Journal Of Sea Research
April 2021, Volume 170 Pages 102009 (6p.)
https://doi.org/10.1016/j.seares.2021.102009
https://archimer.ifremer.fr/doc/00682/79365/

Lack of match between nutrient-enriched marine seafoam and intertidal abundance of long-lived invertebrate larvae

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Abstract :

Since most marine benthic species experience a pelagic larval phase, scales of dispersal are key determinants of population dynamics. Biologically derived marine foam has been suggested to increase chances of fertilisation and reduce dispersal of larvae of short-live duration (hours), thus maintaining localised intertidal populations. The present study examined the role sea-foam plays as a mechanism of physical retention/accumulation for long lived (weeks) invertebrate larvae that are relatively long-lived (weeks). Larvae were collected using a submersible pump at two sites along the south-east coast of South Africa, where intertidal assemblages are dominated by beds of mussels and barnacles. Sampling took place on six occasions in 2015–2016, during events of high sea-foam production and periods of no foam accumulation. Foam/water was collected from the surface and bottom of tidal channels. There was no difference in abundance of larvae of any of the invertebrate taxa examined, whether foam was present or absent. Regardless of foam state, barnacle and polychaete larvae were mostly associated with the surface of the short water column at the tidal channels. This study highlights how the very nearshore environment may play a key role in limiting scales of larval dispersal, but especially how the effects of physical processes can be taxon-specific, depending on the larval duration and characteristics.

Highlights

► Invertebrate larvae of benthic taxa are associated with the surface at the sea-rock interface. ► Presence or absence of foam has no effect on the intertidal distribution of invertebrate benthic larvae in tidal channels. ► Formation of intertidal foam is associated with increased wind-driven turbulence at scales of 2 days. ► Preliminary indication of poor-quality food content of foam due to low PUFA prevalence.

Keywords : Larval connectivity, Mussels, Barnacle, Bio-physical processes, Early life stages

1.1 Introduction

Attention to marine sea-foam goes back to ancient Greek mythology. In “The Theogony”, an 8th-century BC poem on the genealogy of gods, Hesiod provides a dramatic explanation for the origin of sea-foam. The Greek primal gods, Uranus and Gaia, had an argument and the son Kronus, under the mother Gaia’s request, castrated his father Uranus and threw his genitals into the sea, producing white foam. From the foam rose Aphrodite (derived from Aphro-geneia – the foam born), the goddess of love and beauty (Evelyn-White, 1914).

Bio-foam on the sea surface microlayer is a common phenomenon (see Shilling & Zessner, 2011 for a review), especially observed in dynamic coastal boundaries exposed to seasonal or permanent wind forcing and/or upwelling shadows (Velimirov, 1980; Graham & Largier, 1997; Jenkinson et al., 2018). The biological origin of this visco-elastic (Jenkinson, 1993; Jenkinson et al., 2018) mixture of surfactant proteins and carbohydrates (Schilling & Zessner, 2011; Mecozzi & Pietroletti, 2016), is often linked to surface enrichment from phytoplankton blooms (e.g. *Phaeocystis*, Seuront et al., 2006, 2007) or exudates from aquatic vascular plants (Craig et al., 1989) and is associated with binding and transfer of energy from dissolved to particulate organic matter (Seuront et al., 2007). Although the autotrophic formation of foam has been linked to harmful and toxic events (Craig et al., 1989), the positive ecological role of foam in coastal waters as food source for primary consumers and habitat for the marine microbiome (Velimirov, 1980; Bärlocher et al., 1988) has also been highlighted.

Fatty acid (FA) techniques are useful tools that highlight quality of food available to consumers, including planktotrophic larvae (Dalsgaard et al., 2003; Kelly & Scheibling, 2012). Polyunsaturated FA (PUFA) are mostly synthesised by primary producers and maintain organismal function (Parrish et al., 2000). In phytoplankton, PUFA composition varies among taxa, and distinguishes food-quality (high quality, e.g., diatoms or dinoflagellate; Puccinelli et al., 2016; low quality, e.g., cyanobacteria; Brett & Müller-Navarra, 1997).

In marine systems, the production of sea-foam or mucilage has been ascribed a role as a dispersal agent for algae (Santelices, 1990) and linked to synchronised mass-spawning in tunicates (Castilla et al., 2007). Given that tunicates have a very short dispersal phase (hours), the presence of foam can favour immediate fertilisation, and limit the dispersal capacity of larvae and, hence, favour settlement within parental populations (Castilla et al., 2007).

