et al., 2004), research on the processes governing larval fish survival (including trophic-related processes) has also been historically concentrated in high latitudes. In lower latitudes, aside from work on large pelagic species, there has been a relatively greater focus on transport-related processes and the implications for population connectivity, rather than on what might influence the survival of the larvae en route during the planktonic period (Cowen and Sponaugle, 1997). However, recent efforts in low-latitude marine waters have begun to expand our knowledge on larval fish trophodynamics in these regions (Llopiz and Cowen, 2009; Llopiz et al., 2010; Ostergaard et al., 2005; Sampey et al., 2007). From this work, it appears that there could be inherent latitudinal differences in larval feeding success and the trophic role of fish larvae in planktonic food webs. Such differences could be related to the well-documented latitudinal differences in the magnitude and seasonality of primary production (Cushing, 1990; Longhurst and Pauly, 1987), fish and zooplankton diversity (Hillebrand, 2004; Rombouts et al., 2009; Tittensor et al., 2010), and fish spawning strategies (Johannes, 1978). There may also be

46 inherent differences in larval feeding ecologies among taxonomic groupings of fishes, which

47 could underlie any observed latitudinal patterns that may exist at the assemblage level.

48   Despite the extensive accumulated data on the trophic ecologies of fish larvae worldwide,

49 there has yet to be an effort in any context to synthesize the published results from the many

50 single or multi-species studies on the feeding of marine fish larvae in their natural environment.

51 Here, I synthesize results from the literature on the feeding success, diet, and other trophic-

52 related variables of larval fishes with an emphasis on both latitudinal and taxonomic patterns.

53 Specifically examined are patterns in feeding incidence, trophic niche breadth, ontogenetic diet

54 shifts, dominant prey types, relative broadness of diets, and the occurrence of larval piscivory

55 (i.e. fish larvae consuming other fish larvae).

56

57 **2. Material and Methods**

58 *2.1. Literature search*

59   The Aquatic Sciences and Fisheries Abstracts database was searched via CSA Illumina to

60 obtain a list of articles from the peer-reviewed literature meeting the general criteria of reporting

61 empirical results on trophic-related variables of field-collected estuarine or marine planktonic

62 fish larvae. This initial step was conducted with the search: 'fish' (keyword) AND 'larva*'

63 (keyword) AND 'feeding' OR 'diet*' (keyword) NOT 'aquaculture' (keyword) NOT

64 'aquaculture' (source), with keyword and source being categories of the search terms. This

65 combination yielded 2466 journal articles. Based on their titles, 239 of these articles were

66 conservatively selected as potentially containing relevant feeding-related results. Upon reading

67 the abstracts or the articles themselves, the number of papers reporting empirical, feeding-related

68 results on marine or estuarine taxa was 111. This number was supplemented with 18 peer-

69   reviewed articles that were not returned in the search results. Most of these supplemented articles

70   were published prior to the source's inclusion in the ASFA database (the year of a source's initial

71   inclusion in the database varies, but the earliest year that any articles appeared in the search

72   results was 1978). Additionally, some of the supplemented articles were published too recently

73   to, as of yet, be included in the ASFA database. Together, synthesized results were from articles

74   published between 1975 and 2011. To minimize the influence of an incomplete ASFA database

75   on illustrating publishing trends, papers reporting any empirical results related to larval fish

76   feeding were plotted only for articles published between 1980 and 2009 (Fig. 1A).

77   Since the sampling unit for the analyses described below is a unique taxon within a

78   latitudinal region (see section 2.3), it is less essential to gather results from as many articles on

79   larval fish feeding as possible (e.g. those published prior to the ASFA cutoff year of 1978 and in

80   addition to supplemented articles) in order to examine patterns or differences among regions or

81   taxonomic groups. Similar to recent decades, taxa studied prior to 1978 were usually

82   economically important taxa and, as such, have often been studied since 1978. Thus, the

83   inclusion of additional studies on the same taxon could only change the value of the parameter

84   used for that taxon, not add to the sample size. In addition to this, so little was published on low-

85   latitude taxa prior to 1978 that synthesized results for these regions would likely not change at all

86   by extending the literature search farther back. Yet, to evaluate the thoroughness of the articles

87   included herein, cited articles that could potentially contain useful results were noted from the

88   literature cited sections of 12 articles published between 1969 and 1984 that were included or

89   evaluated for inclusion in this synthesis. A total of 25 unique references published between 1925

90   and 1980 were noted. Of these 25, 8 had been included in the present synthesis (or evaluated for

91   inclusion). Within the remaining 17 articles (all published before 1977), a total of only 12 unique

92   taxa were analyzed, and of these 12 taxa, all but 3 had already been included in this synthesis.

93   Types of commonly reported data from gut content studies of fish larvae include feeding

94   incidence (the percentage of larvae containing at least one prey item), diet composition, and

95   relationships related to the sizes of both prey and consumer. Unfortunately, many of the articles

96   initially selected as reporting results on field-collected larvae had methodologies, results formats,

97   or insufficient detail (in the results or methodology) that rendered their results unsuitable for use

98   in this synthesis (recommendations for reporting data and results are made in the Discussion). In

99   all, a total of 81 published articles provided usable results for daytime feeding incidence,

100   numerical diet composition, and/or trophic niche breadth. Since many articles report on multiple

101   taxa, the total number of 'investigations' (taxon-article combinations) was 204, and, as some

102   articles reported results for the same taxon, the total number of unique taxa investigated was 166

103   (73% to the species level, 12% to genus, 15% to subfamily or family). For the analyses below,

104   however, the sampling unit was a unique taxon within a latitudinal region, and since a few taxa

105   were investigated in multiple regions, this number was 175 (Fig. 1B). Investigations with sample

106   sizes less than 20 inspected larvae were excluded. Summary information on each of the

107   investigations used for this synthesis, including the articles from which they came, can be found

108   in Table S1 (supplementary information).

