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The Fate and Impact of Internal Waves in Nearshore Ecosystems

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Abstract

Internal waves are widespread features of global oceans that play critical roles in mixing and thermohaline circulation. Similarly to surface waves, internal waves can travel long distances, ultimately breaking along continental margins. These breaking waves can transport deep ocean water and associated constituents (nutrients, larvae, and acidic low-oxygen waters) onto the shelf and locally enhance turbulence and mixing, with important effects on nearshore ecosystems. We are only beginning to understand the role internal waves play in shaping nearshore ecosystems. Here, I review the physics of internal waves in shallow waters and identify two commonalities among internal waves in the nearshore: exposure to deep offshore waters and enhanced turbulence and mixing. I relate these phenomena to important ecosystem processes ranging from extreme events to fertilization success to draw general conclusions about the influence of internal waves on ecosystems and the effects of internal waves in a changing climate.

INTRODUCTION

Internal waves are ubiquitous features of the global ocean that are responsible for substantial ocean mixing, energy dissipation, and thermohaline circulation and that often (albeit unpredictably) crash into nearshore ecosystems (Alford 2003; Garrett & Munk 1979; Nash et al. 2012a,b; Ray & Mitchum 1996; Simmons et al. 2004; Zhao & Alford 2009). As internal waves approach the coast, they slow down, steepen, and become increasingly nonlinear, similarly to surface waves, and then eventually break and form internal bores (Kundu & Cohen 2004). Nonlinear internal waves and bores transport significant volumes of water along with associated constituents and inhabitants and are characterized by increased turbulence and mixing. The effects of internal waves in nearshore environments are thus widespread, ranging from causation and mitigation of extreme events (hypoxia, acidification, and extreme heat) to fertilization success (Crimaldi & Zimmer 2014; Hofmann et al. 2011; Lucas et al. 2011a,b; Wall et al. 2015).

Nonlinear internal waves can bring deep offshore waters into the nearshore (**Figure 1**). These deeper waters are often colder, lower in oxygen, higher in CO_2 concentration (lower pH), and nutrient enriched. Consequently, internal waves can dramatically change the ambient environment, leading to either extreme oxygen (hypoxia) or pH (acidification) events (Frieder et al. 2012). However, they can also mediate extreme heating events by providing a temporary reprieve from high temperatures (Buerger et al. 2015, Palumbi et al. 2014, Wall et al. 2015).

Deep offshore waters can also provide nutrients and food subsidies to nearshore ecosystems (Jantzen et al. 2013, Leichter et al. 1998, McPhee-Shaw et al. 2007, Shea & Broenkow 1982). Nutrient-deprived nearshore ecosystems, namely coral reefs, can be highly dependent on such subsidies (Leichter et al. 1998, Monismith et al. 2010). Internal waves in these systems can drive the degree of heterotrophy and overall biomass at relatively small spatial scales (Roder et al. 2010). The presence of internal waves on coral reefs may thus provide a mechanism for corals to survive bleaching events by providing temporary refuge from extreme temperatures or energetic subsidies to adapt to them (Palardy et al. 2008). Even in more nutrient-rich waters, such as eastern boundary current upwelling systems, internal waves can provide a critical last push for nutrients into nearshore rocky reefs dominated by large, fast-growing algae that form important habitats for many iconic species (McPhee-Shaw et al. 2007). Transport of offshore waters into the nearshore also brings larvae into adult habitats, an important source of population replenishment that can be manifest in overall population densities at broad spatial scales (Broitman et al. 2008, Ladah et al. 2005, Pineda 1991).

During arrival or retreat, nonlinear internal motions can also enhance local turbulence and mixing, which may resuspend particulate matter and enhance broadcast spawning efficiency (Crimaldi & Zimmer 2014, Johnson et al. 2001). Resuspension of particulate matter can enhance filter feeding rates for sessile benthic invertebrates (Abelson & Denny 1997, Monismith et al. 2010, Pomar et al. 2012, Riisgaard 1998). Enhanced turbulence can improve feeding and survival of recently recruited mobile organisms (MacKenzie 2000, MacKenzie & Kiørboe 2000, Rothschild & Osborn 1988). Internal-wave-associated turbulence can also enhance fertilization rates for both sessile and mobile broadcast spawners during spawning aggregations (Crimaldi & Browning 2004, Crimaldi & Zimmer 2014, Ezer et al. 2011).

Given the wide variety of effects that internal waves have on coastal marine ecosystems, their importance in determining ecological patterns in nearshore environments is a growing avenue for research. However, internal waves are inherently unpredictable, making such research difficult. In this review, I highlight recent progress in our understanding of how internal waves influence broad-scale ecological patterns and discuss how we may target regions or periods that may be particularly insightful for these studies. I begin with a concise review of internal-wave physics in

