SHORT COMMUNICATION

Change in prey selectivity during the larval life of Atlantic cod in the southern Gulf of St Lawrence

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Atlantic cod larvae showed strong selectivity for the medium-size calanoid copepod *Pseudocalanus* spp. Naupliar stages comprised 62.4% of total prey number in the gut of first-feeding larvae. Selectivity shifted to *Pseudocalanus* spp. females at the mid-larval stage, representing 43% of all prey ingested by >12 mm larvae.

KEYWORDS: fish larvae; prey selectivity; ontogeny; *Pseudocalanus* spp.; Atlantic cod; *Gadus morhua*

Recruitment success in marine fish populations is generally considered to be highly dependent on the survival rate achieved during the initial and relatively short larval period (Hjort, 1914; Anderson, 1988; Govoni, 2005; Houde, 2008). Any environmental factor which may induce variability in larval processes (e.g. feeding and growth) may thus potentially impact year-class strength through control of mortality rate. However, apart from a few successful attempts at linking year-class strength to larval environmental characteristics (Beaugrand *et al.*, 2003; Platt *et al.*, 2003; Castonguay *et al.*, 2008), the large majority of field-based studies have failed to reveal the main processes accounting for recruitment variability (Myers, 1998). Coupled physical–biological models of the growth and survival of young fish dispersed in a virtual representation of their environment represent a promising alternative avenue towards elucidating the links between ocean climate variability and year-class strength (Miller, 2007; Houde, 2008). The biological component of such models relies on the quantification of functional relationships linking larval behaviour and/or metabolism (e.g. vertical migration, prey selection, energy intake, growth, survival) to key characteristics of the environment (e.g. prey availability, temperature) (Beyer and Laurence, 1980; Cushing and Horwood, 1994; Runge *et al.*, 2004). Among these functional relationships, effects of prey availability on vital rates are particularly difficult to parameterize because of a general lack of information on prey selectivity during the larval stage (Robert *et al.*, 2008). Using a fine taxonomic resolution, the objective of the present study was to characterize the ontogenetic

evolution of diet and prey selectivity in larval Atlantic cod from the southern Gulf of St Lawrence. This work constitutes a first step prior to quantifying and modelling feeding success, growth and survival for this population.

Southern Gulf of St Lawrence cod larvae were sampled through weekly 1-day surveys from late May to mid-September of 1998 and 1999. This time interval spanned most of the spawning and larval development season of Atlantic cod in the area (Lett *et al.*, 1975; DFO, 2009). Sampling was concentrated in areas located to the south-east and north-east of the Magdalen Shallows (Fig. 1). During each survey, the sampler was deployed 6 to 10 times from 1600 to 2100 hours. Detailed sampling methodology is given in Robert *et al.* (Robert *et al.*, 2007, 2008). Briefly, the

Fig. 1. (**a**) The Gulf of St Lawrence in eastern Canada with delineated study area. (**b**) The Magdalen Shallows with stations where fish larvae and their zooplankton prey were sampled in 1998 (triangles) and 1999 (circles).

sampler consisted of a rectangular metal frame towed from its centre and carrying two plankton nets (750-μm mesh, 1 m^2 aperture) to capture fish larvae and large zooplankton. Two small cylindrical nets (64-μm mesh, 81 cm^2 aperture, 4 m long) were fastened on each side of the sampler to collect the microzooplankton prey of cod larvae. Upon retrieval of the sampler, the cod-ends of the 750-μm mesh nets were immersed in a tricaine methane sulphonate (MS-222) solution to prevent larval cod gut content evacuation. Larvae were then preserved in 95% ethanol, while the 64-μm mesh net microzooplankton samples were preserved in 4% formaldehyde.

A stratified sub-sample of 713 larvae was assembled for gut content analysis by randomly picking larvae among length classes in the 2 years. Prey items found in the digestive tract of each larva were identified to the lowest taxonomic level possible at ×70 magnification. Digested copepods that could not be identified or staged (~25%) were assigned to species/stage in proportion to the relative abundance of identified copepods in the diet of a given larval length class.

