

Preliminary examination of the match-mismatch hypothesis and recruitment variability of yellowtail flounder, *Limanda ferruginea*

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Underlying explanations of recruitment variation among fish stocks have been an issue for several decades. An understanding of biological relationships between larval fish and their zooplankton prey is needed for interpreting recruitment success. Recruitment fluctuations often depend upon events occurring during a critical period between spawning and the time of first feeding by larvae (Hjort, 1914). Conditions affecting these early life stages will also determine the number of individuals that survive in a year class. The timing of spawning can enhance the spatial and temporal affinity between larvae and their food resources (Hjort, 1914; Cushing, 1975, 1990; Cushing and Dickson, 1976).

Once resorption of the yolk sac is complete by yolk sac larvae, their survival depends entirely upon the amount and accessibility of available food. If sufficient prey is not located after the yolk sac has become exhausted, permanent degeneration of the larva's digestive system will occur (Pitcher and Hart, 1983). Not only are early stage larvae and young juveniles vulnerable because of their dependence on nourishment, they are also susceptible to movement caused by ocean currents (Hjort, 1914, 1926), predation, and starvation (Houde, 1987).

Yellowtail flounder (*Limanda ferruginea*) is an economically important species that experiences marked variation in year-class strength. In the present study, time series data of fish eggs, larvae, and zooplankton were used to determine if a match or mismatch in time and space between yellowtail flounder production and its potential

prey existed from Georges Bank and Southern New England 1977 through 1987. Cushing (1975; 1990) hypothesized that links (matches or misses) in time and space among phytoplankton blooms followed by zooplankton and then larval fish lead to year-class variability. A match occurs when there is a close overlap between production curves of fish larvae and their planktonic prey; conversely, a mismatch occurs when there is an extensive temporal difference (Fig. 1) (Cushing, 1975; 1990). A match of peak occurrences would presumably result in a successful year class owing to adequate feeding and growth, and increased chances for survival if other sources of mortality and loss are constrained.

Yellowtail flounder became a key constituent of the U. S. demersal fishery in the early 1930s as a result of stock declines in winter flounder (Royce et al., 1959). There were subsequent drastic reductions in populations and catches during the early 1970s in Southern New England (SNE) and the mid-1970s in Georges Bank (GB). In SNE stocks, landings declined from 3.5 metric tons (t) in 1970 to 1.5 t in 1975. The abundance of New England groundfish declined by 65% from 1977 to 1987 (NEFC, 1991). Three stocks—haddock, redfish, and yellowtail flounder—reached record low levels by the late 1970s.

The present study is the first attempt to examine interannual variability in yellowtail recruitment in the context of the match-mismatch hypothesis. The goal of this study was to test the prediction of the match-mismatch hypothesis for yellowtail flounder stocks that

exist and spawn on Georges Bank (GB) and off Southern New England (SNE) and to observe any correlation between year-class strength and prey abundance. Data from a comprehensive sampling program, the Marine Resources Monitoring, Assessment, and Prediction (MARMAP), structured with broad temporal and geographic coverage, were used for this study. Collections were made during 1977–87 on the U.S. continental shelf from Cape Hatteras to the Gulf of Maine.

Materials and methods

A total of 2496 stations from the western North Atlantic were sampled during an eleven-year period from 1977 to 1987. At each station fish eggs, larvae, and zooplankton were collected with a bongo frame (diameter at the mouth of net: 61 cm) (Posgay and Marak, 1980) fitted with 0.333-mm and 0.505-mm mesh nets and a 45 kg depressor. The volume of water filtered by each net was measured by flowmeters suspended in the center of the net mouth. The plankton nets were lowered at a rate of 50 meters per minute, to within 5 meters of the bottom or to a maximum depth of 200 meters, and retrieved at a rate of 20 meters per minute; nets were towed at 1.5 knots at a 45-degree angle. Net contents were preserved in a mixture of 5% formalin and ocean water. Larvae were measured to within 0.1-mm length increments. For complete descriptions of MARMAP sampling procedures see Sibunka and Silverman (1984, 1989).

For each station, catch values were standardized to the number of individuals under 10 m² surface area. The delta distribution (Aitchison, 1955) provided unbiased estimates of sample means (Berrien et al., 1981; Pennington, 1983). The abundance and distribution patterns of yellowtail flounder eggs and larvae were monitored and compared with those of *Calanus* and *Pseudocalanus* prey species in the GB and SNE regions from 1977 to 1987.

Although feeding habit studies of yellowtail larvae have not been docu-

mented, *Calanus* sp. and *Pseudocalanus* sp. are both dominant representatives of the zooplankton community of the North Atlantic and are important prey for many spring spawned fish larvae (Cushing, 1982; Runge, 1988). The widespread abundance and distribution of *Calanus* and *Pseudocalanus* favor them to be the most likely prey choice of yellowtail flounder larvae. Collectively, monthly distributions and mean densities of zooplankton for May and June coincide with peak occurrences of yellowtail flounder (Figs. 2 and 3). The Spearman's rank-order correlation analysis was used to measure the association between ichthyoplankton and their zooplankton prey.

