

# Ontogeny of critical swimming speeds for larval and pelagic juvenile rockfishes (*Sebastes* spp., family Scorpaenidae)

Neosha S Kashef<sup>1,2,\*</sup>, Susan M. Sogard<sup>2</sup>, Rebecca Fisher<sup>2,3</sup>, John L. Largier<sup>4</sup>

<sup>1</sup>Moss Landing Marine Laboratories, 8272 Moss Landing Rd., Moss Landing, California 95039, USA

<sup>2</sup>Southwest Fisheries Science Center, National Marine Fisheries Service, 110 Shaffer Rd., Santa Cruz, California 95060, USA

<sup>3</sup>Australian Institute of Marine Science, The UWA Oceans Institute, 35 Stirling Highway, Crawley, Western Australia 6009, Australia

<sup>4</sup>Bodega Marine Laboratory, University of California Davis, Bodega Bay, California 94923, USA

**ABSTRACT:** Understanding the mechanisms that affect larval dispersal is critical to management of marine populations. Rockfishes *Sebastes* spp. do not settle to benthic habitats immediately after metamorphosis, but instead remain in the water column for weeks to months. Movements of larvae and pelagic juveniles during their months at sea are largely unknown. It is traditionally thought that young rockfishes are planktonic, moving at the mercy of ocean currents, but this assumption is unverified. In this study, swimming capabilities (critical speed) of larval and pelagic juvenile stages of 6 rockfish species (blue [*S. mystinus*], yellowtail [*S. flavidus*], brown [*S. auriculatus*], kelp [*S. atrovirens*], gopher [*S. carnatus*], and splitnose [*S. diploproa*]) were evaluated to determine their ability to behaviorally influence dispersal. Rockfish larvae have critical speeds of 0.5 to 1.8 cm s<sup>-1</sup> (1 to 3 body lengths per second [bl s<sup>-1</sup>]) at parturition, whereas newly settled juveniles are capable of swimming 8.6 to 53.5 cm s<sup>-1</sup> (5 to 9 bl s<sup>-1</sup>). Swimming ability increases throughout ontogeny and postflexion rockfishes can swim faster than typical water motions in their natural habitat (i.e. mean ocean currents off central California). Critical speeds for *Sebastes* spp. are substantially lower than those for larvae and juveniles of tropical species at similar body sizes. Rockfishes, however, have swimming speeds at settlement comparable to some tropical species, as rockfishes settle at larger sizes. The increasing ability of rockfishes to outswim currents during their pelagic phase (acting as nekton rather than plankton) may promote individual survival as well as enhance retention and/or long-distance dispersal — thus swimming has important implications for population connectivity and sustainability.

**KEY WORDS:** Dispersal · *Sebastes* spp. · Rockfish · Larvae · Swimming

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Effective management of marine ecosystems requires an understanding of the spatial structure of population dynamics. Integral to determination of population persistence is the knowledge of whether individuals are retained in their natal population or received from another geographic region. Much remains unknown about the extent of movement of marine organisms with pelagic early life stages be-

cause larvae and juveniles are challenging to study in the open ocean. Dispersal in rockfishes *Sebastes* spp., viviparous temperate reef fishes with a bipartite life history (pelagic early life stages and benthic adults), is likely dependent on movement during pelagic stages (Larson 1980a, Lea et al. 1999, Jorgensen et al. 2006). To inform their conservation, a greater understanding of population connectivity is necessary — which in turn directs attention to larval and pelagic juvenile dispersal by currents and swimming.