The role of biofoam for enhancing larval retention and providing a high-quality medium has yet not been tested for taxa with planktotrophic larval duration longer than a few hours. Surface trapping of spores (Kohlmeyer, 1984) and plankton (Shanks et al., 2018) induced by the increased viscosity of the water (e.g. Seuront et al., 2010), differential settlement (Alldredge & Gotschalk, 1989) or changes in swimming patterns by microplankton within sea-foam (Seuront & Vincent, 2008) highlight the widespread potential for biological-physical coupling mediated by organic flocs (Jenkinson et al., 2015).

By considering the physical processes that favour the formation of sea-foam and preliminarily linking it to its chemical composition, we hypothesised that larvae of intertidal benthic species are preferentially associated with sea-foam events as they facilitate accumulation within rocky shores and provide a nutrient-enriched environment. We also envisaged that during foam events, larvae would be more abundant at the surface than at the bottom due to the expected direct links between foam formation, waves and wind-driven turbulence.

1.2 Material & Methods

The study was carried out on six occasions at two sites on the south-east coast of South Africa: Sardinia Bay (34°02'06.1"S 25°29'17.5"E) and Seaview (34°00'24.0"S 25°20'08.5"E), between June 2015 and January 2016 (Fig.1), characterised by year-round presence of sea-

foam (pers obs), encompassing the timing of local intertidal invertebrate reproduction (Porri et al., 2006; Simon & Booth 2007; Weidberg et al., 2019). Foam was visually present on two out of the six sampling events (June and October 2015).

Fig. 1 Map of the study sites (Seaview and Sardinia Bay) on the south coast of South Africa. Details of the sampling events are also included below the map

The physical characteristics of each event were determined by calculating the wind-induced upwelling index and turbulence from hourly wind data obtained from the South African Weather Service (SAWS) at the Port Elizabeth Airport weather station. These indexes were computed using standard formulations (Pringle et al., 2007) to account for the dynamics of wind forcing in the region (Weidberg et al., 2015, 2019). Wave height was obtained from Windguru predictions (NOAA Wawewatch3 global model), for the 7 days preceding each sampling. To infer the effect of wind forcing on swell dynamics and its time scales,

temporal correlograms were performed between wave height and wind-derived upwelling, and turbulence averaged over 1 to 7 days prior to each sampling.

Larval samples were collected during ebbing tides, from waters adjacent to rocks where the mussels *Perna perna* and *Mytilus galloprovincialis* co-exist (Bownes & McQuaid, 2006). At each site, water/foam samples were collected from two tidal channels, ≅300m apart. During foam events, sampling occurred over at least three large patches (minimum 2X1m) of foam. At each channel, two 25-L water samples from the surface and bottom respectively were filtered through a 75µm sieve using a rechargeable pump (TruePower; 12V DC, flow rate, 760 Lh^{-1}). All samples were preserved in ethanol and transported to the laboratory for identification.

To assess whether foam enhances food quality for larvae, samples of surface water were collected to determine the FA composition of suspended particulate matter (SPM) during foam and non-foam events. Three 2-L samples were collected from each channel during the last four sampling events (October, November, December and January). Water samples were filtered (< 5cm Hg vacuum) onto pre-combusted (450°C) GF/F filters (0.7 µm pore size and 47 mm diameter). The SPM samples were flash-frozen in liquid nitrogen and transferred to a -80 °C freezer until further processing. Total lipids were extracted and trans-esterified using a modified Indarti on-step procedure (Indarti et al. 2005), described in Puccinelli et. al 2018.

We performed a multivariate permutational analysis for unbalanced data (Permanova; Anderson, 2001), to investigate the effects of Event (sampling occasions of foam or no foam occurrence; 6 levels, fixed factor), Site (nested in event; 2 levels, random factor) and Depth (2 levels, fixed factor), on the abundance of early stages of taxa of invertebrate larvae (polychaete trochophores; mussel veligers; barnacle nauplii). Permanova was based on 9999 permutations of residuals under a reduced model on the Bray-Curtis resemblance matrix of larval abundances, after verifying homoscedascity of data (Permdisp, Anderson et al., 2008). After square-root transformation, the FA composition of the foam was also investigated using the same design for the analyses of the invertebrate larval abundance, excluding the factor Depth and confined to the last four sampling occasions. Non-metric multidimensional scaling (MDS) was used to visualise differences between foam and non-foam events and SIMPER (similarity percentage, on Bray-Curtis dissimilarities) analyses were used to assess the FAs responsible for pattern observed. All analyses were conducted using the PERMANOVA+ add-on package of PRIMER v6 (Anderson et al., 2008).