An adaptation of the "larval food supply model" (Mertz and Myers, 1994) was used to test the match-mismatch hypothesis, the relationship between spawning variability, and the variability of recruitment. The recruitment estimates were obtained from the Northeast Fisheries Science Center (NEFC, 1991). Two aspects were explored: 1) whether or not a relationship exists between spawning duration and recruitment variability and 2) whether deviations from peak spawning between yellowtail flounder larvae and prey are related to recruitment variability.

The mean and standard deviation of observed abundance versus time was calculated for both yellowtail larvae and their prey for each year and for both sub-areas. The width and overlap of the abundance curves for predator and prey were analyzed. Selected methods from the Mertz and Myers (1994) study were applied for partial use of this analysis. The following parameters—

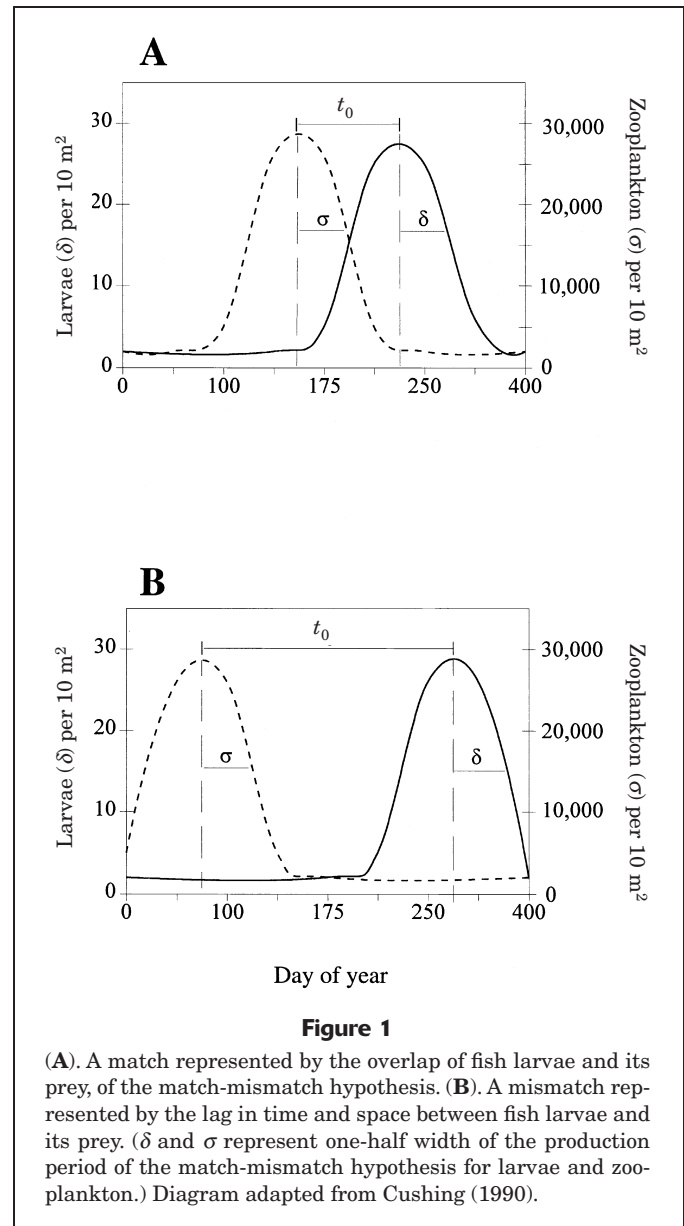
- t_0 = timing between peaks of larval production and food supply;
- Δt_0 = annual differences in (t_0) from its mean value;
- δ = one-half width of the production period for larvae; and
- σ = one-half width of the production period for zooplankton

—were used to calculate 1) variability in peak timing from the mean for individual species (σ and δ), 2) variability in timing between larval spawning and peak zooplankton production (t_0), and 3) year-to-year variability in peak spawning and production (Δt_0). When $t_0 = 0$, the match between the peak larvae and production of zooplankton is exact (Mertz and Myers, 1994).