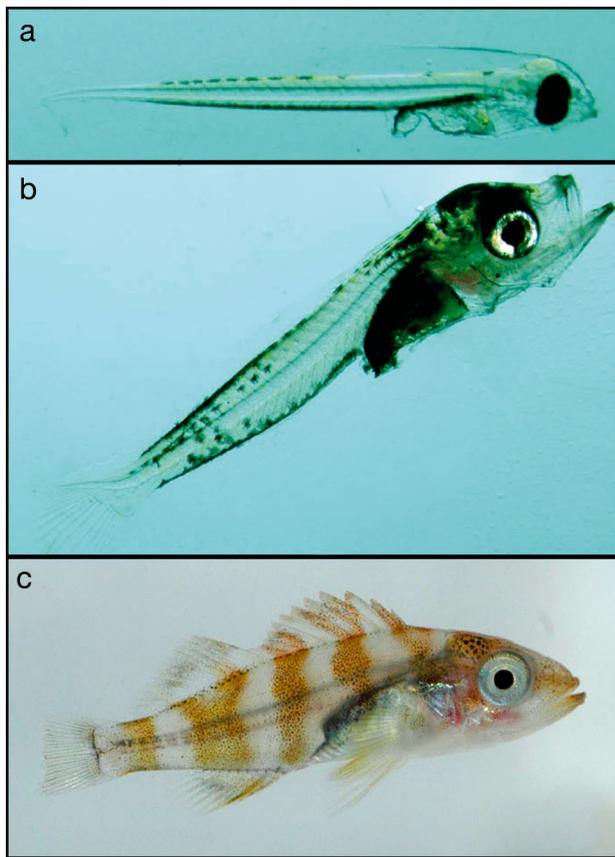


Fig. 1. (a) Kelp rockfish larva at parturition, lacking fully developed fins (5 mm total length [TL]); (b) brown rockfish larva at flexion, showing caudal fin rays forming and development of more muscle mass (9 mm TL); (c) kelp rockfish pelagic juvenile at settlement stage, with fin rays and resembling a miniature adult (20 mm TL)

All *Sebastes* spp. larvae have similar morphology and at parturition possess pectoral fins and an undifferentiated finfold (Moser et al. 1977, Kendall & Lenarz 1987, Fig. 1a). Most species parturite once

annually, typically in winter or spring (Love et al. 2002). Within 1 to 2 mo and at a size of 7 to 8 mm total length (TL), larvae undergo notochord flexion and caudal-fin formation, which is completed at 9 to 10 mm TL (Fig. 1b). At the completion of metamorphosis, fin ray development is complete and the resulting pelagic juveniles resemble miniature adults (Fig. 1c). The pelagic stage lasts 60 to 365 d, depending on species, and in central California most rockfish species settle to structure as 15 to 60 mm TL juveniles in spring and summer (Table 1)—seasons characterized by wind-driven upwelling (Garcia-Reyes & Largier 2012).

Early life stages of rockfishes are patchily distributed over the continental shelf and slope (Love et al. 2002), with higher densities found near upwelling fronts (Lenarz et al. 1991, Bjorkstedt et al. 2002, Woodson et al. 2012). Larval stages are typically distributed throughout the upper mixed layer above the thermocline (Ahlstrom 1959, Boehlert et al. 1985, Moser & Boehlert 1991) or pycnocline (Sakuma et al. 1999), where a mean offshore Ekman transport is observed in the upwelling season (e.g. Dever et al. 2006). Pelagic juveniles of most species are distributed more broadly in the water column, from the surface to 250 m (Lenarz et al. 1991, Love et al. 2002, Ross & Larson 2003).

It has traditionally been assumed that small young fishes are planktonic drifters, at the mercy of oceanic currents, and have little or no behavioral influence on their dispersal. In recent decades this view has been challenged, recognizing the swimming ability of some small young fishes and the importance of even weak swimming of invertebrate larvae in asserting control on dispersal in upwelling areas (Norcross & Shaw 1984, Frank et al. 1993, Fisher et al. 2000, 2005, Sponaugle et al. 2002, Leis 2006, Morgan et al. 2009). Simulations suggest larval behavior can