109

110   *2.2. Data and results synthesized*

111   The specific types of results that were synthesized from investigations included daytime

112   feeding incidence, trophic niche breadth, and descriptors derived from numerical diet

113   compositions. For feeding incidence, a single value per investigation for larvae collected during

114   daylight hours was used. As most larval fish taxa only feed during daylight hours, a daytime

115   feeding incidence is the only value useful as an index of feeding success, and, thus, suitable for

116   making comparisons. Some articles did not explicitly state an overall daytime feeding incidence

117   but instead plotted feeding incidence for time blocks throughout the day (and also included times

118   of sunrise and sunset). In these instances, overall daytime values were estimated from such plots,

119   usually by scaling feeding incidences for each time block by the number of larvae sampled in

120   each block. This is equivalent to a single reported feeding incidence for all larvae collected

121   during the day. In a few instances, sample sizes per time block were not reported, and so an

122   average of the feeding incidences for the daytime time blocks was used as the single feeding

123   incidence for that investigation.

124   It is important to note that feeding incidence can vary with a variety of factors, including

125   ontogeny, time of year, environmental conditions, and location, and there are certainly latitudinal

126   differences in related factors such as production cycles, the seasonal timing and length of

127   spawning, and, occasionally, the objectives of larval fish feeding studies. How such factors

128   might yield any latitudinal differences in feeding success, or any other process, would be

129   difficult to assess—suggesting a possible utility for the present synthesis. One criterion for a

130   study's inclusion in feeding incidence comparisons was that there was a broad size range of

131   inspected larvae, thus minimizing the potential bias that the exclusion of a size class or

132   ontogenetic state may have (e.g. by focusing either on first-feeding or later-stage larvae only).

133   Unaccounted for, however, are any differences among studies in the size-frequency distributions

134   of inspected larvae. Since feeding incidence can vary with ontogeny (but not always and not

135   predictably), an overall feeding incidence can be a function of both feeding success and possibly

136   the size-frequency distribution of the larvae. For a latitudinal difference in feeding incidences to

137 emerge that is not related to average feeding success, the size-frequency distributions of studies

138 would, on average, have to vary systematically with latitude, and there would have to be a

139 similar pattern among studies in how feeding incidence varies ontogenetically. The comparison

140 of a large number of investigations should help minimize these possibilities. Another factor that

141 could clearly influence observed feeding incidences is the taxonomic group (at any level) to

142 which the larval fish consumer belongs, which could then translate to overall regional differences

143 if taxa are pooled and the distributions of species within taxonomic groups vary among locations.

144 Therefore, investigating taxonomic differences at the order level, and accounting for them in

145 latitudinal comparisons where sample sizes allowed, is also a focus of this synthesis.

146   Trophic niche breadth, defined as the standard deviation of the log-transformed prey sizes

147 and usually calculated within larval fish (consumer) size classes (Pearre, 1986), is a way of

148 illustrating the relative variability in the sizes of consumed prey. Rather than using the range or

149 the standard deviation of the raw values, the use of log-transformed values allows for

150 comparisons on a ratio-based (relative) scale, thereby standardizing for differences in the mean

151 prey size (e.g. an increase in mean prey size with larval growth). Of specific interest to

152 researchers has been how trophic niche breadth within a taxon changes with predator size and

153 how universal such patterns may be. Pearre (1986) synthesized data on several species (but over

154 size ranges extending well beyond the larval period) and concluded that niche breadth generally

155 does not change with growth. Pepin and Penney (1997) challenged this conclusion, at least when

156 restricted to the larval stage, by showing significant increases in niche breadth or tendencies

157 toward an increase in 9 of 11 taxa from coastal waters of Newfoundland. Contrasting with this,

158 Llopiz and Cowen (2009) reported significant decreases in niche breadth with larval size for 4 of

159 10 taxa of tropical coral reef fishes (with none increasing). Since the work of Pearre (1986),

160   investigating the relationship between niche breadth and larval size (or another proxy for feeding

161   capability such as jaw length or mouth gape) is often included in larval fish trophic studies. Yet,

162   as for all types of published results on larval fish feeding, there has yet to be a synthesis of

163   results on niche breadth to examine either overall generality or differences in patterns among

164   latitudes.

165   In addition to feeding incidence and niche breadth, the remaining types of synthesized

166   results were diet-related, and were based on the numerical percentages of prey types consumed

167   since numerical percentages were by far the most common type of diet results reported. To make

168   comparisons among investigations, a single overall numerical percentage per consumed prey

169   type was extracted from diet results of each investigation. There is the potential for bias in values

170   of overall numerical percentages that could be introduced by an occurrence of ontogenetic diet

171   shifts in conjunction with a size-frequency distribution of inspected larvae that is different from

172   the population. Yet, a single value per prey type per investigation was the most common type of

173   reported result, and further, if the size-frequency distributions of the inspected larvae are similar

174   to those occurring naturally, overall numerical percentages of prey types are an accurate

175   reflection of the consumer's population as a whole. For the few articles that reported prey-type

176   percentages only within larval subdivisions (e.g. larval size classes, seasons, locations), and did

177   not report the number of extracted prey per subdivision, the percentages for each prey type were

178   averaged across subdivisions to obtain an overall value for the investigation. For each

179   investigation reporting suitable diet data, extracted results were (1) the two most numerically

180   dominant prey types consumed (not to be confused hereafter with being dominant in the

181   plankton); (2) the number of prey types, beginning with the most consumed type, to cumulatively

182 compose 90% of the diet; and (3) the total number of prey types consumed in any amount if prey

183 types were identified to suitable taxonomic levels and not grouped together.