Zooplankton were identified in the 64-μm mesh net sample corresponding to each 750-μm mesh net sample in which at least one cod larva was captured. Successive known aliquots were taken with a Stempel pipette and all organisms were enumerated under the dissecting microscope until a minimum of 300 organisms were identified to species (and developmental stage for copepods). Since late larval Atlantic cod primarily feed on later stage copepods which represented a small fraction of the 300 organisms, the procedure was repeated where only copepodites were enumerated. This added precision to the first estimation of copepodite abundance. Stages CV and CVI of *Calanus finmarchicus* were enumerated from the 750-μm mesh net collections as they are undersampled by 64-μm mesh nets (McLaren and Avendaño, 1995).

Following Govoni *et al.* (Govoni *et al.*, 1986) and Llopiz and Cowen (Llopiz and Cowen, 2008), selectivity of each individual cod larva for its main prey was quantified using Chesson's (Chesson, 1978) α electivity index:

$$\alpha_j = \frac{(d_j/p_j)}{\sum(d_i/p_i)}, \text{ for } i = 1 \ldots \mathcal{N} \tag{1}$$

where $\mathcal{N}$ is the number of prey taxa considered; (d_j/p_j) the relative frequency ratio of prey j in the diet and in the plankton; and $\sum(d_i/p_i)$ the sum of this ratio for all prey taxa. Copepod eggs were not considered an independent prey for larvae of length >6 mm because of the probability of passive ingestion when preying on
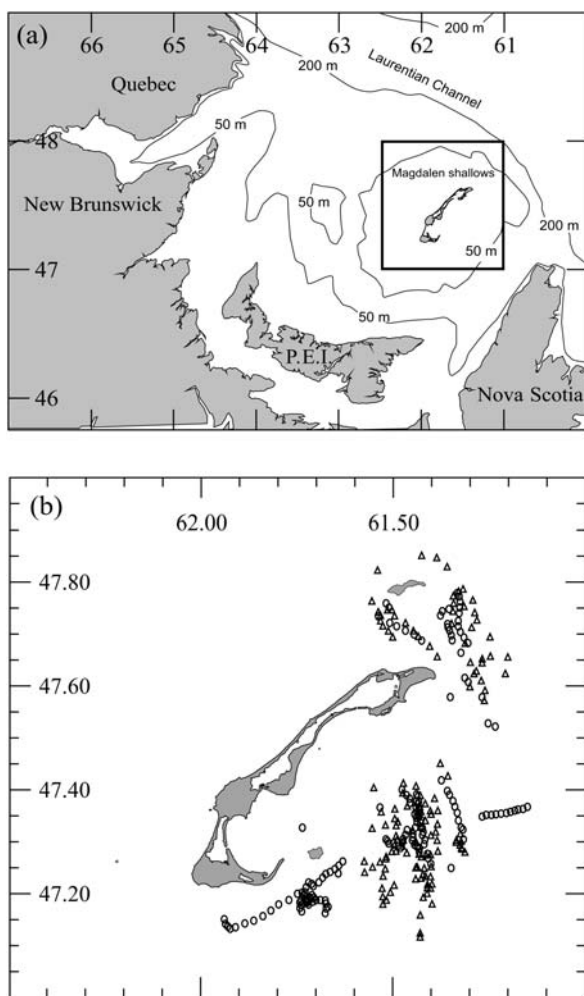
Table I: Diet composition by length classes of Atlantic cod larvae expressed as the per cent contribution by number of different species and stages of prey

