

# Revisiting cross-shelf transport of Dungeness crab (*Metacarcinus magister*) megalopae by the internal tide using 16 years of daily abundance data

Leif K. Rasmuson<sup>\*,1</sup>, Alan L. Shanks

Oregon Institute of Marine Biology, University of Oregon, Charleston, OR 97420, USA

## ARTICLE INFO

### Keywords:

Internal tide  
Larval dispersal  
Dungeness crab  
Wavelet analysis  
Time series analysis

## ABSTRACT

Many marine organisms have a biphasic life beginning with a planktonic larva that undergoes development on the continental shelf. These larvae ultimately need to return to the nearshore environment to settle. One proposed mechanism of transport to the nearshore is the internal tide. The Dungeness crab, *Metacarcinus* (*Cancer*) *magister*, is one species that is hypothesized to be transported by the internal tide. In addition to daily cycles in catch of megalopae being correlated with the internal tide, the annual catch of megalopae is correlated with the Pacific Decadal Oscillation. However, initial studies occurred during a positive phase Pacific Decadal Oscillation. In this study, we analyze an additional 12 years of data (16 years total) to determine if the internal tide continues to be correlated with the transport of Dungeness crab megalopae. We used wavelet analyses and cross-Fourier analysis to relate the catch of megalopae to the daily maximum tidal range, wind speed, and sea surface temperature. We found that over 16 years, the correlation with the daily maximum tidal range continues to be the strongest correlate with the daily catch of megalopae. These results continue to suggest megalopae are transported across the continental shelf by the internal tide. Our use of wavelets allowed us to examine the annual trends in periodicity of returning megalopae. We found that the periodicities at tidal frequencies did not persist throughout the settlement season. We hypothesize this indicates cross-shelf transport is primarily regulated by the internal tide but additional, unknown factors, interact with the internal tide affecting the number of returning larvae. We conclude by discussing why high-frequency sampling is an important component of ecological time series.

## 1. Introduction

Many marine organisms begin their life as a planktonic larva that is released in the nearshore disperses to the offshore and ultimately returns to the nearshore to settle (Cowen and Sponaugle, 2009; Rieger, 1994). Understanding the mechanism(s) employed by larvae to migrate across the continental shelf to their near shore settlement habitats continues to be a key question in marine ecology. Previous work suggests the mechanism is likely a synergistic interaction between larval behavior and hydrodynamics (Metaxas 2001). Swimming behavior of larvae, either vertically or horizontally, is the primary behavior exhibited by larvae (Metaxas 2001). Numerous hydrodynamic processes have been proposed to transport larvae (Shanks, 1995; Queiroga and Blanton, 2005). One such mechanism is transport by the internal tide (either by bores or internal waves) (Criales et al., 2007; Pineda, 1991; Shanks, 1983; Valencia-Gasti and Ladah, 2016).

In marine ecology, the word “tide” is often used to refer to the

barotropic tide, which causes the high and low tides observed at shore (Bertness et al., 2001). However, the barotropic tide can also interact with ocean stratification and bathymetry to generate baroclinic internal waves and bores at tidal frequencies, collectively referred to as the internal tide (Jackson et al., 2012). Since the barotropic tide generates the internal tide, both can exhibit a two-week periodicity in magnitude (Cairns, 1968; Stanton and Ostrovsky, 1998; Suanda and Barth, 2015). However, complex interactions between the barotropic tide and both ocean stratification and topographic features cause the barotropic and baroclinic tides to often be out of phase with one another (Hibiya, 1990; Johnson et al., 2001; Vlasenko et al., 2005). Over the continental shelf, barotropic tidal currents generate the internal tide through lee wave generation at a sharp change in depth, e.g. the shelf break (Hibiya, 1990; Jackson et al., 2012). As the barotropic tide ebbs off the continental shelf, the pycnocline is depressed, generating a lee wave over the continental slope. Lee waves occur at tidal frequencies and are one manifestation of the internal tide. When the barotropic tide reverses

<sup>\*</sup> Corresponding author.

E-mail address: [leif.k.rasmuson@state.or.us](mailto:leif.k.rasmuson@state.or.us) (L.K. Rasmuson).

<sup>1</sup> Present address: 2040 SE Marine Science Drive, Marine Resources Program, Oregon Department of Fish and Wildlife, Newport, OR 97365, USA.

(ebb to flood), the lee wave is reflected offshore and also moves onto and across the continental shelf (Jackson et al., 2012; Vlasenko et al., 2005).

Most work studying the effect of internal waves on transport of larvae has been done by linking time series of numbers of returning/settling larvae with time series of oceanographic indices (Pineda, 2000; Shanks, 1986). Larval abundance in these studies is often pulsed, varying by multiple orders of magnitude between days, and exhibits a two-week periodicity. This suggests only certain internal tidal events are capable of transporting larvae (Pineda, 2000; Shanks, 1983; Valencia-Gasti and Ladah, 2016). Of the studies that sampled with sufficient temporal resolution to resolve the relationship between oceanographic indices and the number of returning larvae on a daily scale, many are only operated for one or two years (Mace and Morgan, 2006; Queiroga et al., 2006; Shanks, 2006). Therefore, interannual variability in the strength and nature of these correlations have received limited study.

The California Current is the predominant ocean current along the continental shelf of the Western United States and is characterized as a monsoonal upwelling system (Checkley and Barth, 2009; Hickey, 1979). On a roughly decadal time scale, the Pacific Decadal Oscillation (PDO) manifests as a warm or cold sea surface temperature anomaly in the North Pacific (Mantua and Hare, 2002). During the cold (warm) phase, the PDO influences flow in the California Current by shifting more (less) water from the West Wind Drift into the California Current (King et al., 2011). On a seasonal scale, wintertime winds are predominantly from the south and generate a poleward inshore current (Davidson Current) with downwelling favorable conditions (Strub et al., 1987). In winter, the thermocline is relatively deep and the water column is weakly stratified (Erofeeva, 2003). During the spring transition relatively consistent north and northwesterly winds replace southerly winds often associated with winter storms causing the Davidson Current to fade and the California Current to flow southward on the continental shelf and conditions become upwelling favorable (Hickey, 1979; Huyer, 1983). Following the spring transition, the thermocline is shallower and the water column is more strongly stratified (Erofeeva, 2003). However, the depth of the thermocline and how stratified the water column is during the upwelling season are both influenced by the upwelling process (Miller, 1996).