1.3 Results

Waves during foam events were more than three meters high and much higher than during no-foam events (Fig.4a).

Fig. 4 a) Wave height during the study period based on 3h Windguru wave predictions. The month of sampling is indicated and the day of sampling is marked by arrows (red for foam events, white for non-foam events). Temporal correlograms between wave height and upwelling index (b) and wind-driven turbulence (c). The dashed lines show the significance level at α=0.05. The best and only significant association for turbulence averaged over 2 days is marked with a circle and shown in panel d.

Temporal correlograms show negative negligible effects of the upwelling index on

wave height at all time scales (Fig. 4b), while turbulence affected wave height when averaged over two days (Fig. 4c), showing a positive association which explained up to 69% of wave height variability (Fig. 4d).

The results of the Permanova for larval assemblages showed a significant effect of Depth ($F_{1, 24}$= 5.93, $p<0.01$), with more larvae accumulating at the surface than at the bottom, regardless of the sampling event or foam state ($F_{5, 24}$= 5.93, $p>0.05$; Fig. 5).

Fig. 5 Mean abundance (+ SD) of polychaete, bivalve and crustacean larvae at the bottom and surface cumulatively collected at Seaview and Sardinia Bay during the months of June, July, October, November, December 2015 and January 2016

SIMPER analysis showed that the structure of the assemblages differed between depths, with the surface characterised by barnacle larvae (12.54%), polychaetes (6.33%) and mussels (1%), whereas assemblages at the bottom constituted polychaete larvae (5.13%), barnacles 3.58% and mussels (1.04%).

The FA composition of the SPM significantly differed among events (MS=1825.7, Pseudo-F 6.57, $p<0.01$), with non-foam events having a higher PUFA than the foam event. Foam samples presented high proportion of BAME, 14:0, 16:3n-4, 18:1n-9, 20:4n-6 and 22:6n-3, whereas non-foam events were typified by 18:0, 18:2n-6, 20:5n-3 and 22:2n-6.

Table 1. Total fatty acid (TFA) composition of suspended organic matter (SPM) from foam and non-foam events. Values are percentages expressed as mean ± standard deviation. Only FA >1 % are displayed. BAME = Bacterial Fatty Acids, SFA = Saturated Fatty Acids, MUFA = Monounsaturated Fatty Acids, PUFA = Polyunsaturated Fatty Acids, EFA = Essential Fatty Acids. 171

1.5 Discussion

Foam events were physically and biochemically well characterised during this study, although only one event of foam was assessed for FA. Knowledge of the influence of onshore winds and wind-driven breaking waves (Cooper & Jackson, 2001; Jenkinson et al., 2015) on foam generation and its persistence in the intertidal is longstanding (Twenhofel, 1921; Bärlocher et al., 1988), with wind speeds above 10m s^{-1} triggering such phenomenon (Velimirov, 1980). Our time series data suggested that high swells were associated with increased wind-driven turbulence on scales of 2 days, but not with downwelling/upwelling events. Thus, wave height depended on wind magnitude rather than on wind direction, The positive relationship between turbulence and wave height suggests that if the kinetic energy reaches a mean value of 2.5 e^{-6} W kg^{-1} over two days, 3-m waves and foam can develop, although a complete long-term record of foam events, wind data and wave climate for the region would be required to definitively confirm such association.

Biochemically, water sampled during foam presence was characterised by the presence of reduced PUFA, indicating a lower water quality compared to non-foam events. Mucilaginous foam originated by massive blooms of colony-forming *Phaeocystis* has been linked to riverine nutrient enrichment in continental coasts in the northern hemisphere (e.g. Lancelot, 1995), which is commonly associated with poor water-quality conditions (Sin et al., 2013). The lower PUFA observed during the foam event might be the result of lipid degradation, which may occur rapidly during the last phase of biofoaming (Hamm & Rousseau, 2003; Balzano et al., 2011) and when conditions for plankton survival are not optimal (Parrish et al., 2000; Budge et al., 2001). Alternatively, the difference in the composition between foam and non-foam events could be linked to the origin of the foam, which varies among different phytoplankton communities (e.g., diatom vs. dinoflagellate, (Parrish et al., 2000; Dalsgaard et al., 2003).