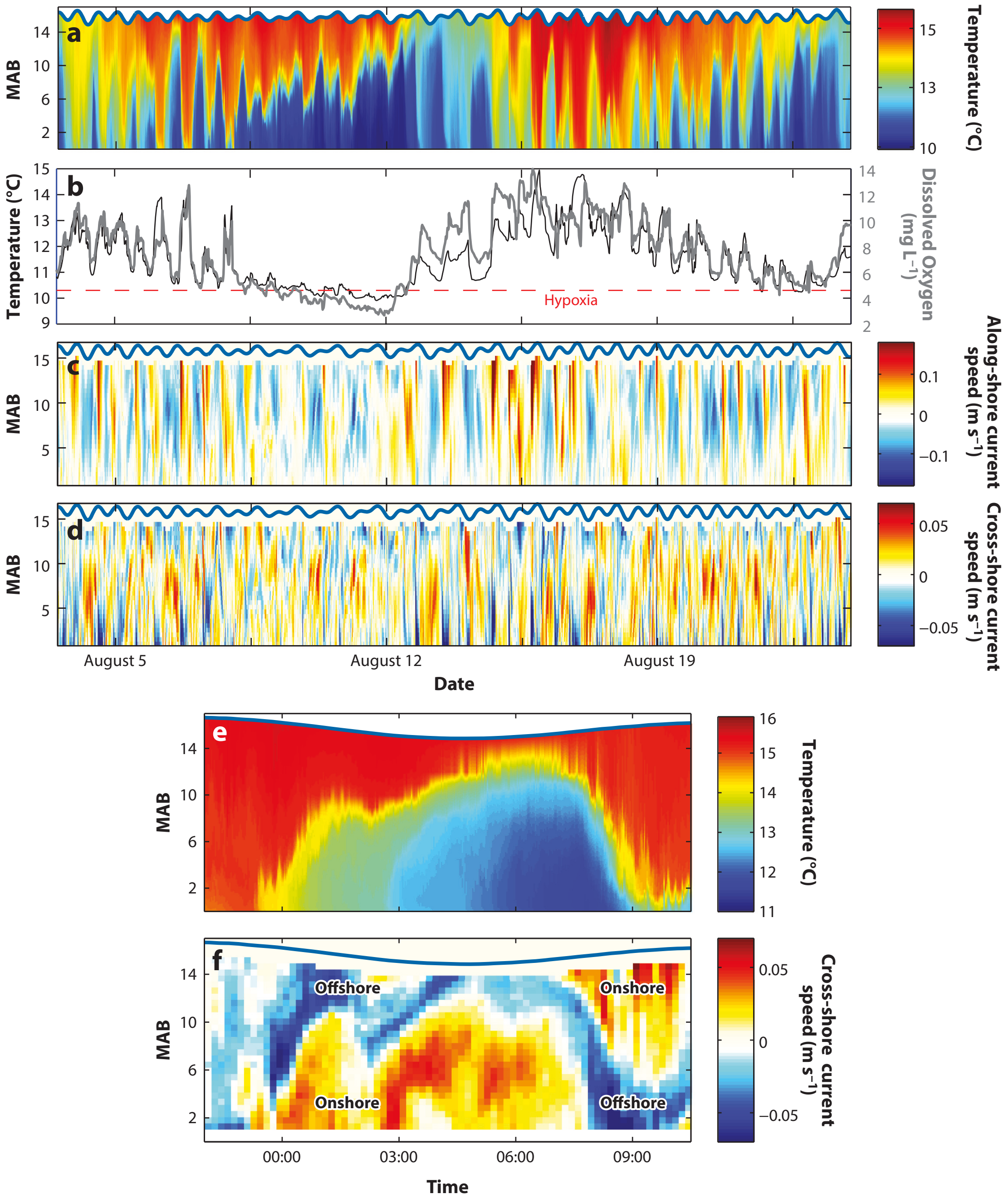

Figure 1

Example of internal waves in the nearshore from near Hopkins Marine Station in Monterey Bay: (*a*) temperature contours, (*b*) bottom temperature and dissolved oxygen, (*c*) along-shore currents, (*d*) cross-shore currents, (*e*) isolated bore temperature contours, and (*f*) cross-shelf currents. The dashed red line in panel *b* denotes a critical biological threshold for dissolved oxygen (i.e., below 4.6 m l^{-1}; hypoxic). Abbreviation: MAB, meters above bottom. Adapted from Walter et al. (2014).

order to dispel a few erroneous concepts about internal waves that appear to have permeated the literature on their impacts in coastal ecosystems. I then give an account of documented impacts of internal waves on a variety of ecosystem processes. Next, I discuss broadly how the effects of internal waves on nearshore environments may shift in a future climate. Finally, in order to guide future research, I highlight how far we have come in recent decades and hypothesize how internal waves may cause some broad patterns in ecosystem dynamics.

INTERNAL WAVES IN THE OCEAN

Before delving into the effects of internal waves in the nearshore, I review some of the basics of internal-wave physics in order to be clear about the physical mechanisms that drive observed changes in nearshore ecosystems.

Linear Internal Waves

Internal waves are a special case of gravity waves that can occur when a fluid is stratified (**Figure 2**), that is, when the density of the fluid changes in space, most commonly in the vertical axis or with

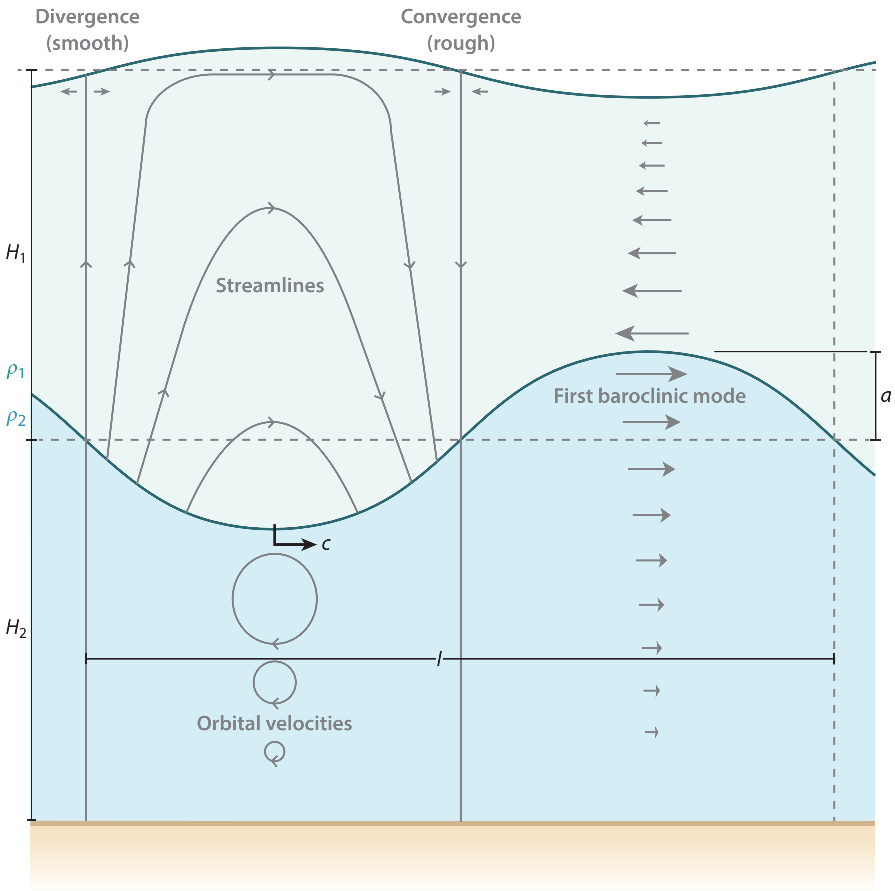

Figure 2

Schematic of an internal wave, along with definitions for a linear internal wave in deep water.

Table 1 General characteristics of nearshore internal waves

Property	Symbol or equation	Typical values
Wavelength	λ	100–1,000 m
Wave number	$k = 2\pi/\lambda$	0.01–0.001 m^{-1}
Frequency	$f = 2\pi/T$	10 min–12 h
Amplitude	a	1–10 m
Stratification	$N = \sqrt{-\frac{g}{\rho_o}\frac{d\rho}{dz}}$	0.001–0.03 s^{-1}
Linear wave speed	$c = (g'h)^{1/2}$	0.03–0.3 m s^{-1}

depth in the ocean and atmosphere (although there are numerous examples of horizontal density gradients, namely fronts). In the simplest case, this scenario can be idealized as a two-layer system with a less dense fluid overlying a denser fluid, as is the approximate case for many situations in the coastal ocean with a strong pycnocline (**Figure 2**). Internal waves are created when this background density field is perturbed, similarly to the formation of a surface wave when the surface is deflected vertically because of the wind or an object thrown into the water. Perturbations in the interior of the ocean can be caused by a variety of mechanisms, most commonly tidal flow over topography (Baines 1986, Bell 1975, Lerczak et al. 2003); flow of a less dense fluid into a denser fluid, such as a river discharging into the ocean, called buoyant flow propagation (Nash & Moum 2005); and wind interactions with hydrography (Lerczak et al. 2001, Walter et al. 2016, Woodson et al. 2011).