The internal tide on the Oregon coast has been studied extensively (Stanton and Ostrovsky, 1998; Jackson and Apel 2004, Moum et al. 2007a). The internal tide varies seasonally due to weak winter and stronger summer stratification (Erofeeva, 2003). In addition, the thermocline depth is often deeper during winter months, leading to more internal waves of elevation and shallower during the summer, leading to more internal waves of depression (Moum et al. 2007b). Although the ocean is more strongly stratified in summer than during winter, upwelling and downwelling dynamics can introduce intra-seasonal changes in stratification (Hayes & Halpern 1976, Kurapov et al. 2010). Work in the nearshore environment has demonstrated that internal waves generated at the shelf break can propagate across the continental shelf to the shore (Apel et al. 1975, Klymak 2003, Lucas et al. 2011). Despite the large amount of work done on the physical characteristics of the internal tide off Oregon, there have been no in situ studies on the transport of larvae.

The dispersal of Dungeness crab, *Metacarcinus (Cancer) magister*, larvae has been studied extensively (reviewed in Rasmuson, 2013). In the California Current, larvae are released in the nearshore during the winter and are dispersed across the continental shelf during their larval development (Lough, 1976; McConnaughey et al., 1994). Following the spring transition, megalopae begin arriving at the nearshore (Shanks and Roegner, 2007). Using a time series of daily abundance of Dungeness crab megalopae, Roegner et al. (2007) demonstrated that the abundance of megalopae was significantly cross-correlated with the daily maximum tidal range and not with other hydrographic variables. Daily abundance of megalopae changed by multiple orders of

magnitude from one day to the next, which is why the researchers in this study (as well as others) hypothesized transport was by the baroclinic rather than barotropic tide (Pineda, 2000; Shanks, 2006; Valencia-Gasti and Ladah, 2016).

In the years since Roegner et al. (2007) was published, Shanks (2013) has continued to monitor the daily abundance of megalopae and has shown that total annual abundance has varied by a factor of 1000, with a large increase in the total annual abundance in 2007. Along with colleagues, he demonstrated that these patterns correlate with the changing of the PDO from positive to negative and attributes the increased abundance of megalopae to a greater retention of larvae in the California Current during negative phase PDOs (Rasmuson, 2015; Shanks et al., 2010; Shanks, 2013). Further, annual abundance is greater when the day of the year of the spring transition occurs earlier in the year and there is more upwelling following the spring transition (Shanks, 2013). No work has assessed whether the cross-correlation between the daily maximum tidal amplitude and daily abundance (a relationship that is assumed to represent shoreward transport of larvae by the internal tides) of megalopae has persisted following the phase change of the PDO.

## 2. Methods

For 16 years (1998–2001 & 2006–2017), daily collections of *Metacarcinus magister* megalopae were made using a light trap in a marina located in Charleston, Oregon (43° 20' 40.75" N, 124° 19' 15.02" W; Roegner et al., 2007, Shanks and Roegner, 2007, Shanks, 2013). Although the trap is located in an estuary, previous work has shown that the pattern of daily abundance of megalopae observed within the estuary are statistically similar to that observed at a nearby coastal ocean sample site (Miller and Shanks, 2004). Further, in the past multiple light traps were operated and sampled each day, but a comparison of the trap catch data demonstrated that the time series were very positively correlated with one another and therefore, due to logistical constraints, only a single trap was operated moving forward (Roegner et al., 2007). From 1998 to 2001 samples were collected for the entire year, while from 2006 to 2017 samples were collected from ~April 1 – September 30, the period when *M. magister* megalopae recruit to the Oregon coast (Rasmuson, 2013). Samples were preserved in buffered formalin and enumerated using a dissecting microscope. When there were more than ~2000 individuals in a daily sample, the number of megalopae was determined by mass (Shanks et al., 2010). Despite well-known limitations of light traps (Doherty, 1987; Hernandez and Lindquist, 1999; Lindquist and Shaw, 2005) the light trap has proven to be an effective tool for studying the causes of variation in daily and annual Dungeness crab megalopae abundance (Roegner et al., 2007; Shanks and Roegner, 2007). We view the daily catch data as a relative index of the abundance of megalopae arriving at the coast.

For each year the light trap was operated, we generated four time series of physical variables (sea surface temperature, daily maximum tidal range and alongshore and cross-shelf wind stress). Mean surface temperature and daily maximum tidal range were obtained from the NOAA station located on the US Coast Guard pier in the Charleston Marina ([http://www.ndbc.noaa.gov/station\\_page.php?station=chao3](http://www.ndbc.noaa.gov/station_page.php?station=chao3)). There was no continuous measure of sea surface temperature in the coastal ocean near Coos Bay, so we used sea surface temperature recorded at high tide in the Charleston Marina (average of the two daily high tide temperatures). At high tide during summer months, water at this location is characteristically oceanic (Roegner & Shanks 2001). Further, there is little difference in sea surface temperature measured on the open coast and at the Charleston Marina (Miller and Shanks, 2004). Sea surface temperature data were only available from 1998 to 2001 and 2006–2015. Daily maximum tidal range was determined by first calculating the difference between the two high tides each day and the subsequent lows. We then considered the maxima of these two values as the daily maximum tidal range. Hourly wind speed and direction were

obtained from the NOAA Newport weather station (NDBC-NWPO3) and converted into daily means of alongshore and cross-shelf wind stress ([http://www.ndbc.noaa.gov/station\\_page.php?station=nwpo3](http://www.ndbc.noaa.gov/station_page.php?station=nwpo3)). The wind stress should be thought of as a pseudo-wind stress because constant values for the coefficient of drag (0.002) and air density ( $1.18 \text{ kg m}^{-3}$ ) were used (Cushman-Roisin & Beckers 2011).

Data analyses were carried out using R (R Core Team, 2018). We first elected to use a wavelet analysis to examine the daily time series of megalopae (Cazelles et al., 2008). A key benefit of using wavelets is that they do not require the data to be stationary or transformed. This is ideal for ecological time series that are highly variable and change seasonally. In other words, rather than just determining the periodicity of the signal of megalopae and assuming the periodicity is consistent across the return season, we can see how periodicities change throughout the summer as ocean conditions change. However, the data can be averaged to also provide an average periodicity of the time series in question. We used a continuous wavelet transform with a Morlet wavelet to examine trends in periodicity in the power spectrum of each years' time series of megalopae catch using the 'biwavelet' package in R (Gouhier et al., 2018). We averaged the wavelet power spectrum for the megalopae catch season at each periodicity to determine at which periodicities the time series exhibited the highest average power spectrum.