Results and conclusions

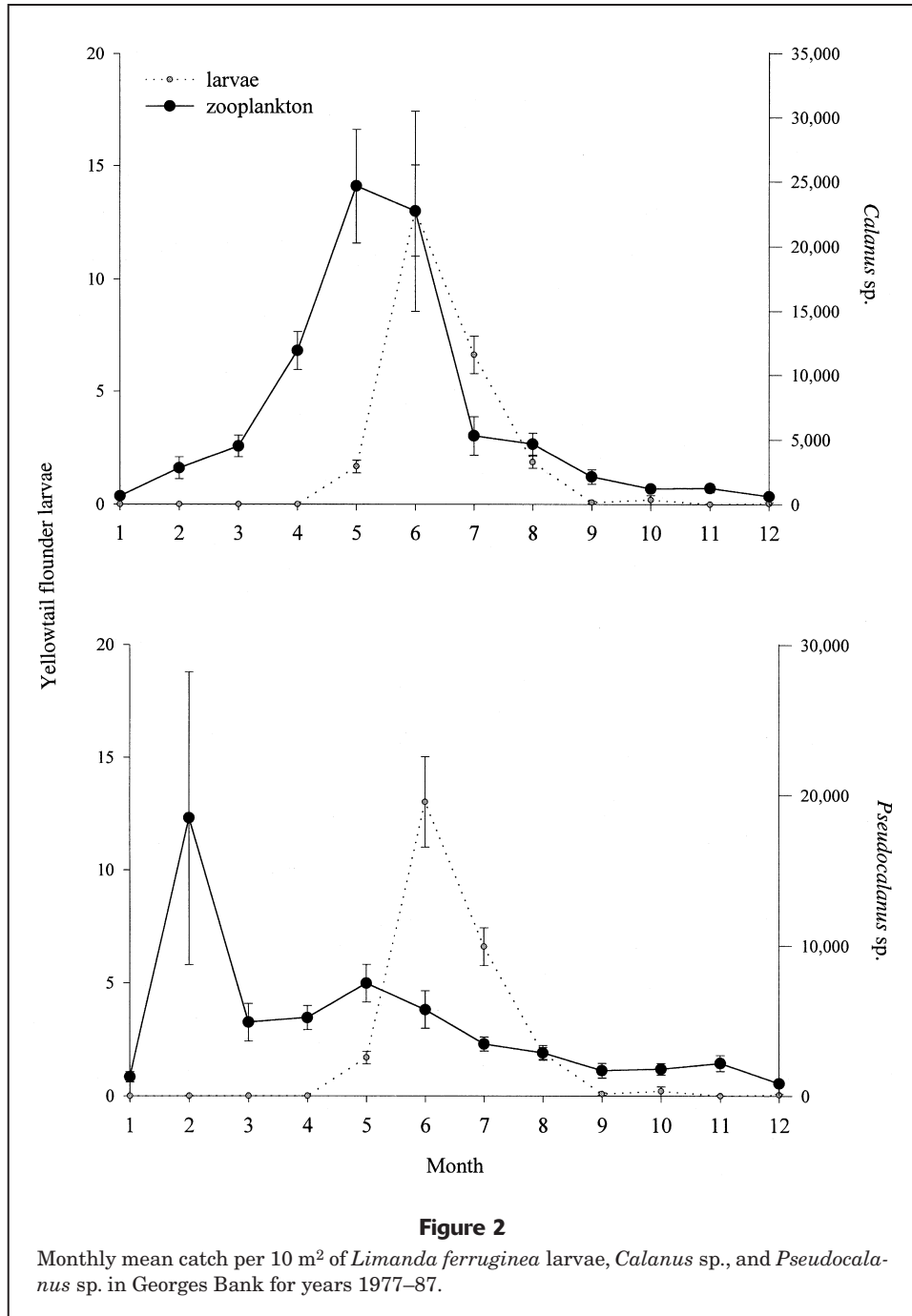
Variability in timing for individual species

Zooplankton The duration of the *Calanus* sp. peak production (σ) varied from 3.4 to 26.5 days for both subareas. The narrowest distribution occurred during 1984 with 3.4 days, and extremes occurred in 1977 with greater than 12 days for GB and 26.5 days for SNE. The greatest span in peak production for *Pseudocalanus* sp. was 33 days. Smallest duration ranged between 7.8 days (GB) to



slightly under 1 day (SNE). The greatest span of time when zooplankton was abundant was 24 days for GB during 1981 and 35 days for SNE during 1982. The low or high zooplankton occurrence was not associated with the strengths or weaknesses of yellowtail recruitment. Both strong (1981) and weak (1982) year classes of yellowtail flounder occurred during times of high variability in peak production of zooplankton.

Ichthyoplankton The difference in timing of peak spawning (Δt_0) from its mean value for yellowtail larvae for both subareas ranged from 1.4 days to approximately 10 days. The largest values of Δt_0 occurred in GB, and again large differences in the timing of spawning did not always reflect years with poor recruitment. Two strong year classes occurred with extreme values of Δt_0 : 1977