184   Regarding prey-type groupings, since articles had zooplankton prey types classified at a

185 variety of taxonomic levels (and to minimize the number of investigations discarded), reported

186 prey types were often combined into higher-level groupings. For the typically common prey

187 types, the groupings used in this synthesis included all copepod nauplii, calanoid copepodites

188 (juveniles and adults together), cyclopoid copepodites by genus (*Oithona*, *Oncaea*, *Farranula*,

189 and *Corycaeus*—though these genera were also summed and graphed as all cyclopoids),

190 harpacticoid copepodites, invertebrate eggs, appendicularians, phytoplankton, and cladocerans.

191 Other types were occasionally dominant, but did not require post-hoc grouping at particular

192 levels to allow for comparisons (e.g. tintinnids, ostracods, bivalve larvae, *Limacina* pteropods,

193 and larval fish).

194 *2.3. Analyses*

195   Each investigation was assigned to a latitudinal region based on the approximate average

196 latitude over which the study was conducted. These regions were high (>60°N/S), high-middle

197 (45–60°N/S), middle (30–45°N/S), low-middle (15–30°N/S), and low (15°S–15°N). Due to low

198 sample sizes in the high and low regions (Fig. 1B), these regions were combined with their

199 respective adjacent regions for analyses. Investigations were also initially classified by

200 planktonic environment ('habitat' hereafter) as estuarine, coastal (bottom depth ca. <100 m and

201 not being separated from shore by water depths >100 m), or oceanic/offshore. However,

202 estuarine investigations were excluded from analyses with the exception of a comparison of

203 feeding incidences only within the low-middle latitude region, because (1) the number of suitable

204 estuarine investigations was low at 16, (2) they were concentrated in the low-middle latitude

205   region with 11 of the 12 from the same study (the four other investigations included one in low,

206   two in middle, and one in high-middle latitudes), and (3) they exhibited clear differences from

207   other habitats within low-middle latitudes. For all comparisons, no patterns were evident

208   between coastal and oceanic/offshore investigations, and therefore, these groupings were

209   combined for analyses other than the initial low-middle latitude comparison of feeding

210   incidences among all three habitat types.

211   A simple metric derived only from diet results for relative diet 'broadness' (i.e. relative to

212   the prey types potentially available in the plankton) was calculated by dividing the total number

213   of all prey types consumed (the best diet-related proxy for what is available to the larvae) by the

214   number of prey types cumulatively composing 90% of the diet (which itself is an indicator of

215   absolute diet 'narrowness').

216   The potential for differences in the prevalence of ontogenetic diet shifts was examined

217   using investigations that subdivided diet results by larval size class or development stage. An

218   ontogenetic diet shift was considered to have occurred if the top prey types that cumulatively

219   compose 50% of the diet in any smaller/younger class are different from those in a larger/older

220   class (either an altogether change in prey types or the addition or loss of a prey type).

221   Relative diet broadness and the number of prey types per taxon (total and those

222   composing 90%) were tested among latitudinal regions using ANOVA and Tukey's HSD test for

223   multiple comparisons. Feeding incidences were often highly skewed toward the upper limit

224   (100%), and, as such, differences among latitudinal regions and taxon orders were tested with

225   either a Kruskal-Wallis or Wilcoxon rank sum test (depending on the number of categories). In

226   the few instances there were multiple investigations for the same larval fish taxon within the

227   same latitudinal region, the mean of the feeding incidences and prey-type percentages for the

228   taxon were used. Statistical analyses were performed with the program R (R Development Core

229   Team, 2011), with multiple comparisons after Kruskal-Wallis (MCKW) tests performed

230   specifically with the R package pgirmess (Giraudoux, 2011).

231

232   **3. Results**

233   The number of published articles reporting empirical, trophic-related results on field-

234   collected fish larvae increased over the last three decades (Fig. 1A). The mean number of articles

235   from 1980 to 1995 was 2.3 yr^{-1} and nearly doubled to 5.4 yr^{-1} for the period 1996 to 2009.

236   Feeding incidences of fish larvae differed by habitat within the low-middle latitude

237   region (Fig. 2A; Kruskal-Wallis, $\chi^2 = 10.6$, df = 2, p = 0.006) where the majority of the few

238   comparable estuarine studies were conducted (12 of 15). Estuarine taxa had significantly lower

239   feeding incidences than both coastal and oceanic/offshore taxa (MCKW, p < 0.01 for both). As

240   described in the Material and Methods, estuarine investigations were excluded from the

241   remainder of the analyses, and coastal and offshore/oceanic investigations were combined.

242   Among latitudinal regions, feeding incidences were significantly different (Fig. 2B;

243   Kruskal-Wallis, $\chi^2 = 15.2$, p < 0.001), exhibiting an increase with decreasing latitude. Low/low-

244   middle latitudes had feeding incidences significantly higher than both high/high-middle latitudes

245   and middle latitudes (MCKW, p < 0.01 for both), while no difference was observed between

246   high/high-middle latitudes and middle latitudes.

247   Feeding incidences were also different among taxonomic orders when all regions were

248   combined (Fig. 2C; Kruskal-Wallis, $\chi^2 = 38.6$, df = 5, p < 0.0001). Clupeiform taxa had

249   significantly lower feeding incidences than both perciforms (MCKW, p < 0.001) and

250   scorpaeniforms (p < 0.01). Similarly, myctophiform feeding incidences were also lower than

251   those of perciforms ($p < 0.05$) and scorpaeniforms ($p < 0.01$). Pleuronectiform feeding

252   incidences were lower than those of scorpaeniforms ($p < 0.05$). Due to sample size constraints,

253   latitudinal differences within orders could only be investigated for Perciformes, and, similar to

254   the results with all taxa combined, significantly higher feeding incidences occurred in lower

255   latitudes (Wilcoxon rank sum test, $W = 275.5$, $p = 0.001$).