Continuous wavelet transforms only allow the user to look at trends in a single variable. To determine if the megalopae catch time series were correlated with any of the time series of abiotic variables we calculated time series cross-correlations between the time series. However, this technique requires the time series to be stationary. We tested for stationarity using both the augmented Dickey-Fuller test and the KPSS tests for stationarity using the R package 'tseries' (Trapletti and Hornik, 2019). None of the time series were stationary. To make the physical time series stationary we fit a least squares linear regression to the time series and then used the residuals from the regression as the new time series. For the biological time series, we first  $\log_{10}$  transformed the data and then used the same linear regression technique to remove seasonal trends. Cross-correlations (covariance) functions were calculated between the megalopae time series and each of the four physical time series for each year using the ccf function in R. The cross-correlations were calculated using the time series deemed to be stationary by the augmented Dickey-Fuller and KPSS tests. Since organisms respond to their environment, the biological variables were lagged relative to the physical variables. Tidal cycles are periodic and an animal may be able to "predict" events, therefore positive lags were examined. Animals should not be able to 'predict' wind stress and sea surface temperature, however, thus only negative lags were considered for these physical variables.

### 3. Results

The annual catch of megalopae differed dramatically between years and catch differed by greater than two orders of magnitude (Fig. 1). At a daily scale, catch showed consistent large day-to-day variations with daily differences in catch of  $> 10,000$  animals being common (Fig. 2). Although the data fluctuate dramatically, no consistent patterns were observable in the raw catch data. In all 16 years, there were no significant periodicities identified by the continuous wavelet transform that persisted throughout the summer (Fig. 3). A consistent significant periodicity would be apparent as a circled horizontal band of light colored. This was not observed in any year, however bands of periodicity were observed at shorter time periods in each year. The most common periodicity in all of the time series was around 16 d. Averaging the wavelets across the catch season, we see that a periodicity of 16 d was the most common annual signal (Fig. 4). However, this periodicity was not observed in all years (e.g. 1999–2001). It is also important to

note that the magnitude of the power at the peak differed between years. Further, the rise in power observed with the larger periodicities is an artifact of the interaction between the length of the time series and the width of the periodicity. The catch of megalopae was consistently cross correlated with the daily maximum tidal range (Table 1). The most consistent cross-correlations were at lags of  $-7$ ,  $-1$ ,  $0$  and  $7$  d; peaks in catch tended to occur around the spring tide when tidal range was maximal. The catch of megalopae was also correlated with other physical time series in a subset of years that the light trap was monitored but no other environmental correlate was significant in all of the 16 years (Table 2).

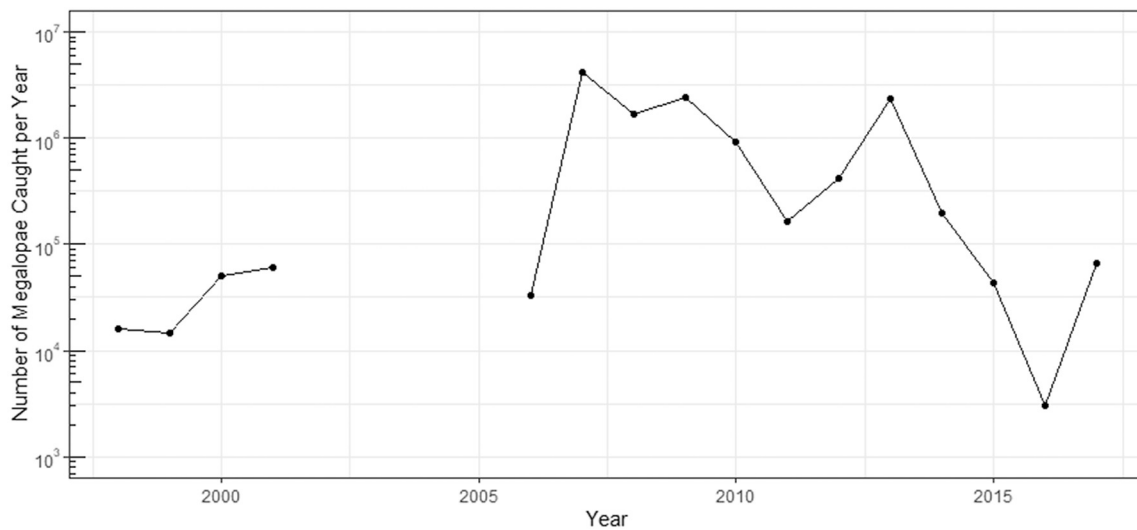
### 4. Discussion

With the inclusion of 12 more years of data, we continue to find that the most consistent environmental correlate with the daily catch of Dungeness crab megalopae was the daily maximum tidal range (Roegner et al., 2007). In the literature, the most common explanation invoked to explain a correlation between the daily maximum tidal range and a larval time series is that larvae are transported across the continental shelf by the baroclinic (internal) tide (Pineda, 2000; Shanks, 1995). Why does a significant cross-correlation between the daily maximum amplitude tidal range and the number of returning megalopae indicate transport by the baroclinic (internal) tide rather than the barotropic tide? For organisms being transported by barotropic tidal currents, the abundance of megalopae should be proportional to the magnitude of the tidal currents, which vary with the two-week spring/neap tidal cycle (Gibson et al., 2001; Queiroga and Blanton, 2005). The abundance of *M. magister* megalopae was, however, highly pulsed; abundance often increased by multiple orders of magnitude between two daily samples. Clearly, abundance was not proportional to the magnitude of the tide. Further, abundance was not in phase with the spring neap cycle. The highly pulsed daily abundance counts suggests that megalopae arrive at the coast in relatively short temporal windows, which previous researchers have suggested indicate discrete transport events (Shanks, 1995).

Although cross-shelf transport is the most common explanation for the combined observation of pulsed returns of larvae and an association between larval abundance and tides, it is possible for other factors such as patchiness of the larvae (McGurk 1986, Blukacz et al. 2009) or trophic interactions (Brodeur & Percy 1992, Baier & Purcell 1997) to influence these patterns. However, the strong relationship between daily abundance of megalopae and the mode-2 baroclinic cross-shelf velocity supports the hypothesis that daily abundance of megalopae is influenced by the internal tide. Therefore regardless of what drives the pulsed returns of megalopae, the internal tide plays an important role.

Our use of wavelets allowed us to demonstrate that the periodicity of significant recruitment events changed throughout the six-month recruitment season. A trend that has been alluded to based on visual examination of raw data but has not been examined using a statistical framework (Cazelles et al., 2008). Recently studies have begun to demonstrate that recruitment and transport of larvae to recruitment sites are not set by a single process but rather are influenced by an interaction of multiple processes (Hare, 2014; Shanks, 1988). Given the considerable variability in the number of returning megalopae, we hypothesize that transport by the internal tide is the primary driver of the variability in the number of returning megalopae but an interaction between multiple physical and biological components operate to influence the number of returning megalopae.