Two parameters that are particularly important in our consideration of internal waves are the wavelength (or frequency), λ (or f), and the amplitude (or wave height), a (**Figure 2**, **Table 1**). Linear internal waves have characteristic wavelengths that are generally constrained by two factors. At the large scale, the Coriolis parameter sets the maximum wavelength (lowest frequency) for sustained motions. Below this frequency, internal waves are ephemeral and rapidly break down (Carter et al. 2005; Lerczak et al. 2001, 2003). At the short-wavelength (high-frequency) end of the spectrum, waves do not contain sufficient energy to overcome the background stratification (buoyancy acts as a restoring force in stably stratified fluids, hence the term gravity wave), thus setting a limit beyond which internal waves are rapidly dissipated. Another important parameter for internal waves is the fluid density (ρ), or, more accurately, the fluid density change ($\Delta\rho$), or rate of change, often called the stratification. Stratification is often reported in the form of the Brunt-Väisälä or buoyancy frequency,

$$N = \sqrt{-\frac{g}{\rho_o}\frac{d\rho}{dz}},$$

where z is the vertical axis or depth. For midlatitude, general ocean conditions, this means that internal waves are commonly constrained to periods ($T = 2\pi/f$) between approximately 20 h and approximately 5 min (**Table 1**).

The amplitude of an internal wave is defined as the height of the perturbation from the resting state of the fluid interface. If the wave amplitude is less than approximately 10% of the layer or water depth, the waves are called linear because they are not affected by the bottom, preserve their shape, and travel at a speed $c_l = (g'H)^{1/2}$. For a more realistic, continuously stratified fluid, $c_l = NH/n\pi$, where n is the mode $= 1, 2, 3, \ldots$. Here, c_l is defined as the celerity, or linear wave speed; g' is the reduced or modified acceleration caused by gravity as $g' = (\Delta\rho/\rho_o)$; and H is the depth of the shallower (most commonly upper) layer. This condition is known in the wavy world as the shallow-water approximation ($kH \ll 1$, where k is the wave number, equal to $1/\lambda$) and ensures that the waves are hydrostatic. The hydrostatic condition means that vertical velocities

Figure 3

Smooth and rough water overlying an internal wave. Smooth water occurs on the rising slope of an individual wave; rough water occurs on the falling slope.

are small enough that they do not affect the background pressure defined by hydrostatics, $P = \rho g H$. (Vertical velocities can cause deviations from hydrostatic conditions because as velocity goes up, P goes down.) Based on common values for the fluid density change across the pycnocline ($\Delta\rho \sim 0.5$ kg m^{-3}) and depth of the surface mixed layer ($h \sim 200$ m) in the open ocean, linear internal waves travel at speeds of $c_{\rm I} \sim 0.5$ m s^{-1}, much slower than their surface-wave counterparts, where $c_{\rm I} = gT/2\pi \sim 16$ m s^{-1} (**Table 1**). Internal waves are almost always affected by the depth of one of the fluid layers, and the gravitational acceleration is modified owing to the small density differences, causing these waves to travel much slower than surface waves. These parameters are not inclusive and are provided as a general guideline in order to fuel the discussion of the impacts of internal waves on nearshore ecosystems in subsequent sections.

Another feature of internal waves that can be important for effects on nearshore ecosystems is that surface flow and the flow in the deeper layer are in opposite directions for these waves, often called the first baroclinic mode (although higher modes are often present in continuously stratified systems; **Figure 2**). In the first baroclinic mode for a two-layer system, the flows under crests and troughs are also in opposite directions, leading to alternating convergence and divergence zones that can be visible from the surface (**Figure 2**). Divergences take the form of smooth water regions where the divergent velocity is greater than the capillary wave speed (the speed of small waves affected by surface tension, such as ripples), and convergences appear as rough patches or foam lines where buoyant material is not submerged by the relatively weak vertical velocities (**Figure 3**).

Linear internal waves, like their surface-wave counterparts, are generally nondissipative and can therefore travel long distances (Alford 2003, Alford et al. 2007, Simmons et al. 2004) (**Figure 4**). Consequently, internal waves generated great distances away from a particular location can have large effects on a local ecosystem. However, local generation of internal-wave-like motions can also be important (Woodson et al. 2011). Similarly to deepwater surface waves, linear internal waves do not transport fluid or things associated with the fluid, such as dissolved nutrients or larval propagules. However, as discussed below for nearshore ecosystems, internal waves are often not linear owing to the shallow water depth, and nonlinear effects must be included (but we need to know when and where). Before considering how internal waves will manifest in the nearshore, however, we should consider where they come from.

Local Versus Remote Generation

Internal waves are generated throughout the world's oceans and can travel long distances from their generation points (**Figure 4**). Unlike surface-wave speeds (approximately 16 m s^{-1} for a

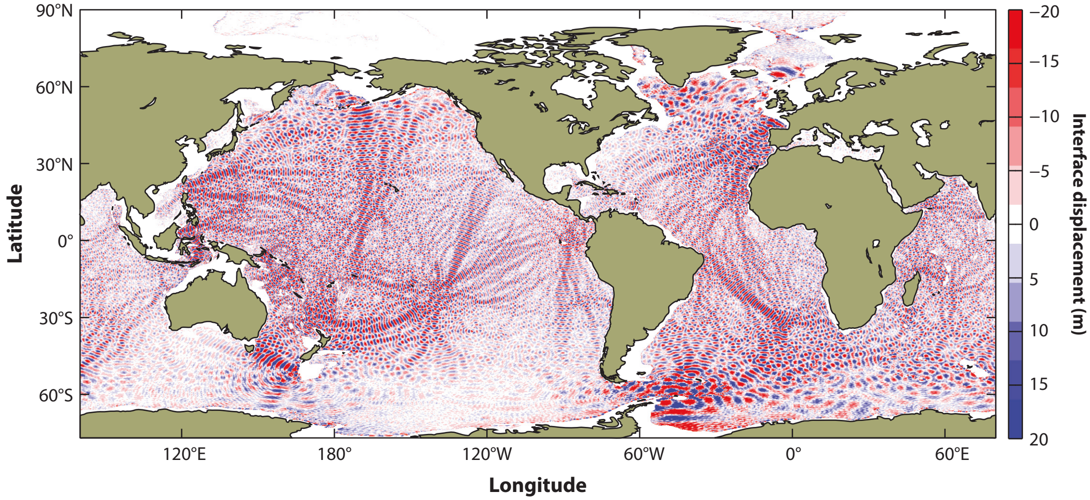

Figure 4

Global map showing the interface displacement (height) of internal-wave beams. Adapted from Simmons et al. (2004).

10-s-period swell), internal-wave propagation (approximately 0.5 m s^{-1}) is of the same order as currents caused by other phenomena (winds, tides, and mesoscale eddies) and is therefore significantly modified by changes in ambient currents and background stratification. Because of the long distances and variability in the background stratification and currents across them, the arrival of remotely generated internal waves is highly irregular and virtually impossible to predict even for internal tides, whose generation is extremely regular and predictable (Nash et al. 2012b). Background currents alter the effective propagation speed and shape of an internal wave (Dunphy & Lamb 2014, Peregrine 1976, Stastna & Lamb 2002, Stastna & Walter 2014). Changes in stratification alter the propagation speed and direction (Holloway et al. 1997). These changes alter the phasing of internal waves between generation and breaking locations such that remotely generated waves are rendered largely unpredictable in nearshore environments (Nash et al. 2012a,b). However, there are locations where observations of distinctly baroclinic motions are regular and clearly modulated by winds and the depth of the local pycnocline (the region of strongest density stratification) (Booth et al. 2012, Frieder et al. 2012, Walter et al. 2014). These waves or wave-like features are likely to be generated locally or regionally through interactions between winds and buoyant surface flows (Walter et al. 2016, Woodson et al. 2011) or in regions with steep nearshore topography similar to continental shelf breaks, such as the southern portion of Monterey Bay (Frieder et al. 2012, Walter et al. 2012) (**Figure 1**). However, local generation can also be intermittent owing to variation in local stratification and forcing mechanisms (Walter et al. 2014). Regardless of the location and mechanism of generation, internal waves have similar effects on nearshore environments, but the regularity and frequency of internal-wave events can change dramatically because of local conditions, location within an internal-wave beam (e.g., **Figure 1**), and other physical characteristics of the ocean and nearshore environment (bathymetric slope and coastline orientation).