We rejected the hypothesis of a close association of invertebrate larvae with foam events, especially at the surface of the water column, where viscosity should be maximal (Seuront et al., 2010; Jenkinson et al., 2018). The occurrence and distribution of larvae were variable, possibly linking to the variability in the timing and location of reproduction (Gaines et al., 1985; Pineda, 2000), the complex association of wave formation nearshore and flow amplification in the surf zone adjacent the rocky shores (Denny et al., 2003), and the dynamic nature of wave-swept environments (Denny, 2014). Spatio-temporal variability in nearshore larval occurrence, even within individual reproductive seasons is common in the region of the study (Porri et al., 2006), hence explaining the spatial patchiness in abundance of all larval taxa at the site.

Regardless of foam state and despite all levels of variability suggested, barnacle and polychaete larvae were distinctly associated with the surface. Under light onshore winds and small waves, zooplankters at surface waters can be transported onshore across the surf zone (Morgan et al., 2017). Barnacle and polychaete larvae can afford some active twilight vertical swimming response, often mediated by phototaxis and ontogeny-mediated vertical swimming (Crisp & Ritz, 1973; Young & Chia, 1982), which can translate into effective upwards shifts, especially considering the limited depth of the tidal channels tackled during this study. Active swimming by polychaetes and barnacle larvae could, hence, ensure an association with the surface even in the absence of foam. Furthermore, an association of larvae and holoplankters is common at the surface of convergent slicks at the inshore waters just off the surf zone (Shanks, 1983; Pineda, 1994; Weidberg et al., 2014), hence a pervasive surface effect that is maintained ashore may also be a contributing factor to the present results. Moreover, a selective pressure for a close link with foam by short-dispersing taxa like tunicates (Castilla et al., 2007), aided by a light-driven increase in swimming speed during the early larval phases (Nakagawa et al., 1999) and a tendency to get entrapped in "sticky" substrata (Szewzyk et al., 1991) could be advantageous to reduce the risk of dispersal before competency. In contrast, taxa with longer dispersal durations may be able to afford such hazards, due to the relatively prolonged time spent in the pelagic environment, as well as any additional alternative strategies they have in place for surface maintenance. Moreover, becoming trapped within foam could be fatal to larvae due to the risks of greater predation by fish, cannibalism by conspecifics (especially for mussels) that dominate the adjacent rocky substrates (Tamburri & Zimmer-Faust, 1996; Porri et al., 2008), delayed metamorphosis (Pechenik 1990), or physiological failure due to increased toxicity and poor food conditions within the foam – as suggested by our study (Craig et al., 229 1989; Jessup et al., 2009).

During non-foam events, the presence of sticky polysaccharides released onsite by adjacent suspension feeders (Li et al., 2008), as well the intertidal presence of transparent exopolymers particles (TEP) and extra-cellular polymeric substances (EPS) (Berman & Passow, 2007; Wotton, 1996) on the surface microlayer can be common in coastlines dominated by large beds of mussels such as *P. perna* (Bustamante & Branch, 1996). In combination with other mechanisms, such as the increased turbulence at the interface of mussel beds and the mechanics of bubble formation of breaking waves (Denny, 2014), the more persistent presence of sticky structures provided by TEP and EPS could favour agglomeration of certain larval taxa at the surface. Such clustering may constitute a temporary safe space for onshore retention/progression and final site selection for settlement by competent stages (Zimmer et al., 2012), with no need for larvae to rely upon ephemeral and/or extreme occurrence of sea-foam.

1.6 Conclusions

While the full dynamics involved in the early/final dispersal of benthic larvae appears still complex, physical structures like sea-foam can favour larval surface residence, but the effectiveness of this mechanism seems taxon-, and most likely, stage-related. Our data provided no evidence that foam serves as a means of retaining larvae of polychaetes, mussels and barnacles near to the shore. They did however, reveal a strong pattern of concentration of larvae in surface waters, irrespective of the presence or absence of foam.

Acknowledgements: This research was funded by the African Coelacanth Ecosystem Programme (ACEP) and it is supported by the National Research Foundation, and the South African Institute for Aquatic Biodiversity. The authors thank S. Mafanya, S. Reddy and T. Mbobo for assistance in the field and laboratory and the constructive comments by the anonymous reviewers.