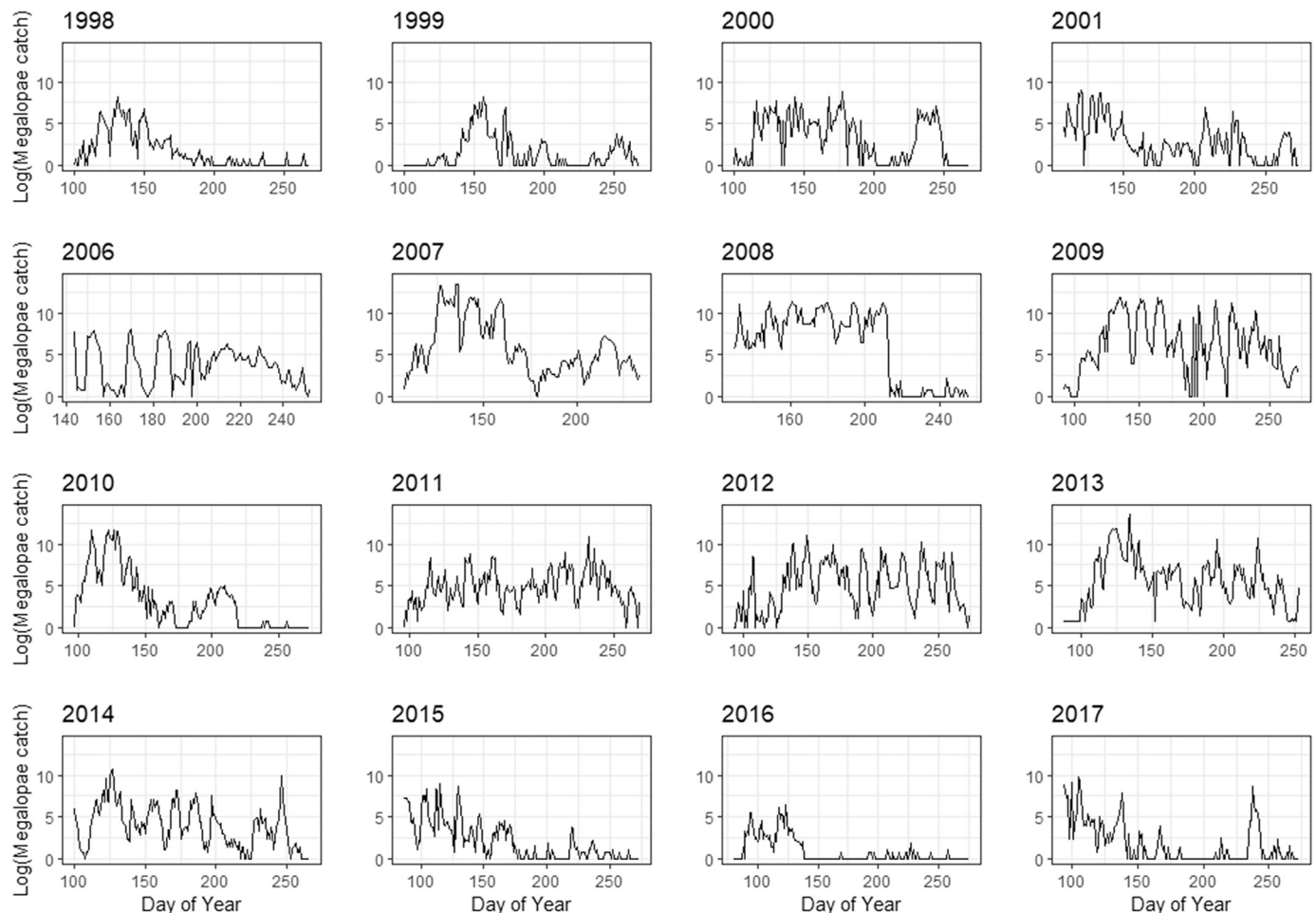
The interaction between water column characteristics and the internal tide is inherently complex. Cairns (1968) demonstrated that the magnitude of the displacement of isotherms was in phase with the spring neap tidal cycle, but the vertical thermal gradient was higher during neap tides than during the spring tides. Moum et al. (2007a)



**Fig. 1.** Total annual catch of megalopae during the 16 years of study. Catch is the sum of the number of megalopae caught in the light trap fished from  $\approx 1$  April through 30 Sept.

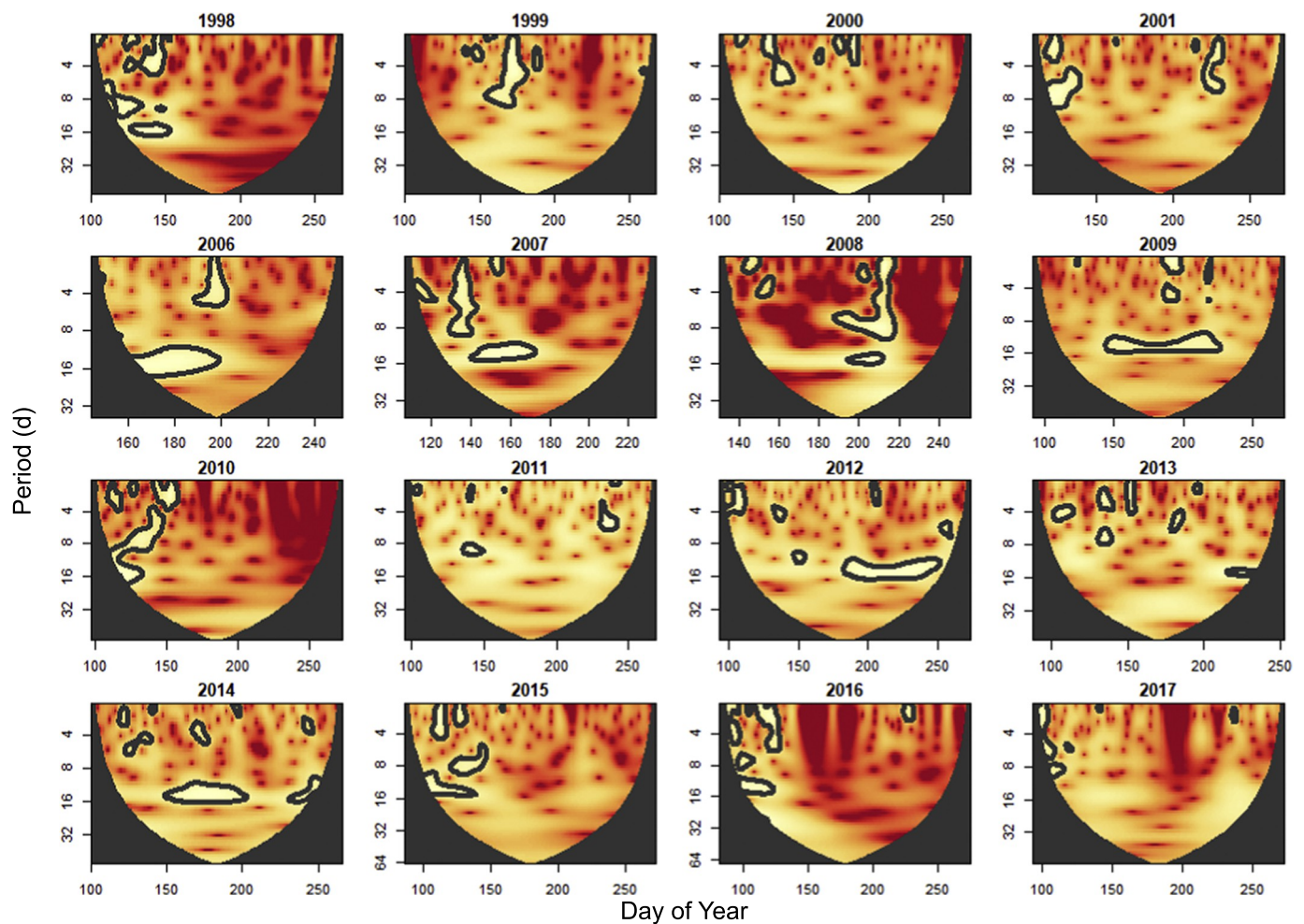
tracked a packet of internal waves as they moved across the continental shelf and demonstrated that they were observable for  $\sim 30$  km. The waves did undergo significant structural changes and energetic losses as they moved across the continental shelf but their speed and amplitude were nearly constant. Although a wave phase change was not observed by Moum et al. (2007a), recent work suggests that the transition from a