256   The percentage of larval fish taxa exhibiting ontogenetic diet shifts in high/high-middle

257   latitudes was 92%, while it was only 58% in middle latitudes and 63% in low/low-middle

258   latitude regions (Table 1). Trophic niche breadth relationships also varied with latitudinal regions

259   (Table 1). In high/high-middle latitudes, 5 taxa had niche breadths that increased significantly

260   with larval size and 9 taxa showed no significant relationship. In middle latitudes, only one taxon

261   had a significantly increasing niche breadth, 14 had no significant relationship, and one had a

262   dome-shaped relationship. In low/low-middle latitudes, 13 taxa had no significant relationship of

263   niche breadth with larval size but 4 had significant decreases in niche breadth.

264   The minimum number of prey types (i.e. those most consumed) to cumulatively compose

265   90% of a taxon's diet was not significantly different among latitudinal regions, averaging

266   approximately 4 prey types per taxon (Fig. 3). However, the total number of different prey types

267   consumed in any amount did differ by region (ANOVA, $F = 7.53$, $df = 2$, $p < 0.001$), with taxa in

268   low/low-middle latitudes having consumed more total prey types than the other regions (Tukey's

269   HSD, $p < 0.01$ for both). The fraction of the total number of prey types represented by the

270   number to reach 90% of the diet was used as a measure of relative diet broadness, which differed

271   among latitudinal regions (Fig. 3; ANOVA, $F = 4.25$, $df = 2$, $p = 0.017$); specifically, low/low-

272   middle latitude taxa had relatively narrower diets than both high/high-middle latitudes and

273   middle latitudes (Tukey's HSD, $p = 0.02$ and 0.04, respectively).

274   Latitudinal patterns in the trophic role of fish larvae as a whole (all taxa combined) were

275   evident when comparing the prey types that were dominant in the diets of larvae among regions

276   (Fig. 4A). The frequency with which appendicularians and cyclopoid copepods occurred as a

277   dominant prey type (this frequency indicating a prey type's overall importance to the larval fish

278   community) increased toward lower latitudes while the frequency for nauplii and phytoplankton

279   decreased. No latitudinal patterns were evident for calanoid copepods (lowest frequency in

280   middle latitudes) or invertebrate eggs (highest in middle latitudes). When only perciform larvae

281   were compared (Fig. 4B), accounting to some extent for potentially influential intrinsic

282   differences among taxa (e.g. morphology), the patterns were similar to those observed with all

283   taxa combined. Without considering latitude, there were clear diet differences among orders for

284   certain prey types (Fig. 4C). For example, clupeiform larvae never relied heavily upon

285   appendicularians or cyclopoids, and this was nearly true for gadiforms (cyclopoids were a

286   dominant type for a small fraction). The lowest dominant prey-type frequencies for calanoids and

287   nauplii were observed for myctophiform larvae, for which cyclopoids had the highest frequency

288   of occurring as a dominant prey type. Phytoplankton was never dominant in either

289   myctophiforms or perciforms.

290   Among latitudinal regions there were clear differences in the frequency with which taxa

291   were piscivorous (Table 2). There were 4 gadid species (cods and haddocks) in high-middle

292   latitudes from one study and a merlucid hake in middle latitudes from another for which a few

293   individuals were observed to have yolk-sac fish larvae in their guts. Aside from these cases, the

294   remaining piscivorous larval taxa were all from the perciform suborder Scombroidei and nearly

295   all occurred in lower latitudes. The only piscivorous scombroid species in high/high-middle

296   latitudes was the Atlantic mackerel (*Scomber scombrus*); in low/low-middle latitudes, 16 taxa

297   from 4 scombroid families were observed to be piscivorous. Among scombroid taxa, there were

298   differences in the relative reliance upon piscivory (not shown), ranging from being nearly

299   exclusively piscivorous throughout ontogeny in *Scomberomorus* spp. (but see Jenkins et al.,

300   1984) to larval fish prey appearing in the diet later and, once appearing, continuing to be

301   supplemented with other prey types (*Scomber* spp.). The standard lengths at which scombrids

302   first exhibited piscivory were ca. 7 mm for *Scomber scombrus* and other lower-latitude *Scomber*

303   spp., 6–8 mm for *Auxis* spp., 6–7 mm for *Thunnus* spp., 5 mm for both *Katsuwonus pelamis* and

304   *Euthynnus* spp., and at first-feeding (ca. 3 mm) for *Scomberomorus* spp. Istiophorid billfishes

305   were piscivorous at 5 mm, swordfish at ca. 9 mm, and gempylids at ca. 8 mm.

306

307   **4. Discussion**

308   Studies on the processes governing larval fish survival have long been recognized as a

309   critical step for understanding not only the early life history of fishes, but also factors influencing

310   population sizes of adult fishes. Given this history, it was possible to use the extensive literature

311   on the feeding ecologies of individual taxa of fish larvae to elucidate large-scale latitudinal and

312   taxonomic patterns. In one of the only general reviews on larval fish feeding ecologies (not a

313   synthesis, and more focused on kinematics, prey-size factors, and other laboratory-based results),

314   Hunter (1981) addressed the relative lack of data at the time for tropical and subtropical larval

315   taxa. Leis (1991) did the same in his brief overview of the feeding of tropical fish larvae. Since

316   these works, a substantial amount of research has been conducted in both high and low latitudes,

317   allowing for the present synthesis of 204 investigations on 166 unique taxa. Emerging from this

318   synthesis were latitudinal differences in the feeding success of fish larvae and the prey types they

319   consume, itself illustrating a change with latitude in the trophic role that fish larvae play in

320   marine planktonic food webs. Identifying large-scale ecological patterns such as those that vary

321   with latitude represents an important step toward gaining an understanding of the underlying

322   mechanisms that might be responsible for the patterns (e.g. Hillebrand, 2004; Willig et al., 2003).