Table 1. Summary of rockfish early life history data: reproductive timing, pelagic duration, and size and swimming capability at parturition and settlement

| Rockfish species | Parturition season      | Pelagic duration (d) | Avg. size at parturition (TL, mm) | Avg. $U_{crit}$ at parturition ( $\text{cm s}^{-h}$ ) | Size at settlement (TL, mm) | $U_{crit}$ at settlement ( $\text{cm s}^{-h}$ ) |
|------------------|-------------------------|----------------------|-----------------------------------|---|-----------------------------|---|
| Blue             | Winter <sup>a</sup>     | 125 <sup>b</sup>     | 5.06 <sup>f</sup>                 | 0.76  | 30–53 <sup>h</sup>          | –   |
| Brown            | Spring <sup>a</sup>     | 75–90 <sup>a</sup>   | 6.25 <sup>f</sup>                 | 1.36  | 18–37 <sup>i</sup>          | 12.8–30.9                                       |
| Gopher           | Spring <sup>a</sup>     | 60–90 <sup>c</sup>   | 5.60 <sup>f</sup>                 | 1.12  | 15–40 <sup>h,j</sup>        | 8.6–24.8  |
| Kelp             | Spring <sup>a</sup>     | 60–90 <sup>d</sup>   | 5.38 <sup>f</sup>                 | 0.77  | 16–40 <sup>h,j</sup>        | 9.4–27.6  |
| Splitnose        | Year-round <sup>a</sup> | 365 <sup>e</sup>     | 4.4–5.2 <sup>g</sup>              | –   | 19–40 <sup>j,e</sup>        | 16.9–31.4                                       |
| Yellowtail       | Winter <sup>a</sup>     | 105–120 <sup>a</sup> | 4.94 <sup>f</sup>                 | 0.87  | 28–60 <sup>h,j</sup>        | 26.7–53.5                                       |

<sup>a</sup>Love et al. (2002); <sup>b</sup>Laidig (2010); <sup>c</sup>Larson (1980b); <sup>d</sup>Gilbert (2000); <sup>e</sup>Boehlert (1977); <sup>f</sup>present study; <sup>g</sup>Moser (1996); <sup>h</sup>Ander-son (1983); <sup>i</sup>West et al. (1994); <sup>j</sup>Ammann (2004)

considerably impact dispersal (Wolanski et al. 1997, Armsworth 2001, Drake et al. 2011); however, most contemporary reef management models continue to assume passive dispersal of larvae by ocean currents (Leis 2007). As rockfishes have well developed fins and are at a significant size at the conclusion of the pelagic stage, it is plausible that they are able to swim at ecologically relevant speeds by the time they reach settlement (first arrival to structure). A greater understanding of swimming behavior is clearly necessary to determine when and where larvae and pelagic juveniles may influence their own dispersal.

In central California, rockfish larvae released in the winter usually encounter nutrient-poor conditions with low plankton densities, and may be subject to downwelling events and onshore surface transport (Skogsberg 1936). Those released in the spring encounter offshore surface transport associated with wind-driven upwelling and nutrient-rich waters with higher concentrations of plankton. Populations that parturite in winter have a longer pelagic larval duration (PLD inclusive of both the larval and early juvenile pelagic stages) than those released in the spring, thus increasing their potential for transport. Rockfishes that parturite in these 2 seasons employ different reproductive strategies, with a trade-off between larval size and larval condition (Fisher et al. 2007, Sogard et al. 2008). Larvae released in the winter (e.g. subgenus *Sebastosomus*) have comparably large oil globules and small body size, whereas those released in late spring (e.g. subgenus *Pteropodus*) have small oil globules and large body size. These contrasting strategies suggest a shift in allocation from enhanced energy reserves to increased swimming capabilities (and other traits associated with larger body size) to match the oceanographic environment encountered by larvae released in different seasons.

In this study, the ontogenetic development of swimming ability in nearshore rockfishes was examined using critical swimming speed ( $U_{crit}$ , Brett 1964) to estimate the physiological limits of prolonged swimming speed for larval and juvenile stages. We evaluated 6 rockfish species, ranging in size from 4.5 to 60 mm TL and progressing in development from newly released larvae to settled juveniles, to determine if  $U_{crit}$  increased with increasing length. These results are considered in the context of observed currents, identifying when rockfishes can swim strongly enough to overcome ocean currents, or at least to behaviorally influence their dispersal during pelagic early life stages. The efficacy of swimming in moving waters depends on speed, direction,

and persistence of swimming relative to the speed, direction and persistence of currents and the spatial extent of water masses. Persistent swimming will affect the advective component of dispersal, whereas variable swimming will affect the diffusive component of dispersal in a population (Largier 2003).