Prey taxon	Stage	Length class (mm)			
		3 to ≤6	6 to ≤9	9 to ≤12	12 to ≤20
Copepods					
Nauplii					
Pseudocalanus spp.	I	–	<0.1	–	–
	II	2.6	1.2	0.2	<0.1
	III	23.6	11.4	3.5	0.5
	IV	33.9	29.9	11.2	2.2
	V	2.0	1.9	0.8	0.2
	VI	0.3	0.5	0.2	0.1
Cyclopoids	I	0.1	–	–	–
	II	2.2	0.6	–	–
	III	4.7	1.6	0.4	<0.1
	IV	0.4	0.3	0.2	<0.1
	V	–	0.1	0.1	–
	VI	–	–	–	–
Temora spp.	I	0.2	–	–	–
	II	1.0	0.1	<0.1	–
	III	1.7	0.1	–	–
	IV	1.5	0.2	0.2	–
	V	1.4	0.5	0.1	<0.1
	VI	0.3	0.1	–	<0.1
Calanus spp.	I	0.1	0.1	–	–
	II	0.5	0.4	–	–
	III	3.4	2.5	0.4	<0.1
	IV	0.9	0.5	0.3	0.1
	V	0.3	0.1	0.3	<0.1
	VI	–	<0.1	–	<0.1
Copepodites					
Pseudocalanus spp.	I	3.8	6.5	3.9	2.3
	II	0.8	3.9	4.1	2.0
	III	1.2	4.1	4.8	2.8
	IV	1.3	3.6	6.1	6.7
	V	0.9	6.8	8.2	8.5
	♀	0.7	8.7	26.4	43.0
	♂	–	0.7	0.6	0.2
Oithona similis	I	–	0.1	0.1	0.1
	II	0.2	0.3	0.4	0.1
	III	0.2	0.3	0.4	0.6
	IV	0.3	0.2	1.6	1.9
	V	0.6	2.2	4.7	6.8
	♀	0.2	3.4	6.4	7.0
	♂	–	–	0.1	0.1
Temora longicornis	I	0.4	0.6	0.3	0.1
	II	0.4	0.6	0.3	0.1
	III	0.1	0.2	0.4	0.4
	IV	–	0.2	0.5	0.2
	V	–	0.3	0.2	0.4
	♀	–	–	0.3	0.2
	♂	–	–	0.2	0.4
Calanus finmarchicus	I	–	0.2	0.4	0.4
	II	0.1	0.2	0.4	0.9
	III	0.1	0.3	0.7	0.9
	IV	–	0.1	0.2	0.6
	V	–	–	0.2	0.6
	♀	–	–	<0.1	0.2
	♂	–	–	–	0.1
Cladocerans		0.1	<0.1	–	1.3
Gastropods		0.1	–	–	<0.1
Bivalve larvae		2.7	0.6	0.2	0.1
Number of larvae analysed		217	177	157	162
Mean number of prey		10.0	16.3	17.5	28.1
Mean carbon ingested (µg)		2.3	8.8	20.3	55.8

egg-carrying females. Selectivity was computed for individual larvae and then averaged over length intervals.

Atlantic cod larvae of all lengths preyed almost exclusively on copepods, which represented on average >95% of all ingested prey (Table I). By number, copepod nauplii comprised 83.5% of the diet of larvae ≤6 mm, and nearly 75% of these were *Pseudocalanus* spp. (primarily NIII and NIV). As larval length increased, the diet shifted from nauplii to copepodites, with *Pseudocalanus* spp. females becoming the dominant prey (Table I). For any length class, *Pseudocalanus* spp. represented over 65% of the total number of prey ingested. *Oithona similis*, *Temora longicornis* and *Calanus finmarchicus* made up the bulk of the remaining copepod prey fraction.

The *in situ* abundance of the four main prey of Atlantic cod larvae (*Pseudocalanus* spp., *O. similis*, *T. longicornis*, *C. finmarchicus*) followed a similar seasonal pattern in 1998 and 1999 (Fig. 2). All developmental stages started to increase in number during the second half of June, with abundance peaking in mid-July 1998 and late June 1999 (Fig. 2). The number of *O. similis* increased again in August 1999, but less so in 1998. Abundance of medium-sized calanoids *Pseudocalanus* spp. and *Temora* spp. rapidly decreased after a mid-summer peak (Fig. 2a–d). The nauplii, copepodites and adult stages of the two genera showed similar abundances throughout the season. Relative to other prey, the abundance of the large *C. finmarchicus* was low.

All length classes of Atlantic cod larvae strongly selected for *Pseudocalanus* spp. (Table II). Selectivity for *Pseudocalanus* spp. shifted from the naupliar stages in larvae ≤6 mm to copepodites and females in larvae 6 to ≤9 mm, and then principally to females in larvae >9 mm. *Calanus* spp. nauplii were selected for by larvae ≤9 mm and *C. finmarchicus* copepodites by larvae >12 mm (Table II). Cod larvae systematically selected against nauplii and copepodites of *O. similis* and *T. longicornis*.