Nonlinear Waves and Bores

As internal waves approach the coast (or continental shelf or slope; the physics are largely the same in either situation), they become increasingly nonlinear (steeper and nonsymmetric) and eventually break and dissipate (Lamb 2014). This nonlinearity results in several important changes in wave characteristics with different and potentially dramatic effects compared with assumptions derived from linear wave theory. As the total water depth decreases, the ratio of the upper and lower water depths (H_U/H_L) approaches 1, and the waves begin to feel the effects of both layers as opposed to just the surface layer in the open ocean. This effect causes the waves to slow down at the leading edge. Because the trailing edge of the wave is still moving faster, the wave steepens and increases in amplitude (**Figure 2*b***). As the wave height grows, the speed of the wave also increases as

$$c_{\mathrm{nl}} = c_1 \left[1 + \frac{a(H_{\mathrm{U}} - H_{\mathrm{L}})}{2H_{\mathrm{U}}H_{\mathrm{L}}} \right],$$

where c_{nl} is the nonlinear wave speed. Assuming that the surface-layer depth (H_U) remains constant, c_{nl} increases approximately as $a/2H_L$. As the wave becomes increasingly nonlinear, the wave orbital velocities (circular velocities associated with the movement of a wave; **Figure 2**) lose symmetry, and the wave can begin to transport fluid and associated constituents (dissolved nutrients and propagules). During this phase, it is also common for a large-period wave (internal tide) to break down into a series of rank-order nonlinear solitary waves (Helfrich & Melville 2006). Eventually, the waves become too steep, with strong shear between the layers (**Figure 2**). When the shear becomes strong enough to overcome the stabilizing effects of the density stratification, turbulence occurs. In fluid mechanics, this stability is often described using the gradient Richardson number [$Ri = N^2/(\mathrm{d}u/\mathrm{d}z)^2$], which defines the ratio of buoyancy forces to shear forces in a fluid. A flow is considered unstable and susceptible to turbulent fluctuations around $Ri < 1/4$, at which point the velocity shear can overcome the fluid's tendency to remain stratified, and mixing is likely to occur. In this situation, the internal waves may begin to shed a turbulent wake that actively mixes the water column (e.g., Woodson et al. 2011). Finally, these nonlinear waves will ultimately break, forming internal bores (or breaking waves), again similarly to a surf break on the shore (**Figure 1**). Internal bores are characterized by strong turbulence and mixing and can transport significant volumes of fluid.

Fate in the Nearshore

Not all internal waves that enter nearshore environments will necessarily form bores, and again, similarly to surface waves near shore, their behavior is dependent largely on the slope of the ocean floor in the region. If the slope is gentle, the internal waves will gradually orient along the shelf because of refraction and then transform, as described above, into internal bores, after which they rapidly dissipate. If the slope is steep, the waves will continue on their existing path and lead to isopycnal (lines of constant density) heaving with no breaking or associated turbulence. The latter situation is common in regions with steep slopes, such as Monterey Bay (**Figure 1**). Here, the incoming internal waves lead to the surface layer being displaced on the leading edge, and then a bore warm front often develops on the trailing edge as buoyant surface waters surge back to the shore (Pineda 1999, Walter et al. 2012).

How an internal wave evolves in the nearshore can be predicted using the internal Iribarren number [$I = S/(a/\lambda)^{1/2}$], which represents the ratio of the bathymetric slope, S, to the internal-wave slope, a/λ (Arthur & Fringer 2014). At low values, the internal wave evolves similarly to a surface wave on a gently sloping sandy beach, as described in the previous section (**Figures 5*a*** and **6*a***). At high values, the internal wave does not break at all and appears similarly to a wave on the edge of a sea wall or bathtub (**Figures 5*b*** and **6*b***). The form of the internal wave will ultimately determine what is transported (deeper waters for low Iribarren numbers or gentle slopes) and when (on the rising wave front). For large Iribarren numbers, surface waters are transported rapidly on the falling wave.

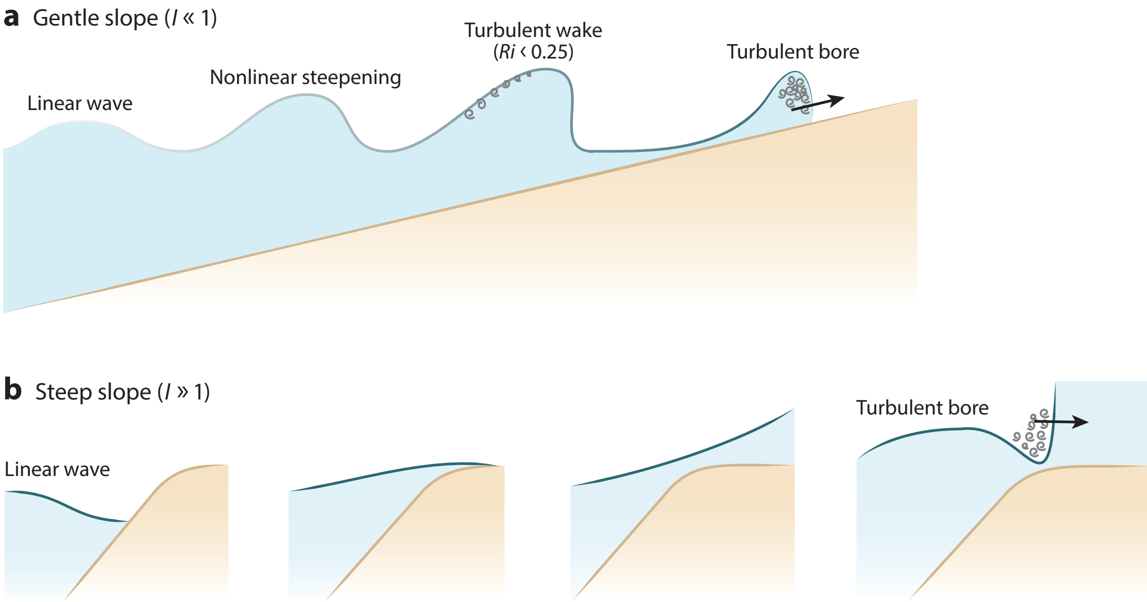

Figure 5

Schematic of nonlinear wave evolution in shallow water for (*a*) a gentle slope [$I = S/(a/\lambda)^{1/2} \ll 1$] and (*b*) a steep slope ($I \gg 1$).