## MATERIALS AND METHODS

Gravid female rockfishes (blue *Sebastes mystinus*, brown *S. auriculatus*, yellowtail *S. flavidus*, kelp *S. atrovirens*, and gopher *S. carnatus*) were obtained via hook and line fishing in Monterey Bay, California, throughout their parturition seasons (spring or winter, Table 1). Fishes were transported in aerated coolers to an aquarium facility at the NOAA Fisheries laboratory in Santa Cruz and housed individually in 575 l flow-through tanks with constant aeration. Seawater temperature was maintained at 12°C for consistent development among broods. Fish were fed squid *Loligo opalescens* to satiation 3 times weekly.

Upon parturition, 30000 to 60000 larvae were transferred to a larval growth tank (300 l) set with low water flow (10 ml s<sup>-1</sup>) to minimize turbulence and disturbance. Larvae were fed 1000000 algae-enriched marine rotifers *Brachionus plicatilis* daily. Upon reaching 4 wk of age, their daily feeding was supplemented with 5000 HUFA-enriched *Artemia* sp. nauplii. *Nannochloropsis* sp. (5 ml) and *Isochrysis* sp. (5 ml) algae were added to each tank at feeding time to provide green-water, which both simulates their natural environment and provides a gradation of light so larvae can choose optimal exposure within the 115 cm tank water column (Muller-Feuga et al. 2007). Full spectrum fluorescent lights over the larval tanks, set to replicate the natural photoperiod at the latitude of Santa Cruz, California (36.97°N), mimicked sunlight.

High mortality rates limited the number of larvae that reached metamorphosis. As it is difficult to obtain pelagic stage rockfishes without physically compromising their swimming abilities (e.g. via damage in a trawl net), wild collections were confined to the capture of later pelagic stages with positively thigmotactic behavior. Swimming capabilities of later-stage pelagic and newly settled juvenile fishes (*Sebastes flavidus*, *S. atrovirens*, *S. auriculatus*, splitnose rockfish *S. diploproa*, *S. carnatus*) were obtained from fish collected in Monterey Bay via standard monitoring units for the recruitment of fishes (SMURFs, Ammann 2004) and dip nets in kelp

canopies. We were not able to obtain gravid female splitnose rockfish nor newly settled blue rockfish. For the other species we were able to test swimming capacity for stages ranging from parturition to settled juvenile.

For the 5 species tested as larvae, swimming trials began for each brood (larvae released by a single female) on the day after parturition and weekly thereafter. A miniature swimming flume (Fig. 2a,b) was used to estimate  $U_{crit}$  of larvae (4 to 20 mm) and a larger swimming flume (Fig. 2c) was used for pelagic juveniles (>20 mm). The smaller apparatus was based on a design by Stobutzki & Bellwood (1994) but miniaturized to be suitable for smaller fishes. The larger swim tunnel was manufactured by Loligo Systems (Model 10). The 2 flumes functioned in identical ways, with a baffle of flow straighteners preceding the swimming chamber to ensure laminar flow and mesh at the downstream end to retain fish when they could no longer swim against the flow. Flow on the smaller flume was manipulated by increasing the opening of a gate valve and on the larger flume by increasing power to a motor. Velocities in both flumes were validated using fluorescent tracer dye at low flows and a digital flow meter at higher flows.

For each trial, an individual was haphazardly selected from the rearing tank, placed in the swimming channel and allowed to acclimate for 15 min. Following acclimation, water flow was increased at intervals of 1 body length per second ( $bl\ s^{-1}$ ) every 2 min until the fish could no longer maintain its position in the channel (Fisher et al. 2000). Interaction of flow with the walls of the chamber creates boundary layers in which flow speeds are reduced; thus, trials in which fish were positioned near the walls were discarded (~5%).

Critical swimming speed was calculated with the following equation (Brett 1964):

$$U_{crit} = U_i + U_{ii}(t_i/t_{ii}) \quad (1)$$

where  $U_i$  = highest velocity maintained for the whole interval (penultimate speed),  $U_{ii}$  = velocity increment ( $1\ bl\ s^{-1}$ ),  $t_i$  = time elapsed at fatigue velocity, and  $t_{ii}$  = set time interval for each velocity increment (2 min).

