

Diel vertical migration in zooplankton: field evidence in support of the predator avoidance hypothesis

Stephen M. Bollens¹, Bruce W. Frost, Dave S. Thoreson & Sidney J. Watts

School of Oceanography, WB-10, University of Washington, Seattle, Washington, 98195, USA

¹*Current address: Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*

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Abstract

We report results of a field test of the predator avoidance hypothesis as an explanation of the adaptive significance of diel vertical migration in zooplankton. We determined the vertical distribution and diel migration of the planktonic copepod *Acartia hudsonica*, concurrently with the abundance of pelagic fish, transparency and thermal stratification of the water column, on six cruises over a one year period in a temperate marine lagoon (Jakles Lagoon, San Juan Island, Washington, USA). Striking seasonal variability was observed in all biological and environmental variables. Linear regressions of the strength of diel vertical migration in *A. hudsonica* on these environmental variables resulted in only one statistically significant relationship, that between copepod diel vertical migration and predator abundance. These results, together with those of previous studies, point to diel vertical migration as a widespread behavioral response of planktonic prey to the presence of their predators.

Introduction

Diel vertical migration (DVM), whereby animals reside in the surface layer at night and descend a few to several hundred meters to spend the day at depth, is widespread among aquatic organisms. Of the several hypotheses put forth to explain the adaptive significance of DVM (Kerfoot, 1985; Lampert, 1989), evidence implicating predator evasion has recently accumulated from field (Bollens & Frost, 1989a; Stirling *et al.*, 1990; Ohman, 1990), theoretical (Frost, 1988; Gabriel & Thomas, 1988; Mangel & Clark, 1988; Ohman, 1990) and experimental (Bollens & Frost, 1989b; Neill,

1990) studies. These studies lead to the prediction that the occurrence of DVM in planktonic animals in the field is positively related to the abundance of their predators. While such relationships have indeed been found (see brief review in Bollens & Frost, 1989a), the locales studied have been limited in number and scope, and only one was marine.

In an effort to broaden the types of field sites used to test the predator evasion hypothesis, and thereby make results collectively more general and far ranging, we undertook the following field study of a temperate marine lagoon. The specific purposes of our study were threefold. First, to de-

scribe the seasonal variation in DVM behavior of the dominant lagoon zooplankter, the calanoid copepod *Acartia hudsonica* Pinhey. Second, to describe the seasonal variation in the abundances of the major species of planktivorous fish in the lagoon, as well as the transparency and degree of thermal stratification of the water column. And third, to relate the strength of DVM in *A. hudsonica* to the magnitudes of these various environmental parameters.

Materials and methods

The field site was Jakles Lagoon, a small (2.6 ha), shallow (max. depth = 3.6–4.0 m, depending on the tides) marine lagoon located on San Juan Island, Washington, USA (48° 28' N, 122° 59' W). The hydrography and bathymetry of Jakles Lagoon are briefly reviewed in Landry (1978). We sampled pelagic fish and zooplankton in the central portion of the lagoon on each of the following six cruises: 21–24 June 1989; 28–31 August 1989; 12–14 October 1989; 6–8 December 1989; 2–4 March 1990; and 26–28 April 1990.

The vertical distribution of the dominant zooplankter, the calanoid copepod *Acartia hudsonica* Pinhey, was determined using a multiple water bottle sampler described in Bollens & Frost (1989b). Duplicate samples were collected near noon and midnight on each of two consecutive days during each cruise. The entire water column was sampled with each deployment of the sampler, save the bottom 10 cm, which consisted of macrophytes and mats of algae. Although the actual strata sampled varied slightly due to tides, on average we sampled the following four discrete depth strata: 0–0.8, 0.8–1.8, 1.8–2.8, and 2.8–3.8 m. As a measure of the strength of DVM in *A. hudsonica* on each cruise, we calculated the proportion of the population migrating on a diel cycle by calculating the difference between the fraction of the population above a reference depth of 2.8 m at midnight and the fraction of the population above 2.8 m at midday (i.e., V as described by Bollens & Frost, 1989a).