Author contributions: FP, PP, EP conceived and designed the experiments, performed the experiment, analysed the data, and wrote the manuscript. NW analysed the data and wrote the paper. None of the authors have competing interests.

Compliance with ethical standards: All applicable guidelines for the care and use of animals were followed. Collection permit from the department of environmental affairs of the Republic of South Africa: RES2015-04. Ethical approval: REF#: 2014/07 from the South African Institute for Aquatic Biodiversity.

1.7 References

Alldredge, A.L., & C.C. Gotschalk 1989. Direct observations of the mass flocculation of diatom blooms: characteristics, settling velocities and formation of diatom aggregates. Deep Sea Research 36:159–71.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46.

Anderson, M., R. Gorley , K. Clarke, 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods. PRIMER-E

Balzano, S., R.D. Pancost, J.R. Lloyd, & P.J. Statham 2011. Changes in fatty acid composition in degrading algal aggregates. Marine Chemistry 124: 2–13.

Bärlocher, F., J.Gordon, & R.J. Ireland, 1988. Organic composition of seafoam and digestion by *Corophium volutator* (Pallas). Journal of Experimental Marine Biology and Ecology 115: 179–186.

Berman, T., & U. Passow, 2007. Transparent Exopolymer Particles (TEP): an overlooked factor in the process of biofilm formation in aquatic environments. Nature Preceedings

Bownes, S.J., & C.D. McQuaid, 2006. Will the invasive mussel *Mytilus galloprovincialis* Lamarck replace the indigenous *Perna perna* L. on the south coast of South Africa? Journal of Experimental Marine Biology and Ecology 338: 140–51.

Brett, M., & D. Müller-Navarra, 1997. The role of highly unsaturated fatty acids in aquatic foodweb processes. Freshwater Biology 38: 483–499.

Budge, S.M., C.C. Parrish, & C.H. Mckenzie, 2001. Fatty acid composition of phytoplankton, settling particulate matter and sediments at a sheltered bivalve aquaculture site. Marine Chemistry 76: 285–303.

Bustamante, R., & G. M. Branch, 1996. Large scale patterns and trophic structure of southern African rocky shores: the roles of geographic variation and wave exposure. Journal of Biogeography 23: 339–51.

Castilla, J.C., P.H. Manríquez, A.P. Delgado, L. Gargallo, A. Leiva, & D. Radic, 2007. Biofoam enhances larval retention in a free-spawning marine tunicate. Proceedings of the National Academy of Science USA 104: 18120–18122.

Cooper, J.A.G. & D.W.T. Jackson, 2001. Surficial beach structures formed by wave generated foam. Journal of Geology 109: 780–788.

Craig, D., R.J. Ireland, & F. Bärlocher, 1989. Seasonal variation in the organic composition of seafoam. Journal of Experimental Marine Biology and Ecology 130:71–80.

Crisp, D.J., & D.A Ritz, 1973. Responses of cirripede larvae to light. I. Experiments with white light. Marine Biology 23: 327–335.

Dalsgaard, J., M. St. John, G. Kattner, D. Müller-Navarra, & W. Hagen 2003. Fatty acid trophic markers in the pelagic marine environment. In: Advances in Marine Biology. Academic Press, pp 225–340.

Denny, M.W., 2014. Biology and the mechanics of the wave-swept environment. Princeton University Press, Princeton, NJ

Denny, M.W., L.P. Miller, M.D. Stokes, L.J.H. Hunt, & B.S.T. Helmuth 2003. Extreme water velocities: Topographical amplification of wave-induced flow in the surf zone of rocky shores. Limnology & Oceanography 48:1–8.

Evelyn-White, H.G., 1914. Hesiod, the Homeric hymns, and Homerica, Harvard University Press

Gaines, S., S. Brown, & J. Roughgarden, 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. Oecologia 67: 267–272.

Graham, W.M., & J.L. Largier, 1997. Upwelling shadows as nearshore retention sites: The example of northern Monterey Bay. Continental Shelf Research 17: 509–532.

Hamm, C.E., & V. Rousseau, 2003. Composition, assimilation and degradation of 307 *Phaeocystis globosa*-derived fatty acids in the North Sea. Journal of Sea Research 50: 271–283.