wave of depression to one of elevation is complex and may cause waves to lose their transporting characteristics as they go through the transition (Scotti 2004). Long term monitoring of the internal tide at different sites on the Oregon shelf have demonstrated that the internal tide is not correlated with the barotropic tide (Suanda and Barth, 2015). Further the upwelling and downwelling dynamics strongly influence how



**Fig. 2.** Daily catch of *Metacarcinus magister* megalopae to a light trap in Charleston, Oregon for each of the 16 years sampled.





**Fig. 3.** Wavelet power spectrum of the daily catch of *Metacarcinus magister* megalopae for 16 years. The color code for power ranges from low (red) to high (white). Data enclosed by the thick black lines are significant at the 5% level. These areas represent times of the catch season where a significant periodicity (as denoted by the y-axis) was observed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

coherent the internal tide remains as it moves across the continental shelf. At a larger temporal scale King et al., 2011 demonstrated that the Pacific Decadal Oscillation altered the magnitude of the alongshore flow in the California Current with strong flows observed during negative phase PDOs. Noble et al. (2009) demonstrated that internal tides were only coherent on the continental shelf off of southern California when there was consistent alongshore flow. Although speculative, it is possible that the increased alongshore flow during negative PDOs creates conditions that are more conducive to coherent movement of internal waves across the continental shelf.

Due to the correlative nature of this study and the relatively “broad” nature of the environmental correlates we considered, our study does not provide sufficient data to analyze the specificities of what is/are driving cross-shelf transport. What our paper does provide is a long-term high frequency dataset that can be used to provide correlations between abiotic factors and daily catch of megalopae. While long term time series are not uncommon (Bograd et al., 2003; Ravier and Fromentin, 2004), having time series of sufficient temporal resolution to resolve processes occurring at time scales occurring at < 1 week are uncommon; standard time series analysis techniques can only resolve periodicities that occur at rates of equal to or greater than twice the sampling frequency. Therefore weekly or monthly sampling only allows researchers to resolve periodicities that occur on the time scales of bi-weekly or bi-monthly, essentially seasonal cycles

(Shumway and Stoffer, 2011). While processes that occur at these lower frequencies undoubtedly affect recruitment of Dungeness crab megalopae, the large day-to-day variations in the number of returning megalopae and the large number of significant periodicities at rates < 8 d indicate that high frequency processes strongly influence the number of returning megalopae. Further, the lack of significant periodicities at time scales > 16 d indicates that a sampling frequency of biweekly or longer would ultimately result in an inability to identify or worse misidentifying significant periodicities. This is not to say that low frequency processes do not influence the return of megalopae or larvae but rather that they may act to modulate the higher frequency processes that are, at least in this data set, the larger drivers of recruitment.

The long time series we used in this study are unique (daily samples over 6-months) and 16 years allows us to investigate how high frequency processes influence recruitment of a species over many years. In this study, we find strong evidence that despite very large differences in inter and intra-annual variability in the abundance of returning megalopae a strong correlation with the daily maximum amplitude tide (e.g., the spring neap tidal cycle) persists which we hypothesize is indicative of transport by the internal tide. Further, the changes in the observed patterns between years indicated that although the internal tide is likely the primary transport mechanism, its ability to act on the transport of megalopae may be modulated by other abiotic factors.