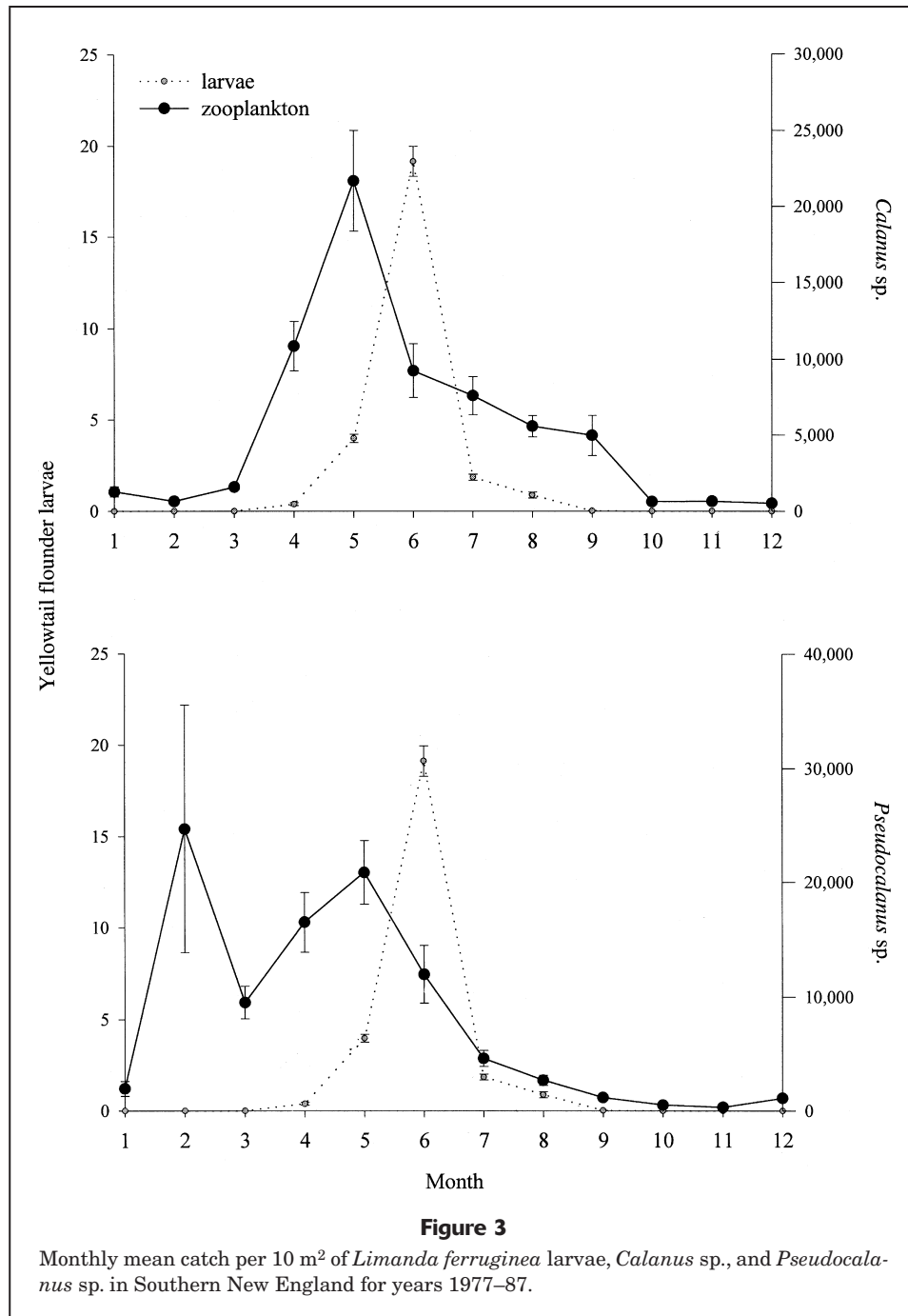
with 7 days and 1980 with 3.9 days in GB. In SNE, the weakest year class (1982) possessed the greatest (Δt_0) span with 9.9 days.

Variability in timing between peaks in predator and prey abundance

Examinations of matches and mismatches of larval food and time of yellowtail spawning are shown by the occurrence of width displacements and overlaps from larvae

(δ) and its zooplankton prey (σ). The relationship between yellowtail larvae and *Calanus* sp. for SNE display definite matches for years 1980, 1986, and 1987. A slightly larger gap existed between peaks for the year class 1982 (Fig. 4).

During the strong year classes 1980 and 1987, density of yellowtail larvae peaked after that of *Calanus* sp., whereas the reverse occurred in the weaker year classes 1986 and 1982. Similar patterns occurred with the peak spawning and peak production relationships between yellowtail larvae and *Pseudocalanus* sp. The year classes 1982 and