Nearshore Internal-Wave Commonalities

A recurring theme throughout this section is the unpredictability and modulation of internal waves by other physical processes (Nash et al. 2012b, Walter et al. 2014). The velocities associated with internal waves (wave-induced and propagation speeds) in nearshore environments are typically on the order of 0.05–0.2 m s^{-1}, values that are of the same magnitude as the common major drivers of nearshore circulation, namely tidal currents and winds. For this reason, it is rare that any two internal waves evolve in the same fashion or occur at regular intervals despite their generation by regular, highly predictable phenomena (tides). Consequently, it is important to pick out particular commonalities of the impacts of internal waves on nearshore ecosystems. In the remainder of this review, I focus on two primary effects of internal waves that occur regardless of their generation location or evolutionary pathway:

1. Internal waves rapidly change the nearshore environment. As internal waves enter the nearshore, they bring deeper offshore waters closer to the surface and into these environments, resulting in a decrease in temperature, a decrease in dissolved oxygen content, an increase in dissolved nutrients, an increase in the concentration of CO_2 (decreased pH), and an increase in other propagules or resources (larvae and zooplankton). These changes can be severe in magnitude and greater than seasonal environmental changes despite occurring over only a few hours.
2. Internal waves bring increased energy and turbulence into the nearshore. As internal waves break, the increased turbulence and associated mixing act to remove nearshore stratification and can resuspend particulate matter on the ocean floor. The intense mixing enables the surface and deeper waters to mix, which, depending on the circumstances, can either increase or decrease residence times for propagules (gametes, larvae, and food resources) and

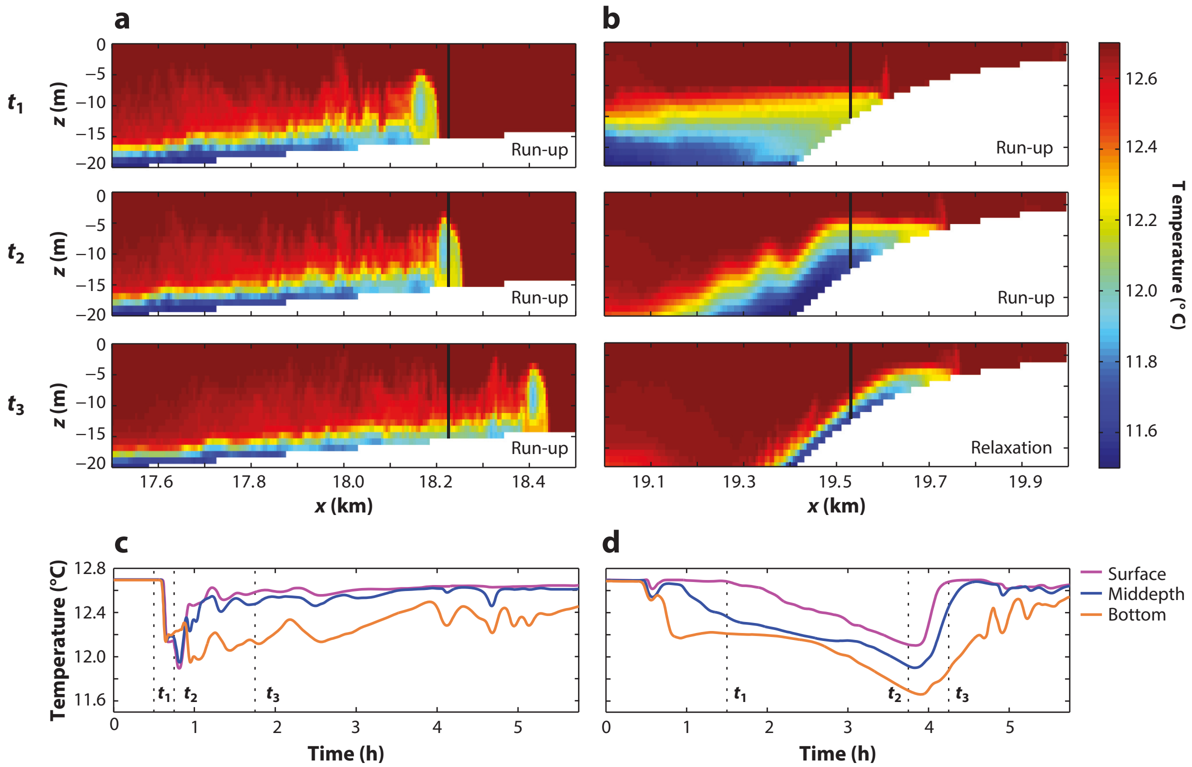

Figure 6

(*a*,*b*) Examples of internal-wave evolution in the nearshore for a gentle slope (panel *a*) and a steep slope (panel *b*). (*c*,*d*) The temperatures measured at the black lines in panels a and b, respectively, at the surface, at middepth, and near the bottom. The vertical dashed lines show the times of the contour plots in panels *a* and *b*. Adapted from Walter et al. (2012).

dissolved constituents (nutrients, oxygen, and CO_2) in the nearshore. Increased residence times allow for more efficient uptake by nearshore plants and animals.

IMPACTS ON NEARSHORE ECOSYSTEM FUNCTION

Internal waves have a wide variety of often counteracting consequences in nearshore ecosystems. For example, internal waves can cause events that lead to hypoxia or ocean acidification exposure but can also modulate large-scale climate extremes. In this section, I discuss some of the more dramatic effects of internal waves on nearshore ecosystems, working from the two main effects outlined above (transport of deep water and increased mixing).

Exposure to Extreme Events

As nonlinear internal waves enter nearshore environments, they bring with them cold, deep offshore waters. These deeper waters are typically low in dissolved oxygen (normally ~8 mg L^{-1}) and enriched in CO_2 (normally ~400 ppm in surface waters with a pH_T of ~8.1). Dissolved oxygen and pH levels can consequently be extremely low (less than 2 mg L^{-1} and 7.6 pH_T, respectively), creating a short-term stress event for nearshore organisms that can last from a few minutes to a few days, again depending on local conditions (Frieder et al. 2012, Hofmann et al. 2011). Unlike larger-scale climate change events, these exposure events have a rapid onset and short duration, which may be more reflective of many early studies of the effects of climate change that used short periods (less than 24 h) of exposure to projected future environmental conditions. Isolated internal waves may therefore increase the susceptibility of nearshore ecosystems to hypoxia and ocean acidification by creating more rapid changes in ambient temperature, oxygen, and CO_2 levels than organisms are accustomed to.

The length and magnitude of each exposure are dependent on transport and mixing: The amount and properties of the fluid transported by the wave determine the magnitude of the exposure event, and the turbulent mixing that occurs with surface waters and the rate at which the deeper waters subside determine the length of the event. These factors are in turn affected by offshore conditions (Walter et al. 2014) and local bathymetric complexity (Leary et al. 2017). For example, highly rugose bathymetry can trap deeper waters within the nearshore, creating exposure hot spots (Leary et al. 2017). Consequently, the characteristic exposure caused by internal waves is likely to be highly specific to a particular locale. However, we can draw a few general rules of thumb. First, bathymetric complexity is likely to prolong extreme events (Leary et al. 2017). Second, the magnitude of an event is determined by its proximity to deeper oceanic waters (e.g., because of upwelling). Third, the mixing available is determined by the difference in wave velocities and densities between surface and deeper waters (e.g., the gradient Richardson number). Regardless of the exposure length for a particular locale, determining the response of organisms to short-term exposure associated with internal waves will help us understand how nearshore ecosystems that are affected by internal waves will respond to ongoing climate change.