323   Together, the observed differences and patterns in larval fish feeding suggest that there may be

324   inherent distinctions in the food web structure of planktonic ecosystems that extend to fish larvae

325   and their evolved feeding strategies. But, whether gradients in variables such as the diversity and

326   abundance of both larvae and their prey; the timing, frequency, and amplitude of production

327   fluctuations; temperature; photoperiod length; or the seasonality and length of spawning periods,

328   among others, are behind any observed latitudinal distinctions remains largely unknown.

329   Feeding incidences, which are inferred to be related to feeding success and feeding

330   frequency, were significantly higher for taxa in lower latitudes than in higher latitudes. This

331   difference appears to be independent of any species composition differences between the regions

332   since it held within the order Perciformes. Given the greater temperatures in low-latitude waters,

333   and the corresponding increase in metabolic rates and energy demands (Houde, 1989), the

334   significant, but not extreme, difference in median feeding incidences in low/low-middle (96%)

335   and high/high-middle (72%) latitudinal regions might be expected if levels of starvation between

336   the regions were similar. This is because larvae in cooler waters would be physiologically

337   capable of withstanding an empty gut for a longer period. A potential caveat to making

338   comparisons of feeding incidences between low and high latitudes is the distinct difference in the

339   productivity cycles of the regions. In higher latitudes, where narrow periods of high productivity

340   would make match-mismatch dynamics more important (e.g. Cushing, 1990), a study's sampling

341   strategy (including the time of year it was conducted relative to peaks in secondary productivity,

342   as well as its time span) could influence feeding incidences. Contrary to higher latitudes, the

343   tropical and subtropical open ocean maintains lower and more stable levels of productivity

344   (Longhurst and Pauly, 1987; Raymont, 1983). Accordingly, fishes in these regions often exhibit

345   more protracted spawning seasons than species in higher latitudes, if not year-round spawning.

346   At scales smaller than those related to seasonal production peaks, the patchiness of planktonic

347   organisms has been well documented (Davis et al., 1992; Folt and Burns, 1999; Llopiz et al.,

348   2010; Wiebe, 1970); however, we still know very little about how this patchiness influences

349   larval fish feeding dynamics, growth, and survival.

350   Within lower latitudes, the consistently high feeding incidences in offshore, oceanic

351   waters are somewhat paradoxical considering the oligotrophy of the habitat, which should result

352   in low prey availability. It is generally hypothesized that an oceanic planktonic environment

353   offers reduced predation mortality (Bakun and Broad, 2003) but with the nutritional tradeoff of

354   low food availability. While growth rates of low-latitude larvae can be influenced by ambient

355   densities of zooplankton prey (Sponaugle et al., 2009), such high feeding incidences, in

356   combination with rapid evacuation rates and the ability to endure an empty gut for the majority

357   of each nightly non-feeding period (Llopiz and Cowen, 2008; Llopiz et al., 2010), call into

358   question the likelihood of high levels of starvation mortality in lower latitudes. But, total

359   mortality rates of larvae are indeed very high in warm, low-latitude waters (Houde, 1989). So if

360   starvation mortality were low, predation mortality would have to be extremely high.

361   Unfortunately, our understanding of both sources of mortality is rather limited, especially in

362   lower latitudes and despite existing techniques and previous efforts to estimate actual starvation

363   mortality rates (e.g. Gronkjaer et al., 1997; Margulies, 1993; Tanaka et al., 2008).

364   The considerably lower feeding incidences of taxa in estuarine waters within the low-

365   middle latitude group was also surprising given the much greater levels of productivity in

366   estuaries. A major limitation to this comparison is that most of the estuarine taxa were from a

367   single study (Houde and Lovdal, 1984) and location (Biscayne Bay, FL, USA). However, the

368   observed differences do appear to be unrelated to taxonomic factors since the median feeding

369   incidence of the 6 perciform taxa in the estuarine group was the same as for the group as a whole

370   (43%). The low number of estuarine articles included in comparisons (n = 6) was a function of

371   few estuarine articles reporting feeding results on field-collected larvae (n = 17) and a larger

372   proportion of articles, relative to studies in other habitats, that had to be discarded for not

373   reporting results suitable for making comparisons (65% vs. 39%). One conclusion, then, is that

374   our knowledge of larger-scale patterns of the feeding ecologies of estuarine larvae, including

375   how they may or may not differ from other habitats, remains limited for now.

376   There were also distinctions in the types of consumed prey among latitudinal regions,

377   with the greatest differences occurring for copepod nauplii, eggs, and cyclopoid copepods. In

378   high/high-middle and middle latitudes, nauplii were the most common dominant prey type and

379   cyclopoids were rarely dominant. In low/low-middle latitudes, there was a more even

380   distribution of dominant prey types, with nauplii equally as common as calanoid and cyclopoid

381   copepods. Consumption of appendicularians was also highest in lower latitudes, and

382   appendicularians were notably absent from the dominant prey of perciforms in high/high-middle

383   latitudes; however, appendicularians were often a dominant, and sometimes exclusive, prey of

384   higher-latitude pleuronectiforms (e.g. Last, 1978). Diet results from all studies were based on gut

385   content analysis, which, though relatively simple and straightforward, is an informative

386   technique that allows for the enumeration of prey and their identification to an often low

387   taxonomic level—but only when those prey are observable. There is growing evidence that

388   organisms that go unnoticed or are altogether unnoticeable (particularly heterotrophic protists)

389   can play an important role in larval nutrition, either through consumption or indirectly due to

390   their presence (de Figueiredo et al., 2005; Overton et al., 2010; Pepin and Dower, 2007).