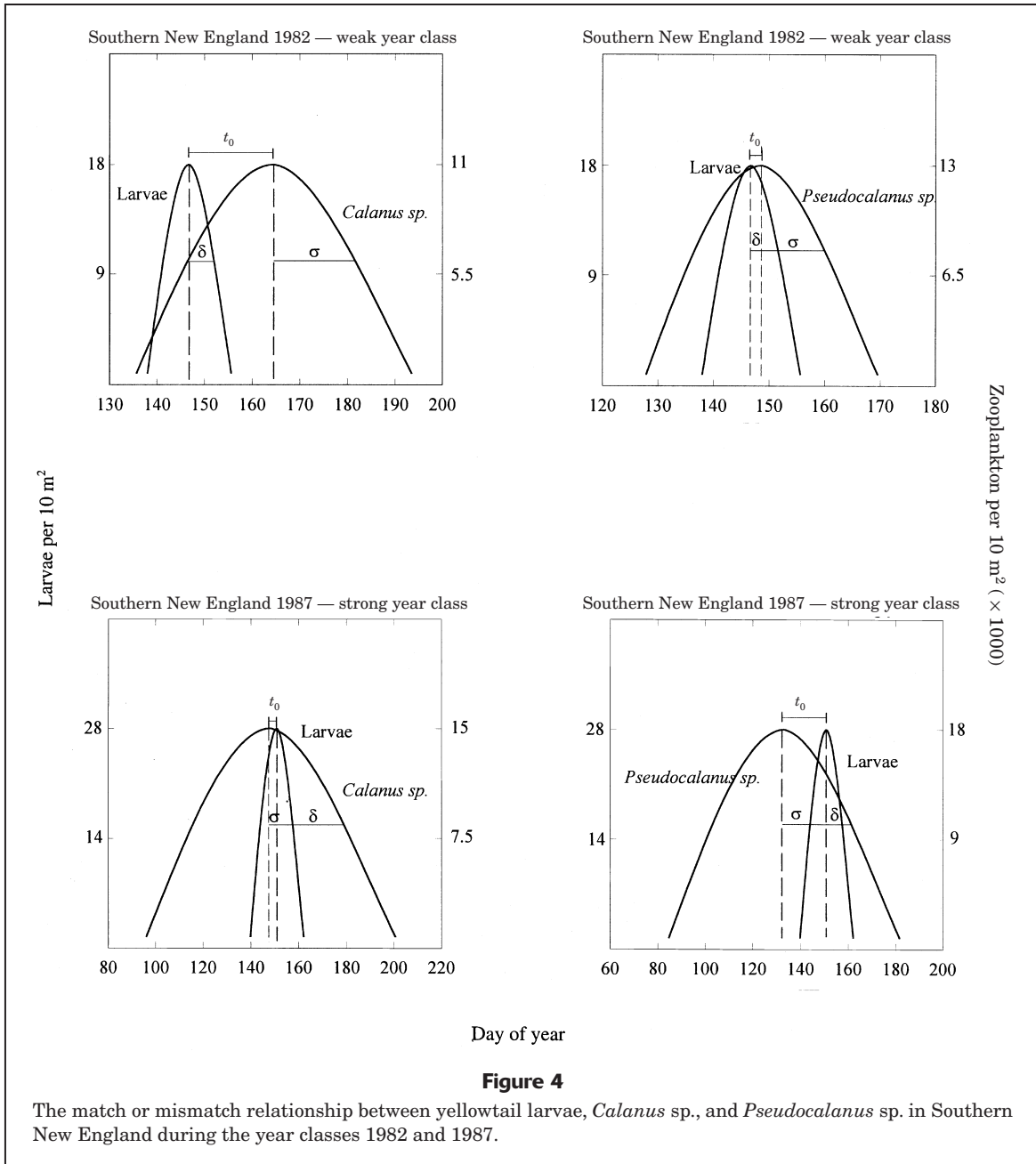


1987 showed matches in peak spawning and prey production (Fig. 4).

Larger gaps exist between predator and prey in GB for many of the year classes (Fig. 5). There was a temporal gap of almost 56 days between yellowtail flounder and *Calanus* sp. abundance during 1980 and 1982. A slightly smaller mismatch occurred during 1977 at 45 days. The poor year class 1986 had the smallest span in time between predator and prey (16 days) when larvae peaked prior to *Calanus* sp.. For the same year class, 1986, the difference between

peaks was slightly greater between larvae and *Pseudocalanus* sp.. There was a smaller mismatch between *Pseudocalanus* sp. and larvae for year class 1982, amounting to 52.6 days (Fig. 5). The stronger year classes, 1977 and 1980, showed more definite matches in spatial timing (<45 days).

To test for a relationship between predator-prey overlap and year-class strength, differences between predator and prey peaks versus year-class strength were plotted for the eleven-year time period (Fig. 6). Two predator and prey combinations (t_0), yellowtail larvae and *Calanus* sp., and