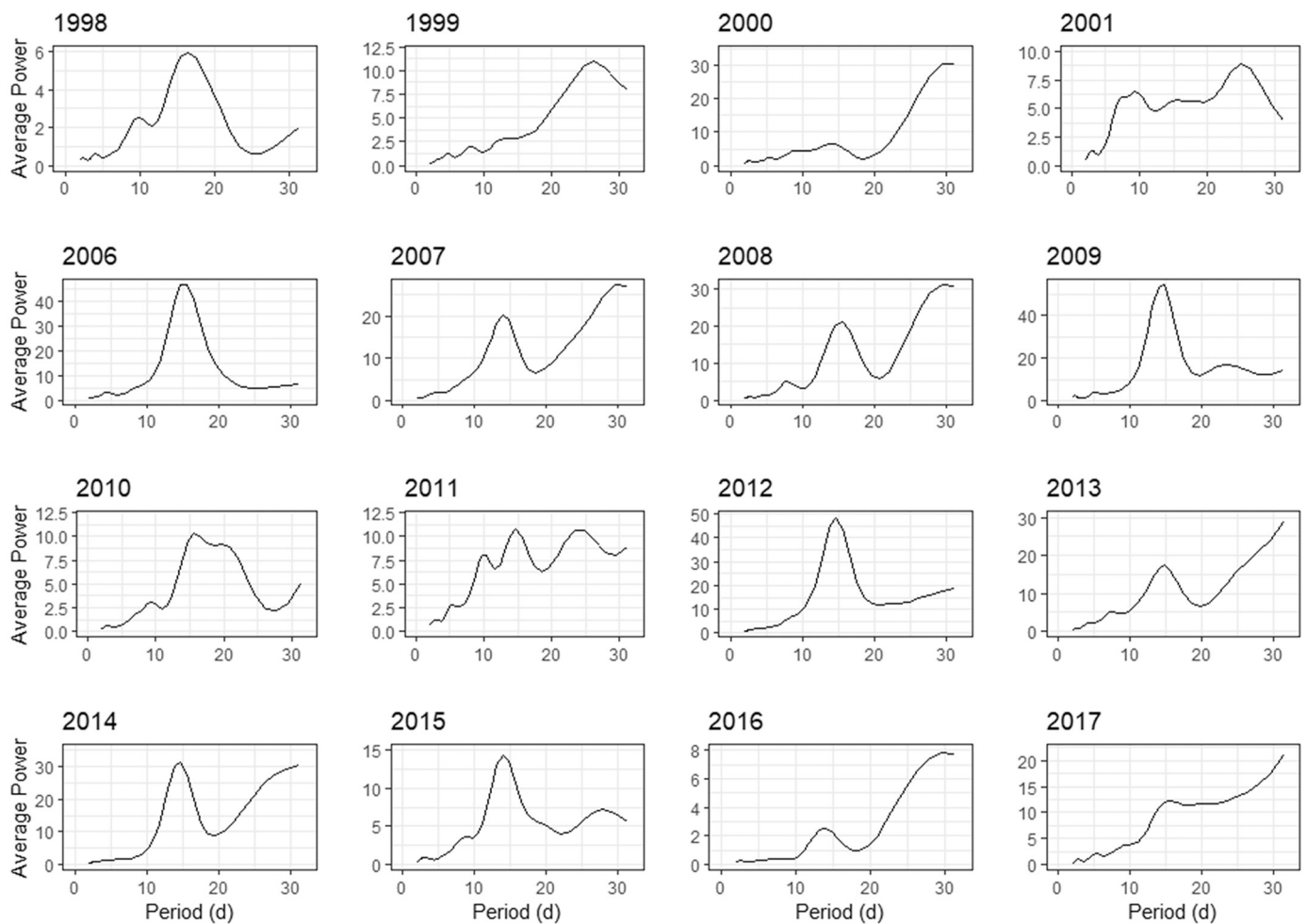


Fig. 4. Average wavelet power spectrum for each year of daily catch of *Metacarcinus magister* megalopae. Peaks in each plot denote periodicities that, on average, had higher overall power throughout the daily catch season. The rise in power at the higher periodicities is an artifact of the decreasing sample size that occurs as the periodicities become longer. Note the y-axis scales are different.

Table 1

Cross-correlations between  $\log_{10}$  transformed daily catch of *Metacarcinus magister* megalopae and daily maximum tidal range. Columns values  $[-7 \ 7]$  denote the number of days the biological data were lagged relative to the daily maximum tidal range. A value of 0 indicates when the two time series are in phase with one another. Seasonal trends were removed from the biological and physical data to ensure data were stationary. Biological data were lagged relative to physical data. Correlation coefficients ( $r$ ) are only reported for significant cross-correlations. Bold numbers denote the largest significant positive and negative correlation for each year.

	Daily Maximum Tidal Range														
	-7	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	7
1998	0.29	<b>0.33</b>	0.27				-0.17	-0.25	<b>-0.27</b>	-0.21				0.16	0.22
1999	<b>-0.17</b>						0.20	<b>0.21</b>							
2000			-0.17				<b>0.17</b>	0.17						-0.19	<b>-0.26</b>
2001						-0.19	<b>-0.21</b>	-0.17				0.26	<b>0.32</b>	0.31	0.26
2006	0.35	0.26	0.13		-0.22	-0.37	-0.46	<b>-0.49</b>	-0.41	-0.26			0.33	0.46	<b>0.52</b>
2007	0.30			-0.21	-0.33	<b>-0.39</b>	-0.35	-0.23			0.32	0.46	<b>0.49</b>	0.42	0.28
2008	<b>0.55</b>	0.54	0.42	0.24		-0.30	-0.38	<b>-0.38</b>	-0.31					0.22	0.31
2009	<b>0.46</b>	0.37	0.21		-0.19	-0.36	-0.45	<b>-0.48</b>	-0.43	-0.30			0.27	0.38	0.42
2010	0.25			-0.26	-0.35	<b>-0.41</b>	-0.39	-0.32	-0.20			0.24	<b>0.30</b>	0.28	0.21
2011	<b>0.33</b>	0.22			-0.21	-0.31	-0.35	-0.34	-0.25			0.22	-0.32	<b>-0.38</b>	-0.34
2012	0.44	0.38	0.24			-0.34	-0.48	<b>-0.53</b>	-0.49	-0.36	-0.16		0.30	0.47	<b>0.55</b>
2013	<b>0.37</b>	0.30	0.18		-0.16	-0.31	-0.41	<b>-0.44</b>	-0.40	-0.29			0.16	0.29	0.36
2014	0.28	0.2			-0.21	-0.35	-0.44	<b>-0.45</b>	-0.39	-0.26			0.25	0.37	<b>0.42</b>
2015					-0.21	<b>-0.28</b>	-0.3		-0.22				<b>0.25</b>	0.23	0.23
2016	<b>0.16</b>							<b>-0.11</b>							
2017			-0.2	-0.31	-0.37	-0.43	<b>-0.46</b>	-0.43	-0.33	-0.21					

**Table 2**

Cross-correlations between  $\log_{10}$  transformed daily catch of *Metacarcinus magister* megalopae and sea surface temperature (SST), alongshore and cross-shelf wind stress. Seasonal trends were removed from the biological and physical data to ensure data were stationary. Biological data were lagged relative to physical data. Correlation coefficients ( $r$ ) are only reported for significant cross-correlations. Bold numbers denote the largest significant positive and negative correlation for each year. NA denotes “No Data” because the weather station was taken offline.

	Alongshore Wind						Cross-Shelf Wind					
	−5	−4	−3	−2	−1	0	−5	−4	−3	−2	−1	0
1998												
1999												
2000												
2001												
2006	<b>0.13</b>	0.11										
2007												
2008												
2009												
2010												
2011				−0.17			−0.16	−0.14	−0.13	−0.13		
2012												
2013												
2014							0.27	<b>0.31</b>				
2015												
2016	0.27	0.28	<b>0.3</b>	0.26	0.24	0.25						
2017		−0.16	−0.19	−0.2	−0.22	−0.27	<b>0.15</b>					

Sea Surface Temperature												
	−5	−4	−3	−2	−1	0						
1998												
1999	−0.2		−0.24				−0.18		−0.23		−0.26	
2000			−0.17			<b>0.18</b>			−0.23		−0.24	
2001									−0.16		−0.19	
2006									0.13		<b>0.16</b>	
2007												
2008												
2009												
2010												
2011												
2012												
2013												−0.26
2014	0.19						0.17		0.21		<b>0.27</b>	
2015	−0.27		−0.21		−0.26		−0.21					
2016	NA		NA		NA		NA		NA		NA	
2017	NA		NA		NA		NA		NA		NA	

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgments

We thank the numerous undergraduate and graduate students who have maintained the light trap over the years. LKR and ALS were funded by the Oregon Dungeness Crab Commission and OCE-1259603. ALS was also funded by OCE-0926923.