391   Not shown for the diet results were the dominant prey types that were in addition to those

392   plotted in Figure 4, most of which occurred in low/low-middle and middle latitudes exclusively

393   or in higher frequencies than in higher latitudes. These included bivalve larvae, cladocerans, and

394   harpacticoid copepods, which were more frequent in lower latitudes, and fish larvae, *Limacina*

395   pteropods, and ostracods, which exclusively occurred as dominant prey types in lower latitudes.

396   Furthermore, within Cyclopoida, *Oithona* was the only genus that was ever dominant in

397   high/high-middle latitudes, while in low/low-middle latitudes there were four cyclopoid genera

398   that were dominant (*Oncaea*, *Farranula*, *Corycaeus*, and *Oithona*). The greater diversity of

399   dominant prey types in lower latitudes certainly follows the general pattern of increasing

400   diversity toward the equator (Hillebrand, 2004; Rombouts et al., 2009; van der Spoel and Pierrot-

401   Bults, 1979); however, comparing the high diversity of dominant consumed prey types to the

402   observations that only a few of these groups are ever dominant in the environment (Hopcroft et

403   al., 1998; Llopiz et al., 2010; Neumann-Leitao et al., 2008) supports the likelihood that fish

404   larvae in lower latitudes, overall, exhibit a higher degree of prey selectivity. Unfortunately, very

405   few low-latitude studies quantitatively examined prey selectivity by comparing diets with prey

406   availability. While Robert et al. (2008) do provide a summary of the preferred prey of larval taxa

407   from published selectivity studies, another hurdle to making quantitative comparisons of prey

408   selectivity across studies and regions would seem to be a lack of a sufficient metric to compare.

409   The approach taken for diet broadness was meant to provide further evidence for

410   latitudinal differences in prey selectivity if they existed. These results showed that larvae in

411   lower latitudes consumed a greater total number of prey types, and, relative to this number

412   (assuming that the total number of prey types is related to the number available to the larvae), the

413   bulk (90%) of their diets was composed of a smaller fraction of the available prey types than

414   larvae in higher latitudes. The results for trophic niche breadth, though limited, illustrated that

415   the distributions by taxa of how niche breadth changes with growth may differ among regions—

416   often increasing (i.e. widening) in higher latitudes, not changing in middle latitudes, and, in

417   lower latitudes, occasionally declining (i.e. narrowing; illustrating these taxa become relatively

418   more specialized with regard to prey size). Together, the patterns of fish larvae in lower latitudes

419   (1) exhibiting potentially greater specialization in the sizes of prey consumed, (2) more often

420   maintaining their diet composition with growth (i.e. not exhibiting an ontogenetic diet shift), and

421   (3) all taxa together having a high diversity of dominant prey types but (4) individual taxa having

422   relatively narrow diets, suggest that there is greater niche partitioning in lower latitudes relative

423   to higher latitudes.

424   One of the clearest differences observed among latitudinal regions was the much greater

425   number of larval taxa in lower latitudes that exhibited piscivory, and this was entirely due to the

426   latitudinal distribution of inspected taxa in the suborder Scombroidei (which includes the

427   families tunas and mackerels, snake mackerels, istiophorid billfishes, swordfish, and, not

428   examined by any included study, barracudas and cutlassfishes [but see D'Alessandro et al.,

429   2011]). Scombroids have distinct adaptations contributing to their evolved strategy of

430   consuming—often at the first-feeding stage—other fish larvae (Govoni et al., 1986; Llopiz and

431   Cowen, 2008; Shoji and Tanaka, 2001; Tanaka et al., 1996). If we assume that all scombroid

432   species exhibit some degree of larval piscivory (none has been shown not to), the striking pattern

433   of the adults (or where they spawn) being concentrated in lower latitudes (Collette and Nauen,

434   1983; Nakamura, 1985; Nakamura and Parin, 1992; Nelson, 2006) results in larval piscivory also

435   being concentrated in lower latitudes. A rough approximation based on the distribution of the

436   adults suggests that, of the nearly 160 species of scombroids, it is likely that less than 10%

437   spawn in latitudes higher than 40° N/S. The only confirmed scombroid larval piscivore of this

438   10%, and likely the most abundant and poleward species, is the Atlantic mackerel (*Scomber*

439   *scombrus*), which exhibits substantial differences from co-occurring non-scombroids in several

440   feeding-related aspects (e.g. Robert et al., 2008). It is possible that not all scombroid species are

441   larval piscivores, and, additionally, species other than scombroids may occasionally display

442   piscivory, including some gadiforms (shown in two investigations here), as well as paralepidids

443   and alepisaurids (pers. obs.). Still, the latitudinally constrained nature of larval scombroids and

444   their behavior of piscivory—a feeding strategy that is effectively dependent upon the timing,

445   location, and intensity of spawning by adult fishes—remains clear and represents one of the

446   largest distinctions among latitudinal regions. Such a difference is paradoxical when considering

447   the low levels of productivity in low-latitude waters together with the decrease in prey

448   abundance and energy lost with each step up in trophic levels.