Many organisms can withstand short-term exposure to low-dissolved-oxygen and low-pH conditions but not longer exposures of more than approximately 24 h (Kroeker et al. 2010). Therefore, understanding how exposure length is set by internal-wave interactions with other forcing mechanisms may be critical to predicting how nearshore organisms will be affected by stressors related to climate change. Additionally, research on multiple stressors is beginning to move in the direction of variable-exposure (as opposed to constant-exposure) scenarios, which may better reflect the variability in these systems (Frieder et al. 2014). In many cases, the dominant variability is at tidal periods (~12 h) associated with internal waves. Therefore, more studies that highlight this short-term variability (e.g., Frieder et al. 2014) for regions exposed to internal waves are needed.

Climate Variability

The transport of deeper ocean waters into nearshore environments can also modulate exposure to extreme climate events. An excellent example of this phenomenon comes from work around Isla Natividad in Baja California Sur, Mexico. In this region, a team from Comunidad y Bioversidad, Stanford University, and the University of Georgia, in partnership with the local fishing cooperative, has monitored ocean conditions at a water depth of approximately 15 m for almost five years on each side of the island (**Figure 7**). The two sites are less than 1 km apart and largely subject to the same large-scale and regional climate variability. However, the northeast site, Punta Prieta, is generally warmer and commonly exposed to regular internal-wave-like features that bring cooler waters into the nearshore. By contrast, the southwest site, Morro Prieto, is generally cooler and has comparatively less internal-wave activity. The result of this contrast is that Morro Prieto is much more sensitive than Punta Prieta to large-scale climate forcing such as El Niño–Southern Oscillation. A good analogy of the conditions at the two sites comes from a comparison with typical weather patterns. The Morro Prieto reef is typical of a temperate continental weather

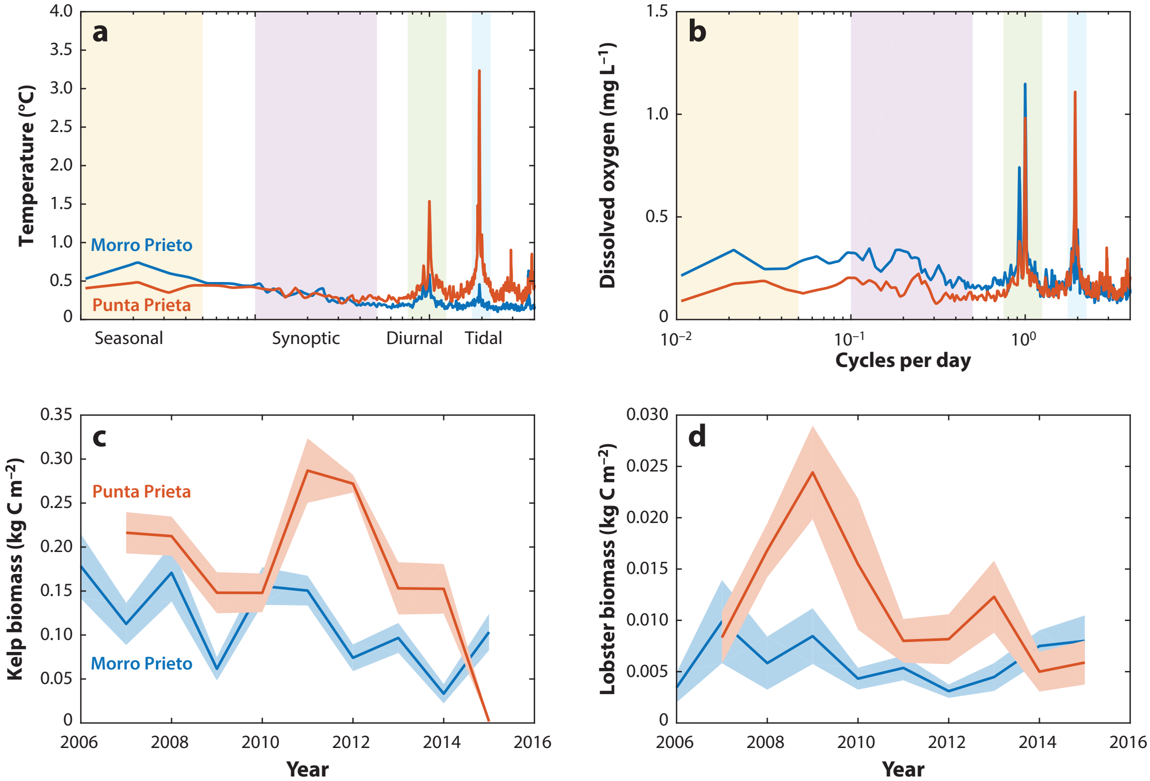

Figure 7

Comparison of (*a*) temperature and (*b*) dissolved oxygen variability, along with the biomass density of (*c*) kelp (*Macrocystis pyrifera*) and (*d*) lobster (*Panuliris interruptus*) on two sides of Isla Natividad: Morro Prieto (southwest) and Punta Prieta (northeast). Punta Prieta is strongly influenced by internal motions, whereas Morro Prieto is not.

pattern, with long, cold winters followed by long, hot summers. The Punta Prieta reef is typical of a temperate coastal weather pattern (such as that of coastal California or the Mediterranean), with warm days and cool nights (e.g., more variability at semidiurnal and diurnal periods) but less seasonal variation. The regular internal-wave activity acts as a modulator of extreme large-scale climate events and the resulting response to them (Pineda et al. 2013). Similar high-frequency variability has been observed in other regions of the California Current (Frieder et al. 2012) and elsewhere around the world (Hofmann et al. 2011, Leichter et al. 2005, Smith et al. 2016, Wolanski & Delesalle 1995). Whether these fluctuations act to exacerbate or mitigate long-term responses of nearshore organisms will play an important role in ecosystem responses to changing climate (Oliver & Palumbi 2011, Palumbi et al. 2014, Wall et al. 2015).

By contrast, internal waves could also exacerbate large-scale climate events if they act synergistically. For example, internal waves could prolong exposure by continually resupplying low-dissolved-oxygen water during a hypoxic event, thus not allowing local primary production (and consequent oxygen generation) to replenish the low-oxygen waters. Internal waves can also increase the exposure of nearshore ecosystems to human impacts by transporting outfall waste or pollution into these regions (Boehm et al. 2002, Omand et al. 2011). Again, the impacts of internal waves are likely to be locale specific. However, general conclusions can be drawn to at least generate initial hypotheses about the impacts of internal waves in these regions.