We examined  $U_{crit}$  in absolute terms ( $cm\ s^{-1}$ ) to facilitate comparisons with current speeds, and in

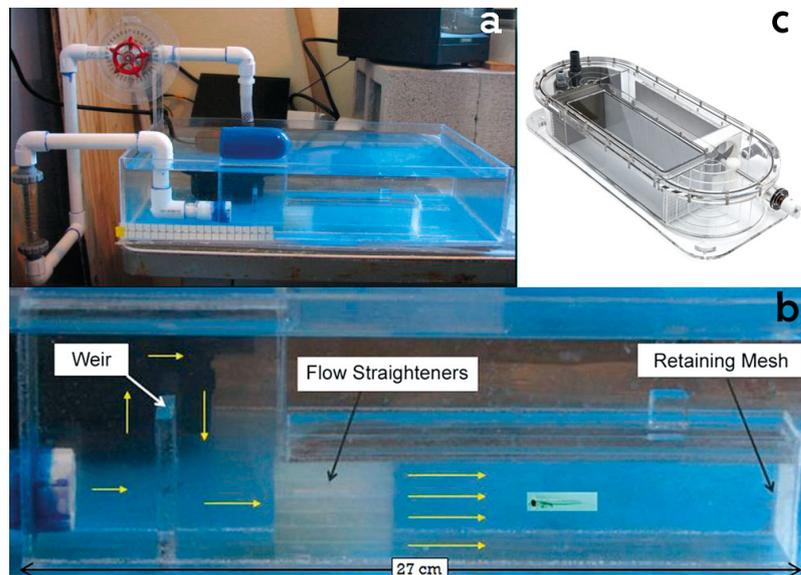


Fig. 2. Swimming apparatuses. (a) General photo of larval swimming system; (b) close-up view of miniature flume. Water enters the flume and hits a weir, which spreads the flow. The straws act as flow straighteners (creating laminar flow) and the mesh at the end retains the larva at exhaustion. (c) Larger swim tunnel (Loligo Systems model 10) used for testing  $U_{crit}$  of pelagic juvenile rockfishes. (Photo credit: LoligoSystems.com)

relative terms ( $bl\ s^{-1}$ ) to facilitate comparisons among species as standardly reported in the swimming literature (e.g. Bellwood & Fisher 2001).

At the conclusion of the swimming trial, each fish was photographed digitally using a camera mounted on a dissection microscope, then euthanized with MS-222. This procedure was repeated weekly for 10 fish from each brood. Pelagic juveniles caught in the field were brought back to the lab, allowed to acclimate in flow-through holding tanks for 24 h and then tested in the swimming flume using the same protocol as for larvae. Each fish (larva or juvenile) was tested only once.

Images were analyzed with Optimas imaging software to precisely measure TL, standard length (notochord length for larvae), and trunk width for each fish as well as oil globule volume (if present) for each larva. Linear regressions were used to examine the relationship of  $U_{crit}$  swimming ability with morphology. For all species examined, relationships of  $U_{crit}$  were strongest with TL; thus, we focused on TL for subsequent analyses. Log transformation was used to normalize the data and linearize the scaling relationship between  $U_{crit}$  and fish length, which is expected to follow a power function. ANOVAs were used to determine if  $U_{crit}$  differed among species during 3 life stages: parturition, preflexion, and postflexion.  $U_{crit}$  estimates were compared with the speed of currents