449   Approximately 43% of the articles initially categorized as having empirical trophic-

450   related results had to be discarded for a variety of reasons. These included inadequate sampling,

451   insufficient detail in the results or methods, or diet categories that were too broad. Some studies

452   had greater objectives than just describing larval feeding dynamics (e.g. investigating feeding in

453   conjunction with other processes) and simply had no need to report details on the feeding-related

454   results that were used in a broader context. However, for future studies with the main goal of

455   describing larval feeding ecologies, following some well-established approaches for reporting

456   metadata, data, and results will ensure future interpretability and broader utility of the published

457   results. These 'best practices' include that (1) if sampling was conducted during both day and

458   night, feeding incidence should be indicated separately for the daytime-collected larvae. Since

459   few species of fish larvae have been shown to feed at night (and even if they do, it would likely

460   be at a reduced level), an overall feeding incidence taken from daytime and nighttime larvae will

461   be influenced not only by feeding success (the variable of interest), but also by gut evacuation

462   rates and the relative sample sizes from each period. Along these lines, (2) if sampling was

463   conducted only during the daytime, this should be stated. (3) Regarding the reporting of diet

464   data, numerical percentages (%N) and frequencies of occurrence (%FO) of prey types (and, if

465   used, any other descriptors such as biomass or volume) should be reported separately. These

466   categories are often combined to calculate an index of relative importance (IRI); but to ensure a

467   study's maximum utility for making comparisons, IRI should not be the only reported descriptor

468   (most journals allow for online supplemental information, where, for example, %N and %FO

469   could be reported while the more condensed IRI could be included in the article). (4) Also

470   regarding IRI, values are most easily interpreted when reported as a percentage rather than a raw

471   product. (5) For %FO, since these values do not sum to 100% across prey categories, values

472   should be given for a variety of taxonomic levels to which the prey type belongs (e.g. for

473   'Copepoda', 'Cyclopoida', and '*Oithona*') to allow for better comparisons among studies. (6)

474   Grouping of prey types should be kept to a minimum, even if the types were of minor importance

475   (e.g. an 'other' category; a thorough table of all prey-type results could also be supplementary

476   information if grouping is necessary to conserve space). Lastly, (7) minimal additional effort is

477   required to identify copepods to at least the order level and doing so provides much more utility

478   than to the level of Copepoda.

479   The results synthesized here on larval fish trophodynamics have highlighted clear

480   differences between higher and lower latitudes and among taxonomic orders. Though these

481   differences are informative, future efforts should also move toward gaining an understanding of

482   the broader-scale ecosystem processes and potential evolutionary mechanisms that are behind

483   these differences. Such an ecosystem approach in the plankton should enhance our understanding

484   of the early life history of fishes and our ability to predict future impacts on important fisheries

485   and planktonic ecosystems.

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489   *Acknowledgements*

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Table 1. Size-related aspects of larval fish feeding by latitudinal region, including the percentages of taxa exhibiting an ontogenetic diet shift (defined as a change with size in the top prey types cumulatively composing 50% of the diet) of the total number of taxa (in parentheses) for which numerical diet composition by size or developmental stage classes were examined; and the number of taxa displaying a non-significant or significantly increasing or decreasing relationship of trophic niche breadth with larval size (or proxy for larval size).

Latitudinal region	Taxa exhibiting an ontogenetic diet shift (of total examined)	Trophic niche breadth with larval size (number of taxa)		
		Non-significant	Increasing	Decreasing
High/High-middle	92% (26)	9	5	0
Middle	58% (38)	11[a]	1	0
Low/Low-middle	63% (32)	13	0	4

[a] One additional taxon observed to have a dome-shaped relationship

Table 2. Number of larval fish taxa within latitudinal regions observed to be piscivorous of the total number of taxa (in parentheses) for which diet results were synthesized. The number of piscivorous taxa is further subdivided at the family level. Taxon names, as well as study information, are in Table S1 (supplementary information).

Latitudinal region	Number of pisciv. taxa (of all taxa examined)	Piscivorous families	Number of pisciv. taxa within family
High/High-middle	5 (33)		
		Scombridae	1
		Gadidae	4*
Middle	6 (52)		
		Scombridae	5
		Merlucciidae	1*
Low/Low-middle	16 (57)		
		Gempylidae	1
		Scombridae	10
		Xiphiidae	1
		Istiophoridae	4

*Prey larvae that were observed in gut contents were yolk-sac larvae and only observed in one study and within a few individuals

Figure captions

Figure 1. (A) Number of journal articles from a search of the Aquatic Sciences and Fisheries

Abstracts database (see Material and Methods) published between 1980 and 2009 in two-year

intervals reporting trophic-related empirical results on field-collected, estuarine or marine fish

larvae (n = 121). (B) Number of articles from which trophic-related data or results were

synthesized, and, from these articles, the number of 'investigations' (taxon-article combinations)

and unique taxa.

Figure 2. Median feeding incidence (percentage of larvae containing at least one prey item) by

(A) habitat type only within the low-middle latitude region, (B) latitudinal region, and (C)

taxonomic order within groups of latitudinal regions (H/HM/M: high, high-middle, and middle;

L/LM: low and low-middle) that emerged as significantly different in B. Upper and lower

boundaries of boxes indicate quartiles and bars indicate 10th and 90th percentiles. For A and B,

pairwise significant differences in feeding incidences are indicated by unshared letters. In C,

unshared letters indicate significant pairwise differences among orders without regard to latitude

(all regions grouped). Only within the order Perciformes was there a significant difference

among region groupings (indicated by the asterisks).