Nutrient and Food Supply

As nonlinear internal waves and associated bores arrive into nearshore ecosystems, they bring with them deeper offshore waters. These offshore waters are generally replete with nutrients that are largely absent from surface waters. In addition, internal waves and bores move the pycnocline (the boundary between the surface and deeper waters) vertically; near the coast, the intersection of the pycnocline with the bottom also moves horizontally. The pycnocline is a region of enhanced primary and secondary productivity. As the pycnocline impinges into the nearshore because of internal waves, high concentrations of phytoplankton and zooplankton can also be transported into the nearshore. These internal-wave subsidies are important resources for many nearshore ecosystems, including pelagic zones (Haapala 1994; Holligan et al. 1985; Sharples et al. 2007, 2009), kelp forests (McPhee-Shaw et al. 2007, Shea & Broenkow 1982, Zimmerman & Kremer 1984), and coral reefs (Jantzen et al. 2013, Leichter et al. 1996, Monismith et al. 2010, Smith et al. 2004, Thompson & Golding 1981).

Transport of nutrients and food into nearshore ecosystems, however, may be short lived because the internal bores propagate shoreward and then retreat at relatively short timescales. Uptake of nutrients or food reserves must occur rapidly, on the order of a few minutes to a few hours. Many species of marine algae have adapted abilities to rapidly assimilate nutrients (Zimmerman & Kremer 1986). However, the dynamics of the internal-wave field may enhance retention within the nearshore, either by mixing with surface waters so that the denser, nutrient-rich water does not retreat to deeper areas or through sustained and repeated internal-wave exposure. Both situations could significantly increase the time for nutrient uptake and grazing.

Larval Transport and Delivery

The transport of larvae to nearshore environments is perhaps the most studied ecological impact of internal waves (Ladah et al. 2005; Pineda 1991, 1999; Shanks 1983). Consequently, larval transport probably suffers from the biggest misinterpretations of the effects of internal waves on nearshore ecosystems. First and foremost, internal waves do not transport fluid or any propagules embedded within the fluid unless they are highly nonlinear or have become propagating bores. For this reason, it is generally unlikely that internal waves are responsible for extended transport across the continental shelf; more likely is that they provide a final push into the nearshore after larvae have been transported through other processes. Regardless, internal waves play significant roles in defining recruitment and connectivity patterns for a wide variety of species in the marine environment (D'Alessandro et al. 2007, Kingsford & Choat 1986, Pineda 1994, Shanks 1988).

Recruitment of larvae to adult habitats by internal waves occurs largely when a propagating bore front accumulates larvae and transports them into adult habitats. Smaller larvae, including many invertebrate species, are unable to swim against the propagating front, are kept suspended by the increased turbulence in the bore, and are therefore swept along with it (Ladah et al. 2005, Pineda 1994). Larger larvae, such as late-stage juvenile fishes, may swim with the wave and effectively surf into a preferred adult habitat (D'Alessandro et al. 2007, Kingsford & Choat 1986, McManus et al. 2008). As the bore moves shoreward, it loses energy, and larvae are then deposited in preferred nearshore habitats.

Persistent internal-wave features can set large-scale recruitment patterns across multiple taxa, with the aggregative process of fronts and clines combined with shoreward transport by internal waves leading to regions of high recruitment (Broitman et al. 2008, Ladah et al. 2005, Woodson et al. 2012). High recruitment can in turn be reflected as regions of high productivity and ecological resilience (Broitman et al. 2008, Woodson et al. 2012).

Predator-Prey Dynamics

A less studied phenomenon associated with internal waves is their role in mediating predator-prey dynamics (Embling et al. 2013, Greer et al. 2014, Kaartvedt et al. 2012). Revisiting our two primary effects of internal waves on the physical conditions in nearshore environments leads to several potential impacts on predator-prey dynamics, namely increased encounter rates in the plankton (mixing of surface and deep waters that causes predator-prey overlap), mediation of behavioral responses resulting from stressful conditions (low-dissolved-oxygen, low-pH waters), and disruption of suitable foraging conditions resulting from sediment resuspension.

As internal waves enter nearshore environments, they can mix surface and deeper waters that contain different levels of prey and predators. In these cases, the overlap (especially in planktonic ecosystems) can greatly increase the encounter rates between predators and prey by increasing habitat overlap (Embling et al. 2013, Greer et al. 2014, Woodson et al. 2007). In addition, trailing turbulent wakes from unstable nonlinear waves can increase turbulence and encounter rates up to a critical level of turbulence beyond which the turbulence prohibits prey capture (MacKenzie & Kiørboe 2000, MacKenzie & Leggett 1991, Rothschild & Osborn 1988, Woodson et al. 2011). The effects of internal waves on encounter rates and prey consumption are likely to be ephemeral, lasting only as long as the temporal duration of the wave ($\sim T$). However, in many regions located within internal-wave beams (**Figure 4**), or with locally generated internal-wave-like features, the repeated occurrence may act to increase overall ecosystem productivity significantly. For a scaling estimate, consider internal waves of $\lambda = 200$ m (20-min period) that effectively increase encounter rates by a factor of 10 (Greer et al. 2014, Rothschild & Osborn 1988). If these waves occur as rank-ordered packets (a series of internal waves of decreasing amplitude) of 3–6 waves and are generated on a tidal cycle, then prey consumption is effectively doubled for $\sim$1 h every tidal cycle, resulting in an overall increase in productivity of $\sim$75% that is largely unaccounted for in ecosystem models, similar to the effects of fronts at longer timescales (Woodson & Litvin 2015). However, the effects of increased predator-prey overlap and turbulence caused by internal waves on prey consumption are likely to be nonlinear and play out in unsuspecting ways. Internal waves can also cause behavioral redistributions of prey and predators with similar outcomes to purely advective (vertical-only) changes (Kaartvedt et al. 2012).

Another aspect of internal waves mediating predator-prey dynamics arises when internal waves bring low-oxygen waters into the nearshore (Frieder et al. 2012, Walter et al. 2014). Low oxygen concentrations can lead to reduced metabolism and affect the abilities of prey to avoid predators (or, conversely, the abilities of predators to capture prey). The relative outcome of the predator-prey dynamic is determined by the relative sensitivity and acclimation rates of the prey to the predator (Breitburg 2002, Holeton 1980). Again, the effects of internal waves on prey consumption are not likely to play a major role in large-scale ecosystem dynamics unless they are regular features of the surrounding physical environment, in which case local generation of these motions will likely play a more important role than sporadic waves from remote locations (Nash et al. 2012b).

Broadcast Spawning and Fertilization

The use of particular spawning sites by large fishes has also been linked to internal-wave activity. Internal waves act to temporarily increase local turbulence, which enhances fertilization rates

(Crimaldi 2012, Crimaldi & Browning 2004, Crimaldi & Zimmer 2014, Ezer et al. 2011, Woodson et al. 2011). For successful fertilization, eggs and sperm must come into contact with each other, a process that is greatly enhanced by turbulent stirring (Crimaldi & Browning 2004). Nonlinear internal waves (and bores) often have trailing turbulent wakes with turbulence levels 10–100 times higher than ambient levels that can persist for several hours after internal-wave passage (Alford 2003, Walter et al. 2012, Woodson et al. 2011). These elevated turbulence levels could enhance the fertilization rates of broadcast spawners 10-fold (Crimaldi & Zimmer 2014). Such immediate impacts of internal waves on fertilization success may explain why many invertebrate species time spawning events to coincide with periods during the lunar cycle when tidal and internal motions are likely to be stronger (Babcock et al. 1986, Ezer et al. 2011, Harrison et al. 1984, Heyman et al. 2005, Paris et al. 2005, Samoilys 1997). This would require local generation of internal motion, or spawning locations within internal-wave beams, because it would be highly unlikely that remotely generated waves would arrive in phase with local lunar cycles (Nash et al. 2012b).