Fish were sampled by two methods. Three to twelve nighttime replicate tows were made on each cruise with a 2.0 m² (1.4 × 1.4 m) ridged-framed midwater trawl (3 mm stretch mesh). The trawl was maintained at the surface with floats and towed behind and slightly to the side of a 4 m skiff, effectively sampling the surface 1.4 m of the water column. The trawl was used to sample only that portion of the lagoon at least 2.0 m deep (approximately 65% of the surface area of the lagoon). Tow speeds averaged 1 m/s, and volumes filtered, measured by a flow meter mounted in the mouth of the trawl, averaged 300 m³ per tow. Samples were preserved in 10% formalin-seawater solution, and all individual fish were subsequently identified, enumerated, and measured for length to the nearest mm in the laboratory (when total catch of any one species was greater than 400 individuals, a subsample of at least 100 fish was taken for measurement of lengths).

Abundance of the dominant fish, threespine stickleback (*Gasterosteus aculeatus* Linnaeus) was also assessed by Petersen type mark-recapture studies during the June, August, and October cruises (abundances proved to be too low during winter and spring to employ this technique). Methods for Petersen type mark-recapture studies are discussed in detail in Ricker (1975) and Southwood (1978). Briefly, a known number of fish were captured by pelagic trawl or seine, marked by immersion in neutral red stain (3-Amino-7-dimethylamino-2-methylphenazine hydrochloride) for 2–4 hours, and dispersed throughout the lagoon. The next day fish were again captured, with both marked (i.e., stained and recaptured) and unmarked fish enumerated. Mortality of stained fish was determined by retaining approximately 200 fish in a pen suspended in the lagoon for 24 hrs; the number of marked fish released was then adjusted accordingly. The size of the population in the lagoon, N , was then estimated according to Ricker (1975) as:

$$N = (M + 1)(C + 1)/(R + 1),$$

where

M = number of marked fish released;
 C = total number of fish caught the next day;
 R = number of recaptured (stained) fish in catch.

95% confidence limits for the abundance estimates were calculated as described by Ricker (1975).

On every cruise except August we determined vertical distributions of temperature and salinity in Jakles Lagoon near noon with duplicate casts of a YSI^R portable CTD, as well as transparency of the water column with a Secchi disk. Although sharp thermoclines were never present, thermal gradients, usually spanning the entire water column, did occur. We have therefore summarized the extent of thermal stratification of the water column, ΔT , by calculating the difference between the temperature just below the surface (0.5 m) and that just above the bottom (3.5 m).

Results

Diel vertical migration in Acartia hudsonica

Striking seasonal variation in the vertical distribution of adult female *A. hudsonica* was present in Jakles Lagoon (Fig. 1). *A. hudsonica* was fairly evenly distributed throughout the water column during the daytime in March and April, but tended to be more concentrated near the bottom in June and August, and to a lesser degree in October and December as well (Fig. 1). In contrast, the nighttime vertical distributions of the copepod changed

