Progress in Oceanography 151 (2017) 1–12

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

A model for shear response in swimming plankton

Justin Shaw *, Marek Stastna

Department of Applied Mathematics, University of Waterloo, Waterloo, Ontario N2L 3G1, Canada

ARTICLE INFO

Article history:
Received 21 January 2016
Received in revised form 24 October 2016
Accepted 24 October 2016
Available online 2 November 2016

Keywords:
Plankton
Individual based model (IBM)
Euphausia pacifica
Internal waves
Shear response
Rheotaxis
Patch formation
Knight Inlet

ABSTRACT

Observations of zooplankton populations below their preferred light level have been attributed to a shear response. We propose a measure of shear based on the second invariant of the rate of strain tensor. This quantification allows the shear response mechanism to be modelled numerically. The importance of this mechanism is examined by modifying a light-biased stochastic swimming model of the run and tumble type for plankton moving in a velocity field induced by internal waves in a channel. It is found that a model which includes the mechanisms of settling, biased swimming, and a “freeze in shear” response predicts aggregation of plankton populations below their preferred light level, which is consistent with acoustic data observations. Depending on the geometry of the high shear region, the population is either shifted downward, or aggregates as a thin layer along the bottom boundary of the high shear region. A pair of timescales is defined in order to determine which of these two cases will occur.

1. Introduction

Water-dwelling organisms continually encounter flow characteristics which act as cues to which they may respond. It is theorized that some species of copepods may avoid regions of high turbulence or shear (Mackas et al., 1993). The reasons for this response are also theoretical: turbulence could potentially enhance encounter rates of predators and prey (Rothschild and Osborn, 1988), which could lead prey to avoid these regions, turbulence may overwhelm their ability to control their own motion (Yen et al., 2008), or high shear could simply be uncomfortable. This avoidance of high shear regions would change the distribution of the population.

Several previous studies have considered the interaction of swimming plankton with the passage of internal waves. Stastna et al. (2011) considered the interaction of internal solitary waves with plankton using Lagrangian models based on the Langevin equation. In the absence of a biased swimming behaviour, plankton followed a diffusion process and hence observations showing an increased concentration of plankton at certain depths were impossible to reproduce. For plankton which would swim vertically to maintain a preferred light level, a fully nonlinear internal solitary wave of depression was found to advect plankton downward as they passed through the wavefront. This caused the plankton to swim upwards to return to their preferred light level. As the plankton population passed the wave’s crest, the wave-induced currents forced it upward again. The combination of advection with the swimming of the plankton led the population to overshoot their preferred light level, creating an aggregation region at the rear of the wave and above the preferred light level. After the wave had passed, the plankton slowly drifted down to their preferred light level. Lennert-Cody and Franks (1999) also discussed perturbation from a preferred light level using an Eulerian perspective with linear and weakly nonlinear waves in a two layer fluid. They found that the interaction of internal waves and swimming plankton could produce along-isopycnal patchiness in plankton blooms. Scotti and Pineda (2007) found that swimming upwards as a response to downwelling currents associated with gravity currents allows for Lagrangian transport of plankton over large distances (on the order of kilometers, also see Lamb, 1997 for additional modelling). All of these examples illustrate that the passing of internal waves can have a direct effect on the spatial distribution of plankton with preferred light levels.

The effect of shear on plankton populations has been studied before as well. Ianson et al. (2011) noted that in Knight Inlet, British Columbia, *Euphausia pacifica* are observed below their preferred light level when close to a sill. The authors simulated a variety of shear responses and found that the model employing a shear response of downward swimming produced output that most closely matched acoustic data. Gyrotactic phytoplankton

---

* Corresponding author.

E-mail addresses: justin_shaw@outlook.com (J. Shaw), mmstastna@uwaterloo.ca (M. Stastna).

http://dx.doi.org/10.1016/j.pocean.2016.10.012
0079-6611/

were found to collect in a shear layer in Durham et al. (2009), and aggregated as a result of interaction with a simple vortical flow in Durham et al. (2011), leading to the prediction that motility characteristics may drive spatial cell distributions. An experimental example of this “unmixing” was presented in Durham et al. (2013), in which upward swimming produced nonuniform plankton distributions in a vortical flow. Gyrotactic trapping in a shear layer was examined in Hoecker-Martínez and Smyth (2012). The primary effect of shear in these last four publications was as a trigger to reorient gyrotactic phytoplankton. Following (Ianson et al., 2011), we examine the response of zooplankton to shear directly, sometimes called rheotaxis (see Pedley and Kessler, 1992). We also follow (Ianson et al., 2011) by using Knight Inlet as a concrete, motivating example of the discussed mechanisms, however the geographic range of the mechanism we propose is far more general.