## References

- Apel, J., Byrne, H., Proni, J., Charnell, R., 1975. Observations of oceanic internal and surface waves from the earth resources technology satellite. *J. Geophys. Res.* 80, 865–881.
- Baier, C.T., Purcell, J.E., 1997. Trophic interactions of chaetognaths, larval fish, and zooplankton in the South Atlantic Bight. *Mar. Ecol. Prog. Ser.* 146, 43–53.
- Bertness, M., Gaines, S., Hay, M., 2001. *Marine Community Ecology*. Sinauer Associates, Sunderland, MA.
- Blukacz, E.A., Shuter, B.J., Sprules, W.G., 2009. Towards understanding the relationship between wind conditions and plankton patchiness. *Limnol. Oceanogr.* 54 (5), 1530–1540.
- Bograd, S.J., Checkley, D.A., Wooster, W.S., 2003. CalCOFI: a half century of physical, chemical and biological research in the California current system. *Deep Sea Res. II* 50, 2349–2353.
- Brodeur, R.D., Pearcy, W.G., 1992. Effects of environmental variability on trophic interactions and food web structure in a pelagic upwelling ecosystem. *Mar. Ecol. Prog. Ser.* 84, 101–119.
- Cairns, J., 1968. Thermocline strength fluctuations in coastal waters. *J. Geophys. Res.* 73, 2591–2595.
- Cazelles, B., Chavez, M., Berteaux, D., Ménard, F., Vik, J.O., Jenouvrier, S., Stenseth, N.C., 2008. Wavelet analysis of ecological time series. *Oecologia* 156, 287–304.
- Checkley, D.M., Barth, J.A., 2009. Patterns and processes in the California current system. *Prog. Oceanogr.* 83, 49–64.
- Core Team, R., 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria URL: <https://www.R-project.org>.
- Cowen, R.K., Sponaugle, S., 2009. Larval dispersal and marine population connectivity. *Annu. Rev. Mar. Sci.* 1, 443–466.
- Criales, M., Browder, J., Mooers, C., Robblee, M., Cardenas, H., Jackson, T., 2007. Cross-shelf transport of pink shrimp larvae: interactions of tidal currents, larval vertical migrations and internal tides. *Mar. Ecol. Prog. Ser.* 345, 167–184.
- Cushman-Roisin, B., Beckers, J.-M., 2011. *Introduction to geophysical fluid dynamics: physical and numerical aspects*. Prentice Hall, Upper Saddle River, NJ.
- Doherty, P.J., 1987. Light-traps: selective but useful devices for quantifying the distributions and abundances of larval fishes. *Bull. Mar. Sci.* 41, 423–431.
- Erofeeva, S., 2003. Tidal currents on the Central Oregon shelf: models, data, and assimilation. *J. Geophys. Res.* 108, 1–25.
- Gibson, R., Barnes, M., Atkinson, R., 2001. Selective tidal-stream transport of marine animals. *Oceanogr. Mar. Biol.* 39, 305–353.
- Gouhier, T.C., Grinstead, A., Viliam, S., 2018. R package biwavelet: conduct univariate and bivariate wavelet analyses. <https://github.com/tgouhier/biwavelet>.
- Hare, J.A., 2014. The future of fisheries oceanography lies in the pursuit of multiple hypotheses. *ICES J. Mar. Sci.* 71, 2343–2356.
- Hayes, S.P., Halpern, D., 1976. Observations of internal waves and coastal upwelling off the Oregon coast. *J. Mar. Res.* 34, 247–267.