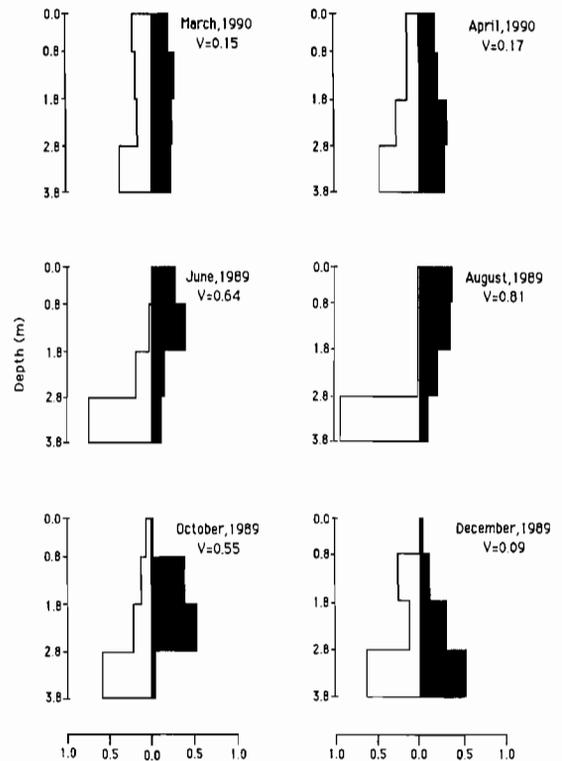


Fig. 1. Vertical distribution of adult female *Acartia hudsonica* in Jakles Lagoon. Each daytime (clear) and nighttime (darkened) vertical distribution is the mean of four vertical series of samples collected in pairs near noon and midnight on each of two consecutive days. The depth range of each histogram is 0–3.8 m. Scales are the proportion of the copepod population in the four sampled layers. Values of V are an index of migration intensity, as described in the text.

from being evenly distributed throughout the water column in March and April to being concentrated in the surface during June and August,

Table 1. Proportion of adult female *A. hudsonica* undertaking DVM (V , as described in text), mean abundance of vertebrate predators (determined from replicate nighttime trawls), secchi disk depths, temperature gradients (DT , difference between 0.5 and 3.5 m), and mean abundance of *A. hudsonica* (replicate nighttime and daytime samples combined) for each date in Jakles Lagoon.

	<i>A. hudsonica</i> DVM index (V)	Predator abundance (#/100 m ³)	Secchi depth (m)	DT (°C)	<i>A. hudsonica</i> density (#/liter)
March	0.15	18.6	4.0	0.2	7.6
April	0.17	3.2	1.1	2.5	14.1
June	0.64	263	1.5	3.1	0.9
August	0.81	1,700	–	–	5.0
October	0.55	181	0.8	0.9	1.1
December	0.09	11.7	1.7	–0.8	3.2

and then became progressively deeper in October and December (Fig. 1). This resulted in variable DVM behavior in adult female *A. hudsonica* (Fig. 1, Table 1); copepods were nonmigratory or very weakly migratory in December, March and April ($V = 0.09-0.17$), moderately migratory in June and October ($V = 0.64$ and 0.55), and highly migratory in August ($V = 0.81$).

Species composition and abundance of pelagic fish

There was very little seasonal variation in the species composition of the pelagic fish assemblage of Jakles Lagoon (Table 2). Threespine stickleback, *G. aculeatus*, was the overwhelmingly dominant species of fish on every date (Table 2), comprising a minimum of 87% of the total number of fish sampled (April) and a maximum of 100% (March). Pacific herring, *Clupea harengus pallasi*, was present on all cruises except March, but never represented more than 3.0% of the total fish sampled (Table 2). Surf smelt, *Hypomesus pretiosus*, represented 8.2% of the total in April, but never more than 0.1% on any other date (Table 2).

Other species occasionally captured, but never representing more than 1.0% of the total number of fish sampled, were Saddleback gunnel (*Pholis ornata*), Arrow goby (*Clevelandia ios*), Pacific sandlance (*Ammodytes hexapterus*), Silverspotted sculpin (*Blepias cirrhosus*), and unidentified poacher (Agonidae), and unidentified surfperch (Embiotocidae), and an unidentified pipefish (Syngnathidae). These rarer species will not be