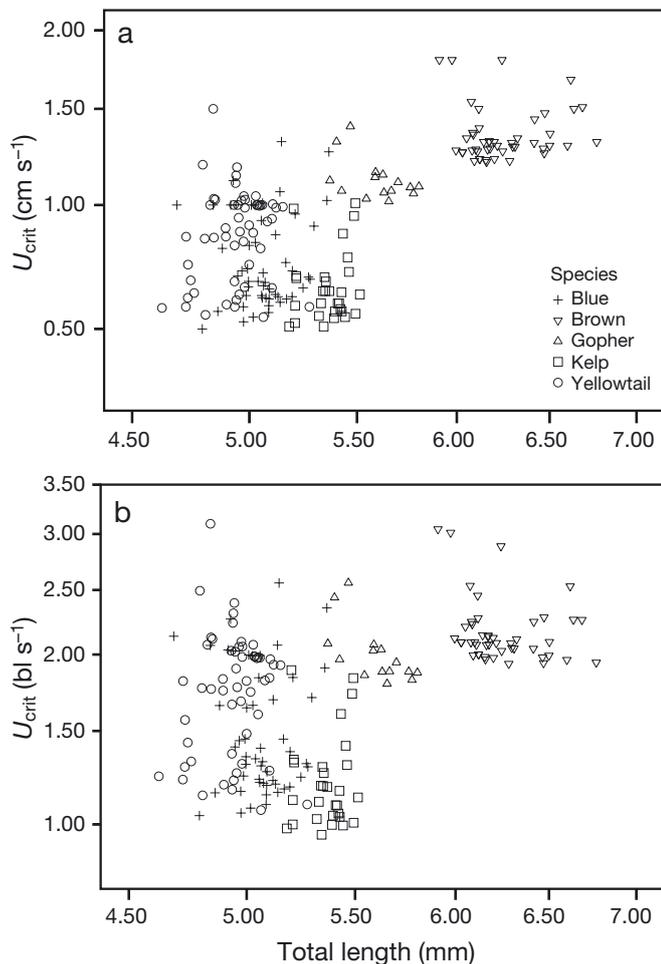


Fig. 3. Relationship between (a) absolute ( $\text{cm s}^{-1}$ ) and (b) relative ( $\text{bl s}^{-1}$ )  $U_{crit}$  and size of 5 species of larval *Sebastes* spp. at parturition. Both axes are displayed on a logarithmic scale

observed off central and northern California, both nearshore (Nickols et al. 2012) and offshore (Largier et al. 1993, Breaker & Broenkow 1994, Rosenfeld et al. 1994, Kaplan et al. 2009) to determine whether young rockfishes can swim strongly enough to behaviorally modify dispersal under natural conditions.

## RESULTS

### Larval rockfishes

At parturition, absolute  $U_{crit}$  of 5 species of *Sebastes* (blue, brown, gopher, kelp and yellowtail rockfish) ranged between 0.5 to  $1.8 \text{ cm s}^{-1}$  with high  $U_{crit}$  variability for a given length (Fig. 3a). Absolute  $U_{crit}$  varied significantly among species at parturition (ANOVA,  $F_{4,189} = 87.6$ ,  $p < 0.001$ ). Brown and gopher