Indarti, E., M.I.A. Majid, R. Hashim, & A. Chong, 2005. Direct FAME synthesis for rapid total lipid analysis from fish oil and cod liver oil. Journal of Food Composition & Analysis 18:161–170.

Jenkinson, I.R., 1993. Bulk-phase viscoelastic properties of seawater. Oceanologica Acta 16: 317–334.

Jenkinson, I.R., X. Sun , & L. Seuront, 2015. Thalassorheology, organic matter and plankton: Towards a more viscous approach in plankton ecology. Journal of Plankton Research 37: 1100–1109.

Jenkinson, I.R., L. Seuront, H. Ding, & F. Elias, 2018. Biological modification of mechanical properties of the sea surface microlayer, influencing waves, ripples, foam and air-sea fluxes. Elementa: Science of the Anthropocene 6: 26.

Jessup, D.A., M.A. Miller, J.P Ryan, H.M. Nevins, H.A Kerkering, A. Mekebri, D.B. Crane, T. A. Johnson, & R.M. Kudela, 2009. Mass stranding of marine birds caused by a surfactant producing red tide. PLoS One 4:e4550.

Kelly, J.R., & R. E. Scheibling, 2012. Fatty acids as dietary tracers in benthic food webs. Marine Ecology Progress Series 446: 1–22.

Kohlmeyer, J., 1984. Tropical marine fungi. Marine Ecology 5: 329–378.

Lancelot, C., 1995. The mucilage phenomenon in the continental coastal waters of the North Sea. Science of the Total Environment 165: 83–102.

Li, B., J.E. Ward, & B.A Holohan 2008. Transparent exopolymer particles (TEP) from marine suspension feeders enhance particle aggregation. Marine Ecology Progress Series 330 357: 67–77.

Mecozzi, M., & M. Pietroletti, 2016. Chemical composition and surfactant characteristics of marine foams investigated by means of UV-vis, FTIR and FTNIR spectroscopy. Environmental Science and Pollution Research 23: 22418–22432.

Morgan, S.G., A.L. Shanks, J. MacMahan, A.J.H.M. Reniers, C.D. Griesemer, M. Jarvis, & A.G. Fujimura, 2017. Surf zones regulate larval supply and zooplankton subsidies to nearshore communities. Limnology & Oceanography 62: 2811–2828.

Parrish, C.C., T.A. Abrajano, S.M. Budge, R.J. Helleur, E.D. Hudson, K. Pulchan, & C. Ramos, 2000. Lipid and phenolic biomarkers in marine ecosystems: analysis and applications. In: Wangersky PJ (ed) Marine Chemistry. Springer Berlin Heidelberg, pp 193– 223.

Pechenik, J.A., 1990. Delayed metamorphosis by larvae of benthic marine invertebrates: Does it occur? Is there a price to pay? Ophelia 32:63–94.

Pineda, J., 1994. Internal tidal bores in the nearshore: Warm-water fronts, seaward gravity currents and the onshore transport of neustonic larvae. Journal of Marine Research 52: 427– 345 458.

Pineda, J., 2000. Linking larval settlement to larval transport: assumptions, potentials, and pitfalls. Oceanography of Eastern Pacific 1: 84–105.

Porri, F., C.D. McQuaid, & S. Radloff, 2006. Spatio-temporal variability of larval abundance and settlement of *Perna perna*: differential delivery of mussels. Marine Ecology Progress 350 Series 315: 141–150.

Porri, F., T. Jordaan, & C.D. McQuaid, 2008. Does cannibalism of larvae by adults affect 352 settlement and connectivity of mussel populations? Estuarine Coastal Shelf Science 79: 687– 693.

Pringle, J.M., 2007. Turbulence avoidance and the wind driven transport of plankton in the surface Ekman layer. Continental Shelf Research 27: 670–678.

Puccinelli, E., C.D. McQuaid, & M. Noyon, 2016. Spatio-temporal variation in effects of upwelling on the fatty acid composition of benthic filter feeders in the Southern Benguela Ecosystem: not all upwelling Is equal. PLOS ONE 11:e0161919

Puccinelli, E., McQuaid, C.D., Ansorge, I.J., 2018. Factors affecting trophic compositions of offshore benthic invertebrates at a sub-Antarctic archipelago. Limnology & Oceanography 63: 2206–2228. https://doi.org/10.1002/lno.10934

Santelices, B., 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. Oceanography Marine Biology: an Annual Review 28: 177–276.