Figure 3. Metrics related to the number of different prey types consumed by fish larvae within

latitudinal regions, including the mean (±SE) total number of prey types, the number of the most

consumed prey types cumulatively composing 90% of the diet, and the relative 'broadness' of

the diet (the fraction of the total number of prey types that the number of types to reach 90%

represents). Significant pairwise differences indicated by unshared letters (among regions for each result category).

Figure 4. Proportions of the dominant prey types (most or second-most numerically dominant in the diets) of fish larvae by (A) latitudinal region for all taxa combined, (B) latitudinal region for perciform taxa only, and (C) taxonomic order with all regions combined.
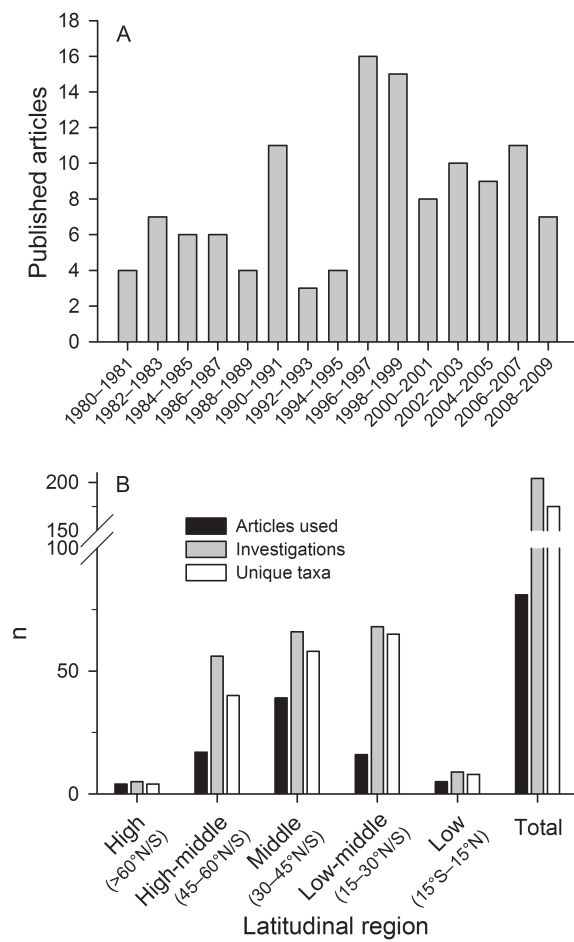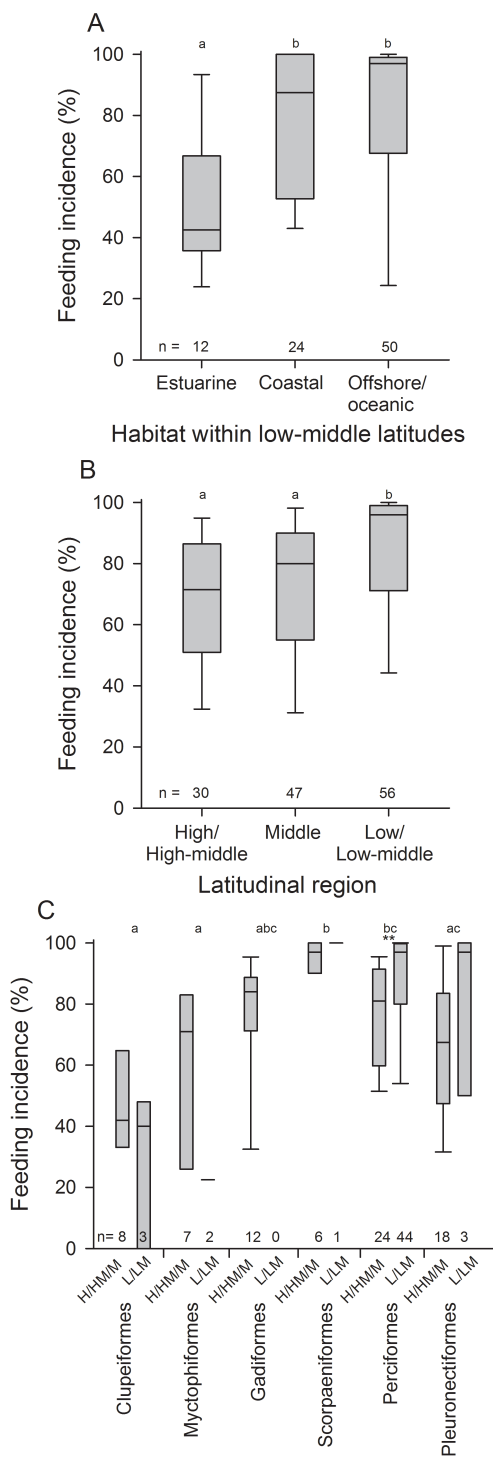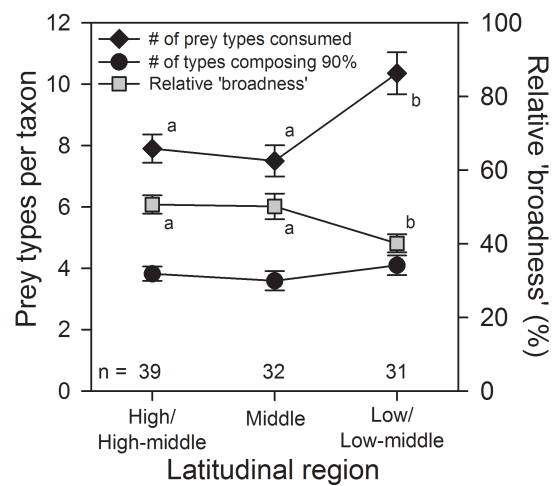
Fig. 1.

Fig. 2.

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Fig. 4.