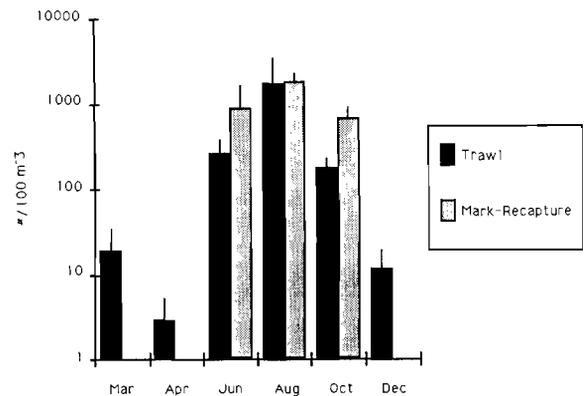


Fig. 2. Abundance estimates (mean $\#/100\text{ m}^3$, with 95% confidence intervals) of threespine sticklebacks, *Gasterosteus aculeatus*, in Jakles Lagoon estimated by nighttime trawling (all cruises) and mark-recapture techniques (June, August, and October only).

considered further. Additional sampling in June and August with a beach seine towed from shore and by boat resulted in no additional species being captured.

In contrast to the relative stability of the species composition, abundances of fish in Jakles Lagoon showed marked seasonal variability, being highest in summer and lowest in winter and early spring. The most striking example of seasonal variation was in *G. aculeatus*, which showed a 560-fold difference between maximum abundance in August and minimum abundance in April (Fig. 2). This seasonal abundance pattern corresponds with changes in the size composition of *G. aculeatus*, as seen from the length-frequency distributions for each cruise (Fig. 3). A clear progression of size over time is evident, with young-

Table 2. Composition (as per centage of total catch by numbers) of the pelagic fish assemblage in Jakles Lagoon on each sampling date.

	Threespine stickleback (<i>Gasterosteus aculeatus</i>)	Pacific herring (<i>Clupea harengus pallasi</i>)	Surf smelt (<i>Hypomesus pretiosus</i>)	Other
March	100.0	0	0	0
April	87.0	3.3	8.2	1.5
June	97.3	2.7	0.0	0.0
August	99.8	0.2	0.0	0.0
October	98.9	0.7	0.1	0.3
December	95.9	3.3	0.0	0.9

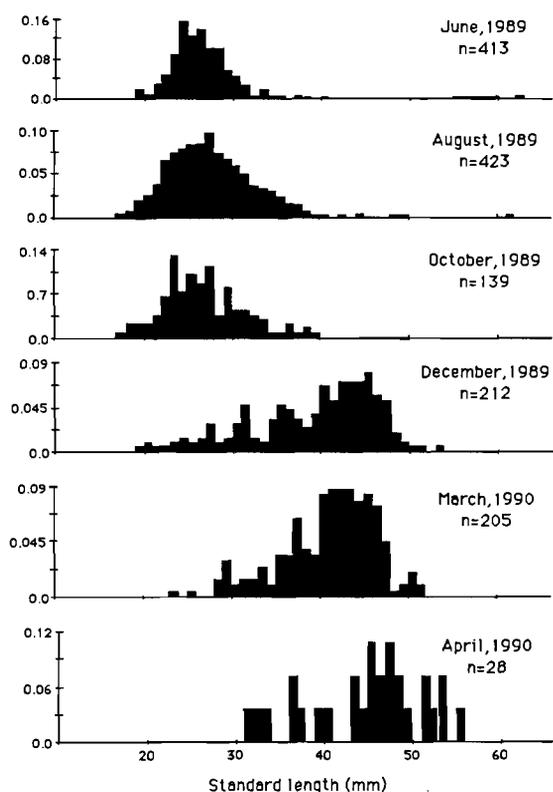


Fig. 3. Length-frequency histograms for threespine stickleback, *Gasterosteus aculeatus*, in Jakles Lagoon on each cruise. *n* is the number of individuals measured.

of-the-year fish first recruiting in June and growing until they disappear, presumably because of death, in the summer of their second year (Fig. 3). The annual nature of the life cycle of *G. aculeatus* has been well documented elsewhere (Wootton, 1984; Giles, 1987; Crivelli & Britton, 1987).