Schilling, K., & M. Zessner, 2011. Foam in the aquatic environment. Water Research 454: 355–4366.

Seuront, L., & D. Vincent, 2008. Increased seawater viscosity, *Phaeocystis globosa* spring bloom and *Temora longicornis* feeding and swimming behaviours. Marine Ecology Progress Series 363: 131–145.

Seuront, L., D. Vincent, & J.G. Mitchell, 2006. Biologically induced modification of seawater viscosity in the Eastern English Channel during a *Phaeocystis globosa* spring bloom. Journal of Marine Systems 61:118–133.

Seuront, L., C. Lacheze, M.G. Doubell, J.R. Seymour, V. Van Dongen-Vogels, K. Newton, A.C. Alderkamp, J.C. Mitchell, 2007. The influence of *Phaeocystis globosa* on microscale spatial patterns of chlorophyll *a* and bulk-phase seawater viscosity. Biogeochemistry 83: 173–188.

Seuront, L., S.C. Leterme, J.R. Seymour, J.G. Mitchell, D. Ashcroft, W. Noble, P.G. Thomson, A.T. Davidson, R. van den Enden, F.J. Scott, & S.W. Wright, 2010. Role of microbial and phytoplanktonic communities in the control of seawater viscosity off East Antarctica (30-80° E). Deep Sea Research Part II: Topical Studies in Oceanography 57: 877– 86.

Shanks, A.L., 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Marine Ecology Progress Series 13: 311–315.

Shanks, A.L., S.G. Morgan, J. MacMahan, A.J.H.M. Reniers, M. Jarvis, J. Brown, A. Fujimura, L. Ziccarelli, & C. Griesemer, 2018. Persistent differences in horizontal gradients in phytoplankton concentration maintained by surf zone hydrodynamics. Estuaries and Coasts 41:158–176.

Sin, Y., B. Hyun, B. Jeong, & H.Y. Soh, 2013. Impacts of eutrophic freshwater inputs on water quality and phytoplankton size structure in a temperate estuary altered by a sea dike. Marine Environmental Research 85: 54–63.

Szewzyk, U., C. Holmström, M. Wrangstadh, M. Samuelsson, J. Maki, & S. Kjelleberg, 1991. Relevance of the exopolysaccharide of marine *Pseudomonas* sp. strain S9 for the attachment of *Ciona intestinalis* larvae. Marine Ecology Progress Series 75: 259–265.

Tamburri, M.N., & R.K. Zimmer-Faust, 1996. Suspension feeding: basic mechanisms controlling recognition and ingestion of larvae. Limnology & Oceanography 41: 1188–1197.

Twenhofel, W.H., 1921. Impressions made by bubbles, rain drops and other agencies. Geological Society of America Bulletin 32: 359–372.

Velimirov, B., 1980. Formation and potential trophic significant of marine foam near kelp beds in the Benguela upwelling system. Marine Biology 58: 311–318.

Weidberg, N., C. Lobón, E. López, L. García Flórez, M.P. Fernández Rueda, J.L Largier, & J. L. Acuña, 2014. Effect of nearshore surface slicks on meroplankton distribution: role of larval behaviour. Marine Ecology Progress Series 506: 15–30.

Weidberg, N., F. Porri F, C.E.O. Von der Meden, J.M Jackson, W. Goschen, & C.D. McQuaid, 2015. Mechanisms of nearshore retention and offshore export of mussel larvae over the Agulhas Bank. Journal of Marine Systems 144: 70–80.

Weidberg, N., W. Goschen, J.M. Jackson, P. Pattrick, C.D. McQuaid, & F. Porri, 2019. Fine scale depth regulation of invertebrate larvae around coastal fronts. Limnology & Oceanography, 64: 785–802.

Wotton, R.S., 1996. Colloids, bubbles, and aggregates – a perspective on their role in suspension feeding. Journal of the North American Benthological Society 15: 127–135.

Young, C.M., & F.S. Chia, 1982. Ontogeny of phototaxis during larval development of the sedentary polychaete, *Serpula vermicularis* (L.). Biological Bulletin 162: 457-68. Zimmer, C.A., V.R. Starczak, & R.K. Zimmer, 2012. Flocs, flows, and mechanisms decoupling larval supply from settlement. Limnology & Oceanography 57: 936–944.