Our results are in agreement with a large body of literature showing that the different species of the *Pseudocalanus* genus (or the morphologically similar *Paracalanus*) constitute the dominant prey for Atlantic cod larvae in populations located in southern portions of the species distribution (reviewed by Heath and Lough, 2007). To our knowledge, the present study, however, provides the deepest insight to date into the ontogeny of larval cod selectivity for their *Pseudocalanus* spp. prey. The naupliar stages of *Pseudocalanus* spp., highly selected by ≤6 mm cod larvae, proved to be the key prey item at the onset of exogenous feeding. First-feeding larvae also selected for the larger *Calanus* sp. nauplii, but the contribution of this relatively rare taxon to total number of prey ingested remained low and could not have sustained the metabolic demand by itself. After the first-feeding stage, larvae 6 to
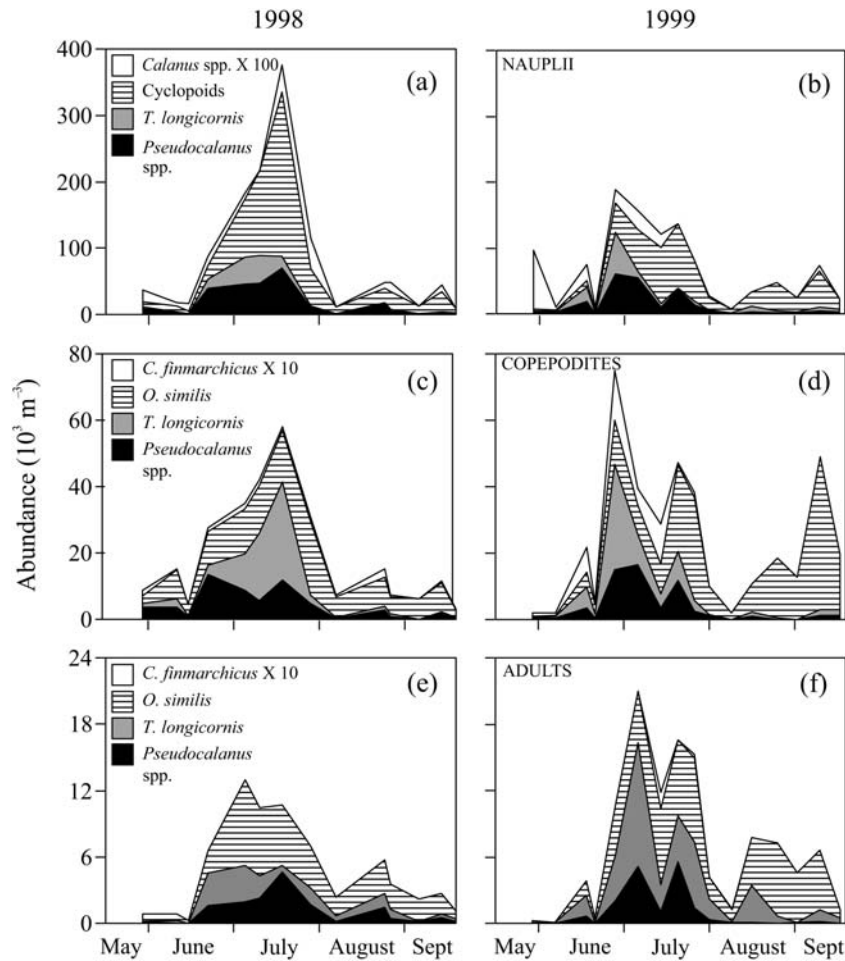
Fig. 2. Seasonal pattern in the abundance of the naupliar (**a**, **b**), copepodite (**c**, **d**) and adult (**e**, **f**) stages of the main copepod prey of Atlantic cod larvae on the Magdalen Shallows in 1998 and 1999. The density of *C. finmarchicus* was multiplied by 100 (naupliar stage) or 10 (copepodite and adult stages) to allow visualization on the same scale as the other species.

≤9 mm underwent a feeding transition period. The increase in body and gape size, combined with increasing energy demand, likely prompted a shift in selectivity from the small *Pseudocalanus* sp. nauplii to copepodite and female stages of the same species. This feeding shift was fully achieved by a body size of 9 mm, when larvae systematically selected against small copepod nauplii and strongly for the female stage of *Pseudocalanus* spp.