G. aculeatus is a visually orienting, predominantly diurnally foraging, zooplanktivorous fish (Wootton, 1976; Wootton, 1984). Likewise, both *C. harengus pallasi* and *H. pretiosus* are also visually orienting zooplanktivores (Hart, 1973). In Jakles Lagoon, all three species are known predators of the planktonic copepod *A. hudsonica* (Landry, 1978; Bollens and Frost, unpublished). Furthermore, planktonic invertebrate predators of *A. hudsonica* are very rare in Jakles Lagoon (Landry, 1978; Bollens and Frost, unpublished). We have therefore summed our abundance estimates of *G. aculeatus*, *H. pretiosus* and *C. haren-*

gus pallasi into a single estimate of abundance of predators of *A. hudsonica* for each cruise (Table 1). However, the vast majority of the striking seasonal variability we observed in abundance of fish in Jakles Lagoon can be attributed to the annual life cycle and dominance of *G. aculeatus*.

Other environmental conditions

Transparency and thermal stratification of the water column also varied seasonally in Jakles Lagoon (Table 1). Secchi disk depths (an indirect measure of transparency) were lowest in spring and autumn, and highest in winter (Table 1). This seasonal cycle corresponds well with the usual occurrence of spring and fall blooms and winter lows of phytoplankton in Jakles Lagoon (Landry, 1978). The degree of thermal stratification of the water column (ΔT) was most pronounced in late spring and summer, and negligible at other times of the year (Table 1).

Relation between variable DVM of A. hudsonica and environmental conditions

Simple linear regression was used to examine the dependence of the strength of DVM in *A. hudsonica* (*V*) on i) abundance of predators, ii) transparency of the water column (Secchi depth), and iii) degree of thermal stratification of the water column (ΔT) (Fig. 4). The abundance of predators was the only environmental condition shown to be statistically significantly related to the strength of DVM in *A. hudsonica*.

Discussion and conclusions

Although our data show no significant relationship between DVM of *A. hudsonica* and thermal stratification of the water column, it should be noted that we were unable to measure thermal stratification in August, a time during which *A. hudsonica* was strongly migratory (Fig. 1) and thermal stratification of Jakles Lagoon is likely