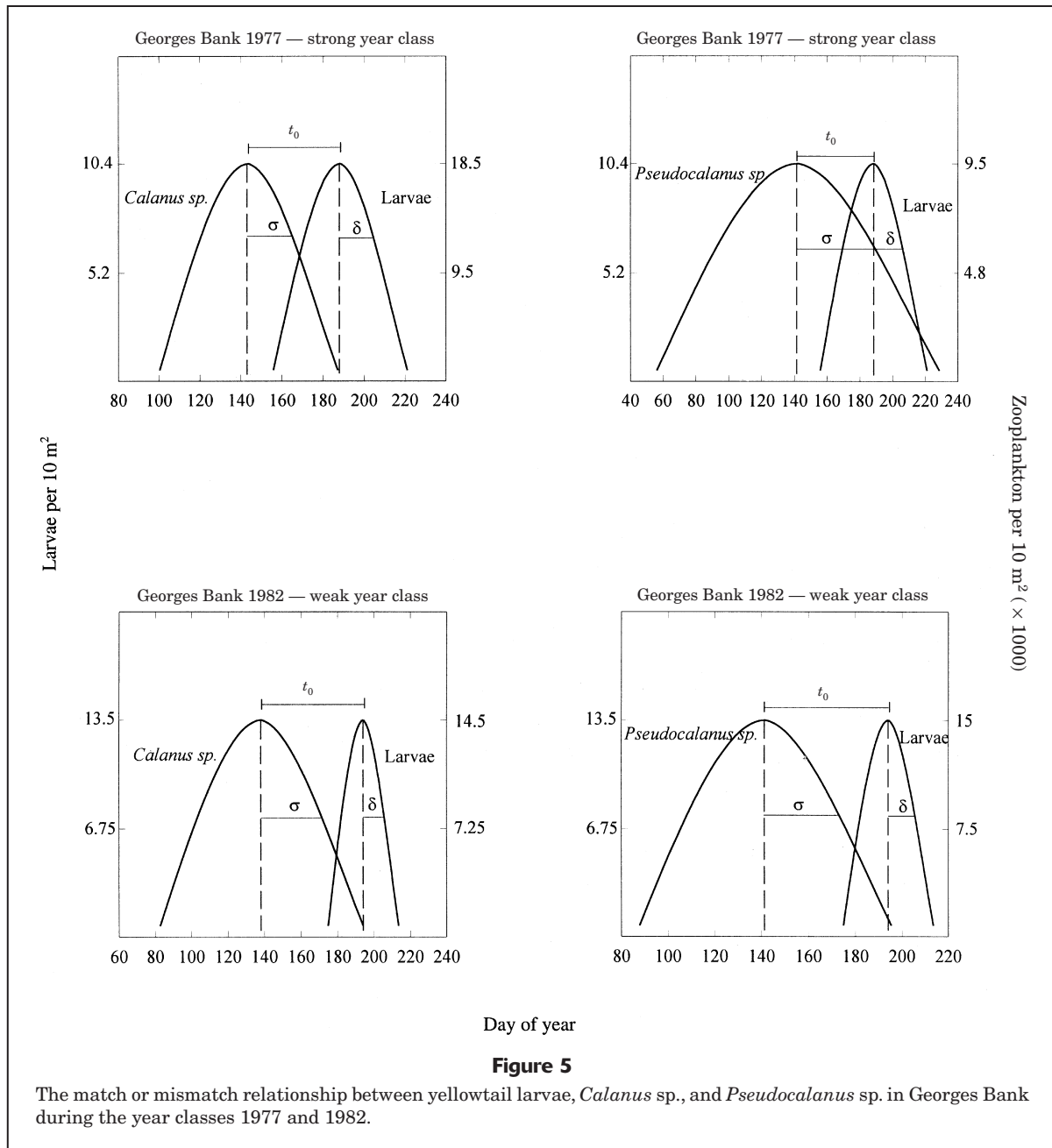
yellowtail larvae and *Pseudocalanus* sp. were examined for each subarea. In both subareas the strong year classes (1980, 1987 SNE; 1980, 1977 GB) were consistently positioned in ranges of t_0 less than zero. The extreme differences in predator and prey peaks frequently reflected the location of poorer year classes (1982, 1986 for both SNE and GB). Unexpectedly, these year classes normally occurred when predator and prey timing was equal to or greater than zero.

Although not statistically significant, the Spearman's rank-order correlation between predator-prey overlap and larval abundance suggested a possible relationship between recruitment variability and the predator-prey

pairs, especially for the combination of larvae and *Calanus* sp. in SNE (Table 1).

Year-to-year variability in peaks of predator and prey abundance

As expected, the greatest anomaly in timing for three of the four predator-prey pairs occurred during the 1982 year class. The large difference in timing between predator and prey was reflected in the contour plot of larvae and zooplankton during 1982 (Fig. 7). There was a mismatch in timing between yellowtail flounder and *Calanus* sp. in GB and between yellowtail flounder and *Pseudocala-*



nus sp. in SNE. Neither predator-prey pair was synchronous. In GB the yellowtail flounder larvae and *Calanus* sp. did not match in time or space. The zooplankton population appeared strong but the spawning of yellowtail flounder occurred during different times, creating low overlap between the two species. Years with the lowest anomalies in timing were 1984 and 1986 for GB and years 1977, 1980, 1986, and 1987 for SNE.

This study relied on extensive data for yellowtail flounder and zooplankton abundances in SNE and GB to test general predictions of the match-mismatch hypothesis. In general no strong support was found for this hypothesis. High overlap between zooplankton and yellowtail floun-

der abundances did not necessarily result in strong yellowtail flounder year classes, and some of the strongest year classes occurred when overlap was low.