The origin of the strong selectivity pattern towards *Pseudocalanus* spp. throughout the larval stage in southern Atlantic cod populations remains unclear, but several hypotheses can be put forward. *Pseudocalanus* spp. usually represents one of the most abundant prey taxa of suitable size in the environment, with relatively stable availability through time (Lough *et al.*, 1996). However, Atlantic cod larvae did not select *Pseudocalanus* spp. on the sole basis of abundance on the Magdalen Shallows, as the equally abundant *Temora longicornis* was selected against (Table II). Another potential reason

explaining this selection pattern is that *Pseudocalanus* spp. are characterized by a high lipid content and fewer robust structures relative to other genera of the same size such as *Temora* (Lough *et al.*, 1996). A relatively high level of activity (Tiselius and Jonsson, 1990; Incze *et al.*, 2001) could also make *Pseudocalanus* spp. an easier prey to detect (Sullivan *et al.*, 1983; Peterson and Ausubel, 1984; Limburg *et al.*, 1997). In a modelling study, Kristiansen *et al.* (Kristiansen *et al.*, 2009) concluded that the strong selectivity for *Pseudocalanus* spp. during the early larval stage likely reflected a passive process and was mainly attributable to combined high abundance and behavioural traits enhancing detection by larval predators. Passive prey selectivity in early larvae would, however, evolve to an active process during the highly motile late larval stage (Rowlands *et al.*, 2008). We propose that on the Magdalen Shallows, strong and active selection for *Pseudocalanus* spp. females occurred as soon as larvae became large enough (≥9 mm) to

Table II: Selectivity (α, Chesson, 1978) of Atlantic cod larvae for their main prey according to different length classes of fish larvae

		Length class (mm)			
	Prey taxon	3 to ≤6	6 to ≤9	9 to ≤12	12 to ≤20
Copepods					
Nauplii	*Pseudocalanus* sp.	0.46 ± 0.03 (+)	0.11 ± 0.02 (+)	0.03 ± 0.01 (−)	0.00 ± 0.00 (−)
	Cyclopoid	0.06 ± 0.01 (−)	0.01 ± 0.00 (−)	0.00 ± 0.00 (−)	0.00 ± 0.00 (−)
	Temora sp.	0.06 ± 0.01 (−)	0.01 ± 0.00 (−)	0.00 ± 0.00 (−)	0.00 ± 0.00 (−)
	Calanus sp.	0.21 ± 0.03 (+)	0.19 ± 0.03 (+)	0.06 ± 0.01 (−)	0.01 ± 0.00 (−)
Copepodites	*Pseudocalanus* sp.	0.11 ± 0.02 (+)	0.22 ± 0.02 (+)	0.16 ± 0.01 (+)	0.14 ± 0.01 (+)
	Oithona similis	0.03 ± 0.01 (−)	0.03 ± 0.01 (−)	0.02 ± 0.00 (−)	0.02 ± 0.00 (−)
	Temora longicornis	0.01 ± 0.00 (−)	0.01 ± 0.00 (−)	0.01 ± 0.00 (−)	0.01 ± 0.00 (−)
	Calanus finmarchicus	0.01 ± 0.00 (−)	0.07 ± 0.02 (−)	0.12 ± 0.02 (+)	0.19 ± 0.02 (+)
Females	*Pseudocalanus* sp.	0.04 ± 0.01 (−)	0.31 ± 0.02 (+)	0.53 ± 0.02 (+)	0.53 ± 0.02 (+)
	Oithona similis	0.01 ± 0.00 (−)	0.09 ± 0.01 (+)	0.05 ± 0.01 (−)	0.04 ± 0.01 (−)
	Temora longicornis	–	–	0.01 ± 0.00 (−)	0.01 ± 0.00 (−)
	Calanus finmarchicus	–	–	0.01 ± 0.01 (−)	0.03 ± 0.01 (−)
Bivalves		0.02 ± 0.01 (−)	0.00 ± 0.00 (−)	0.00 ± 0.00 (−)	0.00 ± 0.00 (−)
Cladocerans		0.00 ± 0.00 (−)	0.00 ± 0.00 (−)	–	0.02 ± 0.01 (−)
Gastropods		0.00 ± 0.00 (−)	–	–	0.00 ± 0.00 (−)
Number of prey taxa considered (*M*)		13	12	13	15
1/*N*		0.08	0.08	0.08	0.07
Number of larvae analysed		213	176	155	162

Mean values ± SE are shown. Signs in parentheses indicate whether the selectivity was positive ($\alpha > 1/N$, + sign) or negative ($\alpha < 1/N$, − sign). Larvae with empty stomach were not included in this analysis.