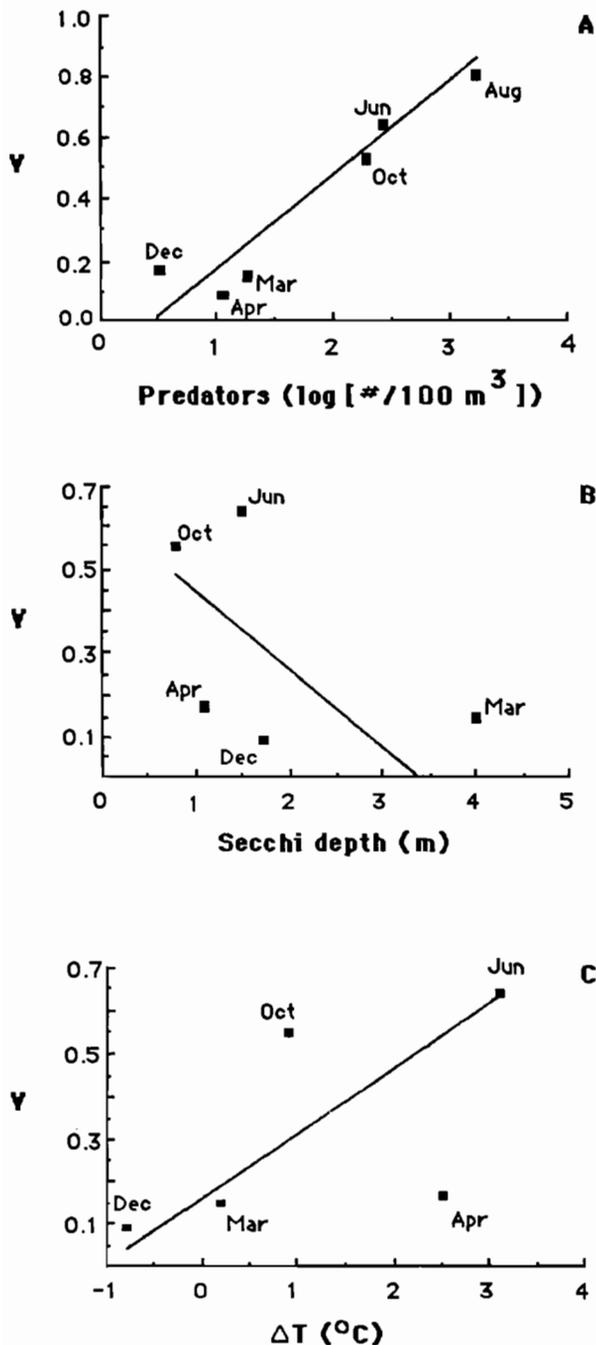


Fig. 4. Linear regressions for the dependence of the strength of diel vertical migration (V) of adult female *Acartia hudsonica* in Jakles Lagoon on A) the log of abundance of predators ($Y = -0.133 + 0.290 X$; $r = 0.948$; $n = 6$; $P < 0.01$), B) Secchi disk depth ($Y = 0.686 - 0.201 X$; $r = -0.443$; $n = 5$; $P > 0.05$), and C) degree of thermal stratification (ΔT) of the water column ($Y = 0.133 + 0.158 X$; $r = 0.593$; $n = 5$; $P > 0.05$). Lines fitted by functional regression (Ricker, 1973).

(Landry, 1978). However, even with the addition of a hypothetical 'best case' August ΔT value that falls directly on the regression line of Fig. 4c (4.3 °C, a very high midsummer value for Jakles Lagoon; Landry, 1978), the result is still a non-significant regression between ΔT and DVM of *A. hudsonica* ($r = 0.771$; $P > 0.05$). While these results are based on low sample size and thus low statistical power, they lend further support to the claims of Frost (1988) and Lampert (1989) that, based on the overwhelming weight of both physiological and field evidence, migration across a thermal gradient, and the accrual of any metabolic or demographic advantage to migrants, is an insufficient explanation of the adaptive significance of DVM behavior in planktonic animals.

Transparency of the water column, and by extension susceptibility of planktonic prey to visual predators, is also inadequate in explaining the observed seasonal pattern of DVM behavior in *A. hudsonica*. Food availability has been suggested to play a role in regulating DVM behavior (e.g., Johnsen & Jakobsen, 1987; Gliwicz & Pijanowska, 1988), but this affect was beyond the scope of the present study.

As mentioned in the introduction, considerable evidence has now accumulated implicating predator evasion as an important adaptive advantage of DVM in zooplankton. In regard to field evidence, the relationship between seasonally variable DVM behavior in zooplankton and variation in abundance of predators has been noted by several investigators (see recent review by Bollens & Frost, 1989a). However, such field evidence is rarer for marine locales, and in only one case has a relationship between prey DVM and predator abundance been shown to be statistically significant (Bollens & Frost, 1989a). By combining two years of field data from Dabob Bay, Washington these authors showed that the marine planktonic copepod *Calanus pacificus* exhibited seasonally variable migration behavior that was statistically significantly related to variations in the abundance of its vertebrate predators.

Thus our results showing a highly significant relationship between extent of DVM in *A. hudsonica* and the abundance of predators in Jakles

Lagoon provide further field evidence in support of the predation hypothesis as an explanation of the adaptive significance of diel vertical migration in zooplankton. Collectively these field studies suggest that such behavioral responses of zooplanktonic prey to predators are likely to be very widespread. In the case of *A. hudsonica*, the mechanism underlying this behavioral response to predators is phenotypic behavioral plasticity of individual copepods (Bollens and Frost, 1989b; Bollens & Frost, in press), mediated through mechanical stimuli or visual cues emitted by planktivorous fish (Bollens & Frost, 1989b). However, a population genetic-level response of prey to predators may underlie other cases of variable DVM behavior in instances where migratory behavior is genetically fixed (e.g., De Meester & Dumont, 1988).