Annual timing of spawning and production cycles from larvae and zooplankton prey (Table 2) also revealed variations between subareas. The spawning production for yellowtail flounder peaked earlier in the more southern subarea SNE than in GB, for all years excluding 1984. Similar results occurred in the production of *Pseudocalanus* sp., with the majority of first peaks cited in SNE for all years except 1978 and 1982. However, opposite patterns were observed for *Calanus* sp. production. Production cycles peaked first in seven of the eleven years in the

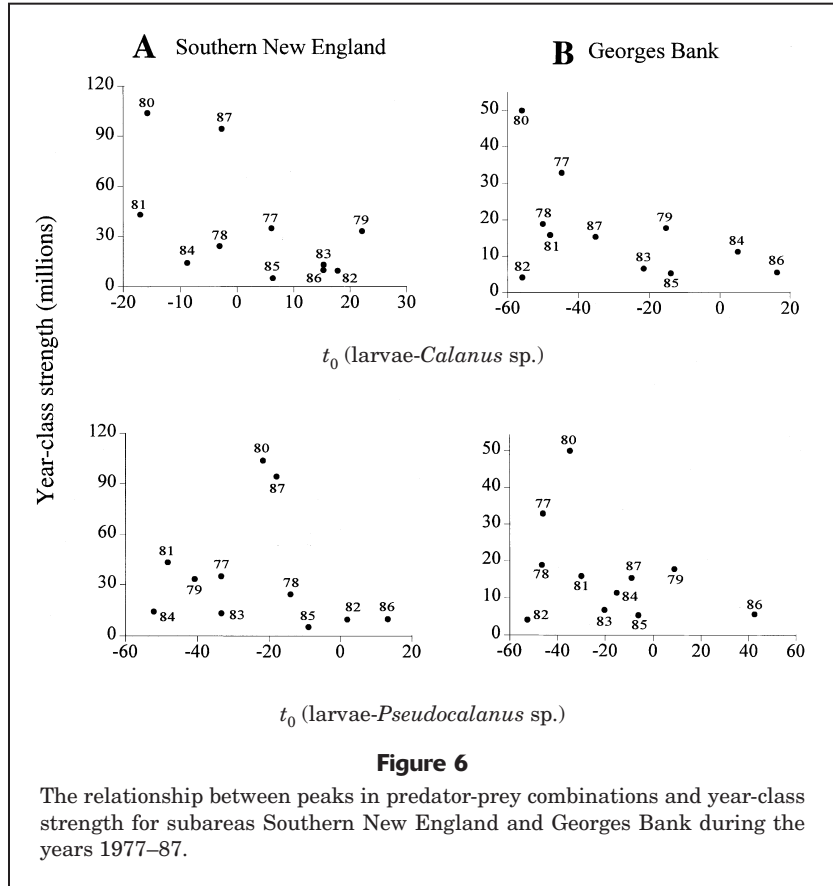


Table 1

Spearman's rank-order correlation coefficients of predator-prey combinations (t_0) for subareas Southern New England (SNE) and Georges Bank (GB) during the 1977–87 time period.

Subarea	Predator-prey combination	r^2	$P > F$
SNE	larvae- <i>Calanus</i> sp.	-0.31	0.077
SNE	larvae- <i>Pseudocalanus</i> sp.	-0.21	0.160
GB	larvae- <i>Calanus</i> sp.	-0.20	0.170
GB	larvae- <i>Pseudocalanus</i> sp.	-0.07	0.417

GB subarea; the exceptions were the years 1984 through 1987. The mean differences in peaks for all years was 22.5 for larvae, 26.6 for *Pseudocalanus* sp. and -9.8 for *Calanus* sp.

Although this eleven-year study did reveal some possible relationships between predator and prey, there was no clear demonstration of a match or mismatch for strong or weak year classes. Results from this study were unable to conclude if high or low ratios between predator and prey abundance could determine or even predict the growth and survival of first-feeding larvae and their ultimate

year-class success. Questions for future research should include 1) stomach-content analyses of larvae to determine prey, 2) incorporation of abiotic influences, and 3) sampling at a much smaller spatial scale. These additional features would increase the feeding success and growth rate estimation of young yellowtail flounder.