ROLE IN A CHANGING CLIMATE

The Internal-Wave Field

Future climate scenarios suggest that surface waters will warm by up to 4°C by 2100. Stratification is also expected to increase because surface waters warm more quickly than deeper ocean waters. Increased stratification will require more energy input into internal-wave formation, resulting in weaker, more stable waves (e.g., with less propensity for instabilities and turbulent mixing) if other factors remain constant. Such changes in background density fields will thus likely have a substantial effect on global-scale energy and heat budgets. In addition, the effects of internal waves in nearshore environments will also change. As coastal ecosystems become more stratified, they will become more stable to perturbations from internal waves. As stratification increases, and assuming other characteristics (λ and c) of a particular internal wave stay the same, the wave will be less likely to generate significant mixing because stratification acts to suppress turbulence and vertical motions. Changes in the amount of mixing could have significant effects on several aspects of internal-wave impacts in nearshore ecosystems. Regardless, how the global internal-wave field is affected by global climate change is a relative unknown and an important topic for future research, given the feedback loop between internal-wave-driven mixing and ocean circulation.

Nutrient Supply

As stratification increases, internal waves are likely to become smaller if the energy input into the baroclinic mode remains constant (as occurs during topographic generation of internal waves). Smaller internal waves are less likely to reach nearshore environments and will likely have weaker (if any) turbulence associated with them. Consequently, the total nutrient flux and the retention time for high-nutrient water could be reduced, and the benefits of mixing with surface waters to provide a persistent nutrient pump may disappear. In regions where the nutrient supply from internal waves is a large component of the total supply, such as many tropical coral reefs, this effect could be massive and lead to large-scale die-offs (Leichter et al. 1998).

Extreme Events

Internal waves often play competing roles when considering exposure to extreme events such as warming, hypoxia, or ocean acidification (Booth et al. 2012, Wall et al. 2015). In tropical regions, where the primary stresses associated with climate change are extreme warming events, internal waves can mitigate stress responses by providing either a refuge from heat stress or additional energy needed for metabolism during stress periods (Leichter et al. 1998, 2005; Wall et al. 2015). In temperate habitats, by contrast, internal waves in the nearshore cause periods of exposure to stressful conditions (Frieder et al. 2012, Hofmann et al. 2011, Walter et al. 2012). In tropical regions, the pulsing of subthermocline water may reverse effects as deeper waters become more hypoxic and acidic. Therefore, refuges provided now by internal waves impinging on coral reefs may turn into a double hit in future climate scenarios.

A central question with regard to internal waves and extreme events or climate change is whether high environmental variability caused by internal waves acts to increase the resilience of animals over ecological or evolutionary timescales or actually reduces resilience to long-term exposure. Animals in regions of high temperature variability may be more resilient to long-term increases in temperature. However, these assertions assume that the high variability is maintained in future ocean scenarios. If the internal-wave field is reduced or absent, such animals would lose the temporary reprieve from the extreme event, a condition to which they are not acclimated.

Turbulence, Spawning, and Predator-Prey Dynamics

Reduced turbulence in more stratified waters will likely lower overall fertilization success (Crimaldi & Browning 2004, Crimaldi & Zimmer 2014). Changes in stratification and thermocline depth could also change the timing and location of internal-wave breaking. In this case, spawning aggregations may be mismatched with internal-wave-associated turbulence that enhances fertilization, reducing recruitment and population viability. Similarly, reduced turbulence could affect predator-prey dynamics. If internal-wave-generated turbulence was previously high, predation rates could increase; if this turbulence was moderate, predation rates could decrease. How these effects play out in a future climate will be important to the function of marine ecosystems but often nonintuitive, thus requiring additional investigation.

WHERE DO WE GO FROM HERE?

The effects of internal waves on nearshore ecosystems will likely change in future climate scenarios. However, these effects will be difficult, if not impossible, to predict until we understand how internal waves themselves will respond to changes in stratification, wind forcing, and thermocline depth. Regardless, some general, testable hypotheses can be formulated from our current understanding of internal-wave dynamics and expected climate change outcomes: (*a*) Reduced mixing resulting from increased stratification will prolong exposure to extreme hypoxic or acidification events; (*b*) nutrient and food supplies will be reduced in nearshore ecosystems because of smaller-amplitude internal waves with less overall transport and mixing; (*c*) reduced turbulence could have large effects on predation rates in the plankton, especially for critical life stages such as larval fishes; and (*d*) reduced mixing and disruption of timing between internal-wave activity and spawning events could reduce fertilization rates for mass broadcast spawners. Each of these hypotheses is testable now using common techniques or outplant experiments that compare sites along an internal-wave activity gradient (C.A. Boch, F. Micheli, C.B. Woodson, M. Al-Najjar, J. Beers, et al., manuscript in review).

The fate of internal waves and the intricacies of their effects on nearshore ecosystems are a growing area of investigation in marine science. Although it is clear what the first-order effects of internal waves in coastal systems are—namely increased turbulence and transport of deeper waters that can be replete with nutrients, food, and larvae (as well as CO_2, and depleted in O_2)—how these effects play out in complex coastal systems is not clear and will be sensitive to the frequency and duration of internal-wave events. Nevertheless, there are regions where the internal-wave activity is significantly higher than it is elsewhere, which could lead to regional-scale ecosystem patterns similar to the impacts of fronts (Woodson et al. 2012). Determining how these regions, which can be more or less susceptible to climate factors, will respond to global climate change will likely provide key insights into the potential for climate refuges or hot spots in the future. Regardless, it is becoming clear that internal waves may modulate nearshore ecosystem patterns as strongly as their surface-wave counterparts (Blanchette 1997, Paine 1974, Raimondi 1990, Underwood & Jernakoff 1984).

SUMMARY POINTS

1. Internal waves are common features of nearshore ecosystems.
2. Internal waves in the nearshore can originate locally or arrive from far away.
3. Internal waves cause two main environmental effects on nearshore ecosystems: transport of deeper waters and enhanced turbulence and mixing.
4. Transport of deeper waters can either cause or alleviate exposure to extremes in temperature, dissolved oxygen, or pH.
5. Transport of deeper waters can also provide nutrients and subsidies to resource-depleted ecosystems such as coral reefs.
6. Enhanced turbulence can increase the net flux of nutrients, increase predation rates, and increase fertilization rates for broadcast spawners.
7. Internal waves can be important, if not primary, drivers of function in nearshore ecosystems.
8. How internal waves change in future climate scenarios may determine the fate of vulnerable coastal habitats.

FUTURE ISSUES

1. The role internal waves play in vulnerable coastal ecosystems relative to other processes needs to be better understood.
2. The effects of internal waves on exposure to extreme events for a diverse array of organisms should be quantified.
3. How internal-wave dynamics will change in a future ocean requires further study.
4. The degree of enhancement of important ecological rates (predation and fertilization) resulting from regular internal waves needs to be determined.
5. The role of internal waves in structuring ecosystems needs to be evaluated.

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Errata

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