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References

- Bollens, S. M. & B. W. Frost, 1989a. Zooplanktivorous fish and variable diel vertical migration in the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.* 34: 1072–1083.
- Bollens, S. M. & B. W. Frost, 1989b. Predator-induced diel vertical migration in a planktonic copepod. *J. Plankton Res.* 11: 1047–1065.
- Bollens, S. M. & B. W. Frost, In Press. Diel vertical migration in zooplankton: rapid individual response to predators. *J. Plankton Res.*
- Crivelli, A. J. & R. H. Britton, 1987. Life history adaptations of *Gasterosteus aculeatus* in a Mediterranean wetland. *Envir. Biol. Fishes* 18: 109–125.
- De Meester, L. & H. J. Dumont, 1988. The genetics of phototaxis in *Daphnia magna*: existence of three phenotypes for vertical migration among parthenogenetic females. *Hydrobiologia* 162: 47–55.
- Frost, B. W., 1988. Variability and possible adaptive significance of diel vertical migration in *Calanus pacificus*, a planktonic marine copepod. *Bull. mar. Sci.* 43: 675–694.
- Gabriel, W. & B. Thomas, 1988. Vertical migration of zooplankton as an evolutionary stable strategy. *Am. Nat.* 132: 199–216.
- Giles, N., 1987. Population biology of the three-spined sticklebacks, *Gasterosteus aculeatus*, in Scotland. *J. Zool.* 212: 255–265.
- Gliwicz, M. Z. & J. Pijanowska, 1988. Effect of predation and resource depth distribution on vertical migration of zooplankton. *Bull. mar. Sci.* 43: 695–709.
- Hart, J. L., 1973. Pacific fishes of Canada. *Bull. Fish. Res. Bd Can.* 180.
- Johnsen, G. H. & P. J. Jakobsen, 1987. The effect of food limitation on vertical migration in *Daphnia longispina*. *Limnol. Oceanogr.* 32: 873–880.
- Kerfoot, W. C., 1985. Adaptive value of vertical migration: comments on the predation hypothesis and some alternatives. *Contrib. mar. Sci. (Suppl.)* 27: 91–113.
- Lampert, W., 1989. The adaptive significance of diel vertical migration of zooplankton. *Funct. Ecol.* 3: 21–27.
- Landry, M. R., 1978. Population dynamics and production of a planktonic copepod, *Acartia clausii*, in a small temperate lagoon on San Juan Island, Washington. *Int. Revue ges. Hydrobiol.* 63: 77–119.
- Mangel, M. & C. W. Clark, 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, New Jersey.
- Neill, W. E., 1990. Induced vertical migration in copepods as a defence against invertebrate predation. *Nature* 345: 524–526.
- Ohman, M. D., 1990. The demographic benefits of diel vertical migration by zooplankton. *Ecol. Monogr.* 60: 257–281.
- Ricker, W. E., 1973. Linear regressions in fishery research. *J. Fish. Res. Bd Can.* 30: 409–434.
- Ricker, W. E., 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Bd Can.*, 191.
- Southwood, T. R. E., 1978. Ecological methods. Chapman and Hall, London.
- Stirling, D. G., D. J. McQueen & M. R. S. Johannes, 1990. Vertical migration in *Daphnia galeata mendotae* (Brooks): demographic responses to changes in planktivore abundance. *Can. J. Fish. aquat. Sci.* 47: 395–400.
- Wootton, R. J., 1976. The biology of the sticklebacks. Academic Press, London.
- Wootton, R. J., 1984. A functional biology of sticklebacks. Croom Helm, London.