Acknowledgments

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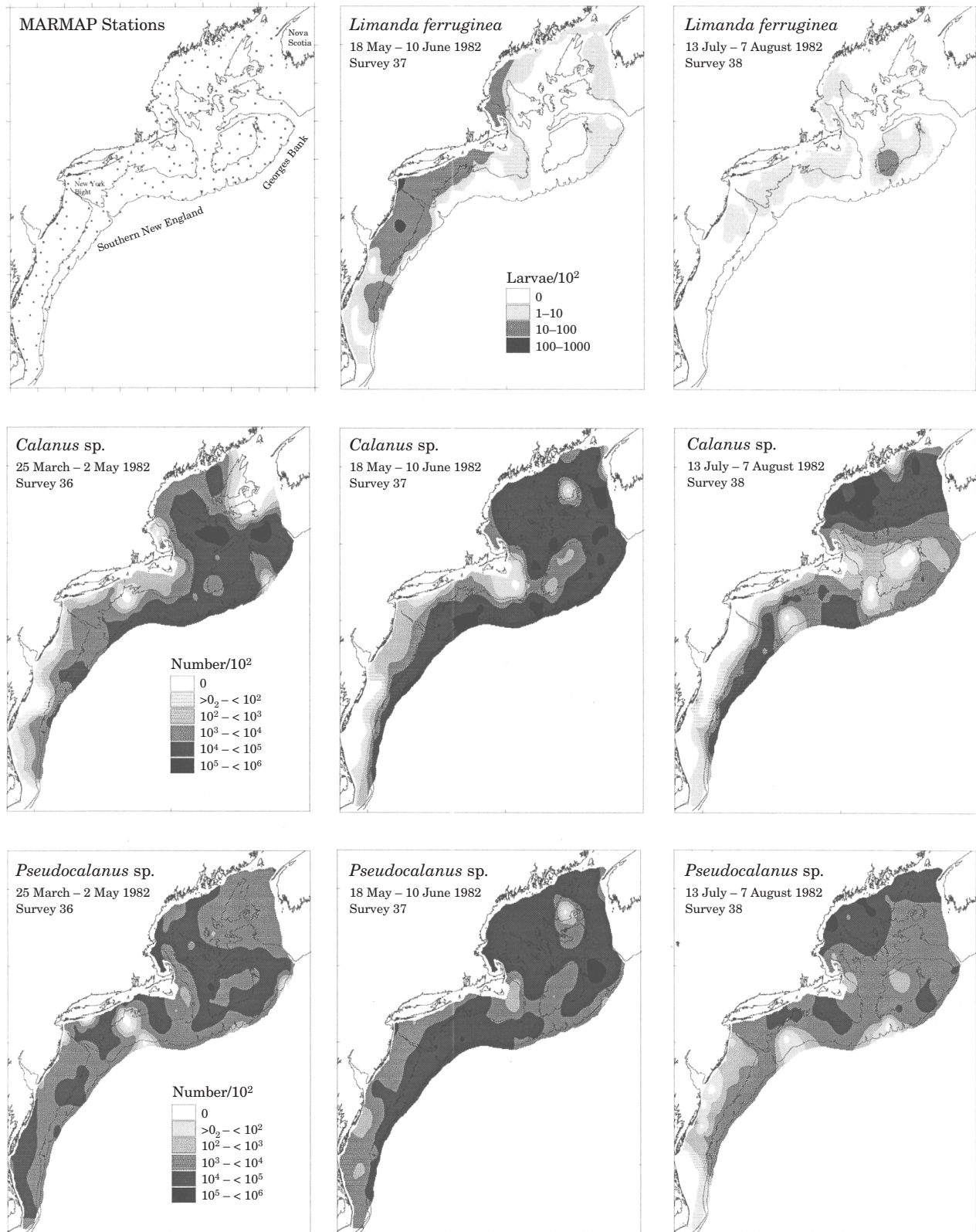


Figure 7

Distribution and abundance of predator *Limanda ferruginea*, and prey *Calanus* sp. and *Pseudocalanus* sp. during the production months of 1982.

Table 2

Mean dates of peak occurrence between spawning and production for yellowtail larvae and zooplankton. C – L = the difference between *Calanus* sp. (C) and larvae (L); and P – L = the difference between *Pseudocalanus* sp. (P) and larvae. (Values in bold were omitted from some parts of the analyses). SNE = Southern New England; GB = Georges Bank.

Subarea	Year	Mean numeric date (Julian calendar)			t_0	
		Yellowtail	<i>Calanus</i> sp.	<i>Pseudocalanus</i> sp.	C – L	P – L
SNE	1977	142.165	148.283	108.849	6.118	-33.316
	1978	163.409	160.381	149.433	-3.028	-13.976
	1979	157.900	180.044	117.218	22.144	-40.682
	1980	165.692	149.971	144.097	-15.721	-21.595
	1981	162.881	145.877	114.694	-17.004	-48.187
	1982	146.877	164.653	148.749	17.776	1.872
	1983	156.263	171.619	123.027	15.356	-33.236
	1984	167.729	158.964	115.622	-8.765	-52.107
	1985	145.375	151.724	136.489	6.349	-8.886
	1986	146.906	162.182	160.195	15.276	13.289
1987	151.111	148.470	133.289	-2.641	-17.822	
GB	1977	188.486	143.828	142.521	-44.658	-45.965
	1978	190.935	141.003	144.407	-49.932	-46.528
	1979	158.285	143.063	167.135	-15.222	8.850
	1980	198.189	142.306	163.603	-55.883	-34.586
	1981	173.270	125.278	143.250	-47.992	-30.020
	1982	194.324	138.514	141.743	-55.810	-52.581
	1983	168.289	146.770	148.058	-21.519	-20.231
	1984	162.345	167.399	147.164	5.054	-15.181
	1985	171.862	157.967	165.720	-13.895	-6.142
	1986	158.822	175.171	201.425	16.349	42.603
1987	188.463	153.322	179.525	-35.141	-8.938	

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