capture them. Such a selectivity pattern could be explained by the fact that unlike other calanoid copepods found in the area, *Pseudocalanus* spp. are egg-bearers. We argue that larvae actively selected for the relatively abundant, conspicuous and weakly protected egg-carrying females of *Pseudocalanus* as a means to maximize energy intake per attack. The results of Lough *et al*. (Lough *et al.*, 2005) suggest that the same type of selection occurred on Georges Bank, as post first-feeding cod larvae consumed *Pseudocalanus* spp. adults in larger numbers than copepodites, and among adults, females dominated the gut contents over males by up to an order of magnitude. Interestingly, Atlantic mackerel from the Magdalen Shallows have also been reported to select for *Pseudocalanus* spp. nauplii at the first-feeding stage (Robert *et al.*, 2008). This suggests that spatiotemporal variations in the abundance of this copepod may simultaneously impact early survival of several commercially important species in the area.

Death is the fate of the vast majority of fish larvae dispersed in the plankton. The infrequent survivors (typically 10^{-6} for an annual fecundity of 10^{6} in cod) are often considered to be those individuals that encountered an improbable sequence of favourable feeding events during the transition period from endogenous to exogenous feeding (Hjort, 1914; Platt *et al.*, 2003). Alternatively, survivors may be those individuals that benefited from optimal growth conditions (including prey supply) throughout larval life (Houde, 1987; Anderson, 1988; Cushing, 1990). The strong prey selectivity pattern exhibited by larval Atlantic cod as well as its evolution through ontogeny, thus, bear large implications for modelling larval growth, survival or recruitment. If testing the "Critical Period" hypothesis (Hjort, 1914), the model should essentially focus on *Pseudocalanus* sp. nauplii density as the effective prey field at first feeding. If the model is alternatively based on the "Growth-Predation" hypothesis framework (Anderson, 1988), it should explicitly take into account the ontogenetic shift in prey selectivity by considering in turn *Pseudocalanus* sp. nauplii at first feeding, and *Pseudocalanus* sp. females from the mid-larval stage.

REFERENCES

Anderson, J. T. (1988) A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *J. Northwest Atl. Fish. Sci.*, **8**, 55–66.

Beaugrand, G., Brander, K., Lindley, J. A. *et al.* (2003) Plankton effect on cod recruitment in the North Sea. *Nature*, **426**, 661–664.

Beyer, J. E. and Laurence, G. C. (1980) Stochastic-model of larval fish growth. *Ecol. Model.*, **8**, 109–132.

Castonguay, M., Plourde, S., Robert, D. *et al.* (2008) Copepod production drives recruitment in a marine fish. *Can. J. Fish. Aquat. Sci.*, **65**, 1528–1531.

Chesson, J. (1978) Measuring preference in selective predation. *Ecology*, **59**, 211–215.

Cushing, D. H. (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.*, **26**, 249–294.

Cushing, D. H. and Horwood, J. W. (1994) The growth and death of fish larvae. *J. Plankton Res.*, **16**, 291–300.

DFO (2009) Assessment of cod in the southern Gulf of St. Lawrence. *DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2009/007*, 15 pp.

Govoni, J. J. (2005) Fisheries oceanography and the ecology of early life histories of fishes: a perspective over fifty years. *Sci. Mar.*, **69**, 125–137.

Govoni, J. J., Ortner, P. B., Al-Yamani, F. *et al.* (1986) Selective feeding of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae in the northern Gulf of Mexico. *Mar. Ecol. Prog. Ser.*, **28**, 175–183.

Heath, M. R. and Lough, R. G. (2007) A synthesis of large-scale patterns in the planktonic prey of larval and juvenile cod (*Gadus morhua*). *Fish. Oceanogr.*, **16**, 169–185.

Hjort, J. (1914) Fluctuations in the great fisheries of northern Europe viewed in light of biological research. *Rapp. P-V. Réun. Cons. Int. Explor. Mer.*, **20**, 1–228.

Houde, E. D. (1987) Fish early life dynamics and recruitment variability. *Am. Fish. Soc. Symp.*, **2**, 17–29.

Houde, E. D. (2008) Emerging from Hjort's shadow. *J. Northwest Atl. Fish. Sci.*, **41**, 53–70.