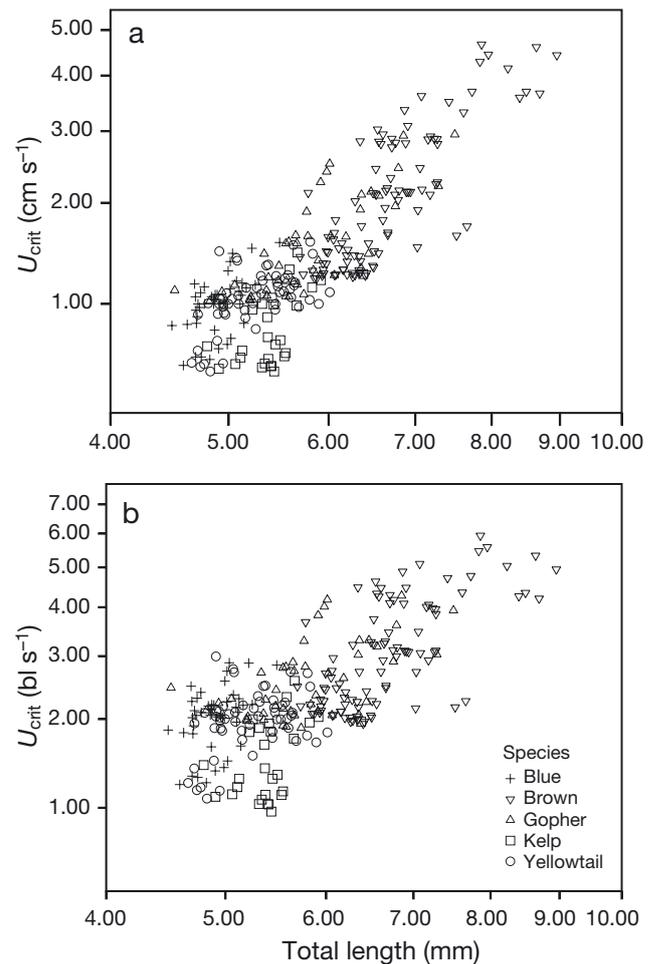


Fig. 4. Relationship between (a) absolute and (b) relative  $U_{crit}$  and size of 5 species of lab-reared *Sebastes* spp. larvae from 1 wk old to the start of flexion (6 to 8 wk old). Both axes are displayed on a logarithmic scale

were the fastest, yellowtail was intermediate, and kelp and blue were the slowest with mean speeds differing amongst groups by 0.01 to  $0.60 \text{ cm s}^{-1}$  (Tukey post-hoc tests). Relative  $U_{crit}$  at parturition ranged from 1.0 to  $3.1 \text{ bl s}^{-1}$  (Fig. 3b) and species differences in  $U_{crit}$  were similar to those observed for absolute  $U_{crit}$  ( $F_{4,189} = 49.2$ ,  $p < 0.001$ ). Brown and gopher rockfishes, the largest 2 of the study species, had significantly higher relative  $U_{crit}$  than the other 3 species, which did not differ from each other (Tukey post-hoc tests).

For parturition to flexion stages, absolute  $U_{crit}$  increased with TL for all of the *Sebastes* species (Fig. 4a; note that splitnose were not tested as larvae). There was no difference among species in the slope of the relationships (ANCOVA,  $F_{4,262} = 1.8$ ,  $p = 0.12$ ) but there were significant differences in the elevation of the relationships (ANCOVA,  $F_{4,266} = 23.7$ ,  $p < 0.001$ ,