- Hernandez, F., Lindquist, D., 1999. A comparison of two light-trap designs for sampling larval and presettlement juvenile fish above a reef in Onslow Bay. North Carolina. *Bull. Mar. Sci.* 64, 173–184.
- Hibiya, T., 1990. Generation mechanism of internal waves by a vertically sheared tidal flow over a sill. *J. Geophys. Res.* 95, 1757–1764.
- Hickey, B., 1979. The California current system- hypotheses and facts. *Prog. Oceanogr.* 8, 191–279.
- Huyer, A., 1983. Coastal upwelling in the California current system. *Prog. Oceanogr.* 12, 259–284.
- Jackson, C.R., Apel, J.R., 2004. An atlas of internal solitary-like waves and their properties. In: *Global Ocean Associates.*, 2nd ed. . <http://www.internalwaveatlas.com>.
- Jackson, C., Silva, J., Jeans, G., 2012. The generation of nonlinear internal waves. *Oceanography* 25, 108–123.
- Johnson, D., Weidemann, A., Pegau, W., 2001. Internal tidal bores and bottom nephoid layers. *Cont. Shelf Res.* 21, 1473–1484.
- King, J.R., Agostini, V.N., Harvey, C.J., McFarlane, G.A., Foreman, M.G.G., Overland, J.E., Di Lorenzo, E., Bond, N.A., Aydin, K.Y., 2011. Climate forcing and the California current ecosystem. *ICES J. Mar. Sci.* 68, 1199–1216.
- Klymak, J.M., Moum, J.N., 2003. Internal solitary waves of elevation advancing on a shoaling shelf. *Geophys. Res. Lett.* 30, 2045.
- Kurapov, A.L., Allen, J.S., Egbert, G.D., 2010. Combined effects of wind-driven upwelling and internal tide on the continental shelf. *J. Phys. Oceanogr.* 40, 737–756.
- Lindquist, D., Shaw, R., 2005. Effects of current speed and turbidity on stationary light-trap catches of larval and juveniles fishes. *Fish. Bull.* 103, 438–444.
- Lough, R., 1976. Larval dynamics of the Dungeness crab, *Cancer magister*, off the Central Oregon coast, 1970–71. *Fish. Bull.* 74, 353–376.
- Lucas, A.J., Franks, P.J.S., Dupont, C.L., 2011. Horizontal internal-tide fluxes support elevated phytoplankton productivity over the inner continental shelf. *Limnol. Oceanogr.* 56, 56–74.
- Mace, A.J., Morgan, S.G., 2006. Biological and physical coupling in the lee of a small headland: contrasting transport mechanisms for crab larvae in an upwelling region. *Mar. Ecol. Prog. Ser.* 324, 185–196.
- Mantua, N., Hare, S., 2002. The Pacific decadal oscillation. *J. Oceanogr.* 58, 35–44.
- McConnaughey, R., Armstrong, D.A., Hickey, B., Gunderson, D.R., 1994. Interannual variability in coastal Washington Dungeness crab (*Cancer magister*) populations: larval advection and the coastal landing strip. *Fish. Oceanogr.* 3, 22–38.
- McGurk, M.D., 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. *Mar. Ecol. Prog. Ser.* 34, 227–242.
- Metaxas, A., 2001. Behaviour in flow: perspectives on the distribution and dispersion of meroplanktonic larvae in the water column. *Can. J. Fish. Aquat. Sci.* 55, 86–98.
- Miller, A., 1996. Recent advances in California current modeling: decadal and interannual thermocline variations. *CalCOFI Rep.* 37, 69–79.
- Miller, J.A., Shanks, A.L., 2004. Ocean-estuary coupling in the Oregon upwelling region: abundance and transport of juvenile fish and of crab megalopae. *Mar. Ecol. Prog. Ser.* 271, 267–279.
- Moum, J.N., Farmer, D.M., Shroyer, E.L., Smyth, W.D., Armi, L., 2007a. Dissipative losses in nonlinear internal waves propagating across the continental shelf. *J. Phys. Oceanogr.* 37, 1989–1995.
- Moum, J.N., Klymak, J.M., Nash, J.D., Perlin, A., Smyth, W.D., 2007b. Energy transport by nonlinear internal waves. *J. Phys. Oceanogr.* 37, 1968–1988.
- Noble, M., Jones, B., Hamilton, P., Xu, J., Robertson, G., Rosenfeld, L., Largier, J., 2009. Cross-shelf transport into nearshore waters due to shoaling internal tides in San Pedro Bay, CA. *Cont. Shelf Res.* 29 (5), 1821–1835.
- Pineda, J., 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* 253, 548–551.
- Pineda, J., 2000. Linking larval settlement to larval transport: assumptions, potentials, and pitfalls. *Oceanography of the Eastern Pacific* 1, 84–105.
- Queiroga, H., Blanton, J., 2005. Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustacean larvae. *Adv. Mar. Biol.* 47, 109–214.
- Queiroga, H., Almeida, M.J., Alpuim, T., Flores, A.A., Francisco, S., González-Gordillo, I., Miranda, A.I., Silva, I., Paula, J., 2006. Tide and wind control of megalopal supply to estuarine crab populations on the Portuguese west coast. *Mar. Ecol. Prog. Ser.* 307, 21–36.
- Rasmuson, L.K., 2013. The biology, ecology and fishery of the Dungeness crab, *Cancer magister*. *Adv. Mar. Biol.* 65, 95–148.
- Rasmuson, L.K., 2015. The Influence of Behavior and Hydrodynamics on the Dispersal of Dungeness Crab, *Cancer magister*, Larvae. Doctoral Thesis. University of Oregon.
- Ravier, C., Fromentin, J.M., 2004. Are the long-term fluctuations in Atlantic bluefin tuna (*Thunnus thynnus*) population related to environmental changes? *Fish. Oceanogr.* 13, 145–160.
- Rieger, R., 1994. The biphasic life cycle-a central theme of metazoan evolution. *Am. Zool.* 34, 484–491.
- Roegner, G.C., Shanks, A.L., 2001. Import of coastally-derived chlorophylla to South Slough, Oregon. *Estuar. Coasts* 24, 244–256.
- Roegner, G., Armstrong, D., Shanks, A., 2007. Wind and tidal influences on larval crab recruitment to an Oregon estuary. *Mar. Ecol. Prog. Ser.* 351, 177–188.
- Scotti, A., 2004. Observation of very large and steep internal waves of elevation near the Massachusetts coast. *Geophys. Res. Lett.* 31, L22307.
- Shanks, A., 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. *Mar. Ecol. Prog. Ser.* 13, 311–315.
- Shanks, A.L., 1986. Tidal periodicity in the daily settlement of intertidal barnacle larvae and an hypothesize mechanism for the cross-shelf transport of cyprids. *Biol. Bull.* 170, 429–440.
- Shanks, A., 1988. Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish. *Fish. Bull.* 86, 703–714.
- Shanks, A., 1995. Mechanisms of Cross-Shelf Dispersal of Larval Invertebrates and Fish, in: *Ecology of Marine Invertebrate Larvae*. CRC Press, Boca Raton, FL, pp. 323–367.
- Shanks, A.L., 2006. Mechanisms of cross-shelf transport of crab megalopae inferred from a time series of daily abundance. *Mar. Biol.* 148, 1383–1398.
- Shanks, A.L., 2013. Atmospheric forcing drives recruitment variation in the Dungeness crab (*Cancer magister*), revisited. *Fish. Oceanogr.* 22, 263–272.
- Shanks, A.L., Roegner, G.C., 2007. Recruitment limitation in Dungeness crab populations is driven by variation in atmospheric forcing. *Ecology* 88, 1726–1737.
- Shanks, A., Roegner, G., Miller, J., 2010. Using megalopae abundance to predict future commercial catches of Dungeness crabs (*Cancer magister*) in Oregon. *CalCOFI Rep.* 51.
- Shumway, R.H., Stoffer, D.S., 2011. Time series analysis and its applications. In: *Springer Texts in Statistics*. Springer, New York, New York, NY.
- Stanton, T., Ostrovsky, L., 1998. Observations of highly nonlinear internal solitons over the continental shelf. *Geophys. Res. Lett.* 25, 2695–2698.
- Strub, P.T., Allen, J., Huyer, A., Smith, R., Beardsley, R., 1987. Seasonal cycles of currents, temperatures, winds, and sea level over the Northeast Pacific continental shelf: 35°N to 48°N. *J. Geophys. Res.* 92, 1507–1526.
- Suanda, S.H., Barth, J.A., 2015. Semidiurnal baroclinic tides on the Central Oregon inner shelf. *J. Phys. Oceanogr.* 45, 2640–2659.
- Trapletti, A., Hornik, K., 2019. tseries: Time series analysis and computational Finance. Valencia-Gasti, J., Ladah, L., 2016. Synchronous settlement of barnacle larvae at small spatial scale correlates with both internal waves and onshore surface winds. *Mar. Ecol. Prog. Ser.* 552, 195–210.
- Vlasenko, V., Stashchuk, N., Hutter, K., 2005. Baroclinic Tides: Theoretical Modeling and Observational Evidence. Cambridge University Press.