Incze, L. S., Hebert, D., Wolff, N. *et al.* (2001) Changes in copepod distributions associated with increased turbulence from wind stress. *Mar. Ecol. Prog. Ser.*, **213**, 229–240.

Kristiansen, T., Lough, R. G., Werner, F. E. *et al.* (2009) Individual-based modeling of feeding ecology and prey selection of larval cod on Georges Bank. *Mar. Ecol. Prog. Ser.*, **376**, 227–243.

Lett, P. F., Kohler, A. C. and Fitzgerald, D. N. (1975) Role of stock biomass and temperature in recruitment of southern Gulf of St. Lawrence Atlantic cod, *Gadus morhua. J. Fish. Res. Board Can.*, **32**, 1613–1627.

Limburg, K. E., Pace, M. L., Fischer, D. *et al.* (1997) Consumption, selectivity, and use of zooplankton by larval striped bass and white perch in a seasonally pulsed estuary. *Trans. Am. Fish. Soc.*, **126**, 607–621.

Llopiz, J. K. and Cowen, R. K. (2008) Precocious, selective and successful feeding of larval billfishes in the oceanic Straits of Florida. *Mar. Ecol. Prog. Ser.*, **358**, 231–244.

Lough, R. G., Caldarone, E. M., Rotunno, T. K. *et al.* (1996) Vertical distribution of cod and haddock eggs and larvae, feeding and condition in stratified and mixed waters on southern Georges Bank, May 1992. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **43**, 1875–1904.

Lough, R. G., Buckley, L. J., Werner, F. E. *et al.* (2005) A general biophysical model of larval cod (*Gadus morhua*) growth applied to populations on Georges Bank. *Fish. Oceanogr.*, **14**, 241–262.

McLaren, I. A. and Avendaño, P. (1995) Prey field and diet of larval cod on Western Bank, Scotian Shelf. *Can. J. Fish. Aquat. Sci.*, **52**, 448–463.

Miller, T. J. (2007) Contribution of individual-based coupled physical–biological models to understanding recruitment in marine fish populations. *Mar. Ecol. Prog. Ser.*, **347**, 127–138.

Myers, R. A. (1998) When do environment-recruitment correlations work? *Rev. Fish Biol. Fish.*, **8**, 285–305.

Peterson, W. T. and Ausubel, S. J. (1984) Diets and selective feeding by larvae of Atlantic mackerel *Scomber scombrus* on zooplankton. *Mar. Ecol. Prog. Ser.*, **17**, 65–75.

Platt, T., Fuentes-Yaco, C. and Frank, K. T. (2003) Spring algal bloom and larval fish survival. *Nature*, **423**, 398–399.

Robert, D., Castonguay, M. and Fortier, L. (2007) Early growth and recruitment in Atlantic mackerel: discriminating the effects of fast growth and selection for fast growth. *Mar. Ecol. Prog. Ser.*, **337**, 209–219.

Robert, D., Castonguay, M. and Fortier, L. (2008) Effects of intra- and inter-annual variability in prey field on the feeding selectivity of larval Atlantic mackerel (*Scomber scombrus*). *J. Plankton Res.*, **30**, 673–688.

Rowlands, W. L., Dickey-Collas, M., Geffen, A. J. *et al.* (2008) Diet overlap and prey selection through metamorphosis in Irish Sea cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*). *Can. J. Fish. Aquat. Sci.*, **65**, 1297–1306.

Runge, J. A., Franks, P. J. S., Gentleman, G. C. *et al.* (2004) Diagnosis and prediction of variability in secondary production and fish recruitment processes: developments in physical-biological modeling. In Robinson, A. R. and Brink, K. H. (eds), *The Global Coastal Ocean: Multiscale Interdisciplinary Processes*. Vol. 13. Harvard University Press, Cambridge, pp. 413–473.

Sullivan, B. K., Buskey, E., Miller, D. C. *et al.* (1983) Effects of copper and cadmium on growth, swimming and predator avoidance in *Eurytemora affinis* (Copepoda). *Mar. Biol.*, **77**, 299–306.

Tiselius, P. and Jonsson, P. R. (1990) Foraging behaviour of six calanoid copepods: observations and hydrodynamic analysis. *Mar. Ecol. Prog. Ser.*, **66**, 23–33.