Knight Inlet, British Columbia, Canada is a fjord with strong tidal flows driving internal wave generation over the large amplitude bottom topography of a glacial sill. It has been the site of a number of field studies, including the well-documented Knight Inlet Sill-Flows experiment (Klymak and Gregg, 2003), as well as a number of theoretical/numerical studies (Lamb, 2004; Afanasyev and Peltier, 2001; Stastna and Peltier, 2004; Cummins et al., 2003). The flow over the Knight Inlet sill is extremely rich dynamically, yielding examples of flow separation from the bottom, shear instability, large amplitude breaking internal waves (see for example Figs. 10 to 16 in Lamb (2004)), as well as an upstream response that includes internal solitary waves (Farmer and Armi, 2001), and significant spatiotemporal variation in the intensity of turbulence (Klymak and Gregg, 2004). The field situation is further complicated by an asymmetry in the vertical stratification profile between the two sides of the sill (Klymak and Gregg, 2003), and significant transverse flows due to flow separation from the complex shoreline (Figs. 6 and 7 of Klymak and Gregg (2001)). The coherent dynamical features near the sill are depicted schematically in Fig. 1. A more dynamic picture based on numerical experiments is presented in Figs. 10 to 16 of Lamb (2004). This is one point of view on the dynamics, a viewpoint based primarily on coherent structures such as large amplitude internal waves. The temporal averages of the turbulent dissipation shown in Fig. 3 of Klymak and Gregg (2004) offer a different point of view.

While Knight Inlet is a well known and well studied geographical location, an energetic high shear environment associated internal waves is a generic feature of the coastal oceans. Stonewall Bank provides an example of three-dimensional topography that yields hydraulic behaviour (see Fig. 5 of Nash and Moum (2001), as well as the colour plates for the same paper) without the focusing provided by the fjord sidewalls in Knight Inlet and similar locations. Other examples of fluid mechanical mechanisms that have been identified as leading to a high shear state in the coastal ocean include shear instability within internal solitary waves themselves (Lamb and Farmer, 2011), the interaction of internal wave trains with the bottom boundary layer leading to instabilities and sediment resuspension (Quaresma et al., 2007), and the breakdown of internal solitary wave trains as they shoal and pass through the turning point at which they cannot maintain their original polarity (Shroyer et al., 2009). While the modelling developed below was motivated by observations in Knight Inlet, the approach taken is generic and not tied to a particular geographical location. It is also not tied to a particular species of zooplankton. So long as the zooplankter in question is thought to have a freeze in shear response and motion well approximated by the given swimming model, the same mechanisms outlined below will apply (although their relative strengths may vary). In Section 4 we briefly discuss the manner in which the results developed may be generalized to the broader coastal environment.

A hierarchy of physical models can be employed to describe the effects of the ocean environment on plankton. Direct numerical simulations which resolve both turbulence and nonhydrostatic motions could be used to completely describe the stratified turbulent flow experienced by plankton on scales relevant to the plankton themselves. However, the manner in which the turbulent flow is coupled to the complex shape of the plankton is beyond the ability of current numerical models to simulate for ensembles as large as those used in this study. On larger scales, such as those associated with hydraulic flows in fjords (Lamb, 2004) approximations are required in order for the model to handle the discrepancy between vertical horizontal scales as well as the full range of motions. As an example, the model employed by Lamb (2004) uses a finite volume method that allows for an accurate representation of the non-hydrostatic flow over the Knight Inlet sill. This model has the drawback that it can only simulate a two-dimensional (along-fjord vs depth) slice. Larger scale models often make even more drastic approximations in order to facilitate reasonable run times, most notably the hydrostatic approximation which neglects vertical acceleration. In the context of Knight Inlet, the hydrostatic Hallberg Isopycnal Model was used by Klymak and Gregg (2003), and a modification of the two-dimensional, non-rotating, hydrostatic Princeton Ocean Model outlined in Cummins (2000) was employed in Ianson et al. (2011). While many of the commonly used approximations are successful in answering targeted scientific questions, it is important to not lose sight of the approximations, especially when attempting to link motions on different scales (e.g., internal waves and their effects on plankton). The model employed below is conceptual in the sense that it is simple to write down analytically, but it does include the effects of vertical acceleration. It is well grounded in the physical oceanography literature since linear internal waves are commonly discussed in many introductory physical oceanography textbooks (e.g., Gill, 1982; Simpson and Sharples, 2012). Linearity implies that we are free to superpose solutions, and beyond the understanding that linear theory is less and less accurate as amplitude increases, amplitude can be chosen at our discretion. This gives us a parameter to vary while we focus on the plankton's shear response mechanism. The flow should be contrasted with the internal solitary waves in Stastna et al. (2011), which are exact solutions of the stratified Euler equations, but whose properties are difficult to tune *a priori*.

The remainder of the paper is organized as follows. We discuss the Euler equations and linear internal waves (Section 2.1) which provide the flow conditions, and describe the model initialization rationale (Section 2.2). The particle and swimming model is then outlined (Section 2.3), along with the modelling of the shear response (Section 2.4). The model is tuned to the parameters of the zooplankter *E. pacifica* to provide a concrete example. We then move on to the results of our experiments (Section 3), which show that the mechanisms of settling, biased swimming, and a freeze in shear response predicts aggregation of plankton populations below their preferred light level.

2. Methods

2.1. The Euler equations and linear internal waves

In order to model a horizontal strip of the water column consider a flow in a two dimensional channel where the x axis is taken to be horizontal and the z axis as vertical. The vertical extent of the domain is given by $H = 20$ m in this case. We employ the stratified