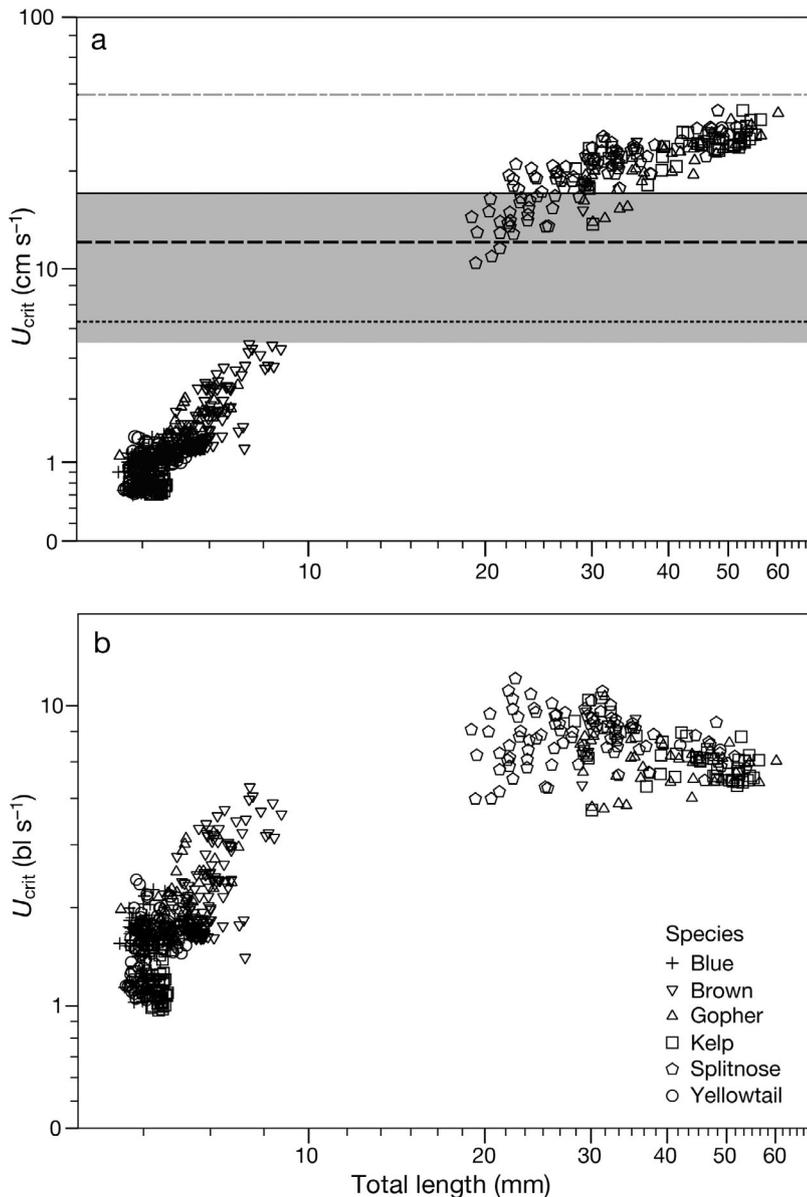


Fig. 5. Relationship between (a) absolute and (b) relative  $U_{crit}$  and total length of *Sebastes* spp. through ontogeny from parturition to settlement. Both axes are displayed on a logarithmic scale. See Table 2 for regression equations. The shaded area represents current speeds between 5 and 20  $\text{cm s}^{-1}$  (reported for Monterey Bay surface circulation by Breaker & Broenkow (1994) and the grey dashed line above the shaded area represents 50  $\text{cm s}^{-1}$ , a typical speed for an upwelling jet (Largier et al. 1993, Rosenfeld et al. 1994, Kaplan et al. 2009). With reference to Fig. 8, the dotted line represents a 3 wk mean alongshore current speed at Terrace Point, CA (5.9  $\text{cm s}^{-1}$ ), the bold dashed line represents the 95<sup>th</sup> percentile for 33 h filtered data (12.8  $\text{cm s}^{-1}$ ), and the solid line is the 95<sup>th</sup> percentile for 2 min data (20.4  $\text{cm s}^{-1}$ )

length covariate  $F_{1,266} = 302.2$ ,  $p < 0.001$ ), reflecting differences among species. Kelp rockfish had a significantly slower  $U_{crit}$  for a given size than brown, gopher, blue and yellowtail, which did not differ from each other (Tukey post-hoc tests).

Relative  $U_{crit}$  of preflexion rockfishes ranged from 1.0 to 5.9  $\text{bl s}^{-1}$  (Fig. 4b). There was no significant difference among the slopes of relative speed versus length for the 5 species (ANCOVA,  $F_{4,262} = 1.8$ ,  $p = 0.12$ ), but values of speed for a given length again differed significantly among species (ANCOVA,  $F_{4,266} = 23.7$ ,  $p < 0.001$ , length covariate  $F_{1,266} = 126.9$ ,  $p < 0.001$ ). Kelp rockfish had significantly slower relative  $U_{crit}$  for a given size compared to the other species (Tukey post-hoc tests).

### Pelagic juvenile rockfishes

The 5 wild-caught pelagic juveniles rockfishes (brown, gopher, kelp, splitnose, yellowtail; note that blue rockfish was not tested at the pelagic juvenile stage) ranged in size from 19.0 to 60.2 mm TL. Absolute  $U_{crit}$  ranged from 10.6 to 43.4  $\text{cm s}^{-1}$  (Fig. 5a) and relative  $U_{crit}$  ranged from 5.1 to 11.8  $\text{bl s}^{-1}$  (Fig. 5b). For statistical comparison among species, yellowtail and brown rockfishes were omitted due to low sample size and data were restricted to a size range of 28.2 to 60.2 mm TL to ensure overlap in size among species and meet assumptions of normality and homogeneity of variance. There was no significant difference among the slopes of absolute speed versus length for the 3 species ( $F_{2,136} = 1.0$ ,  $p = 0.355$ ). Swimming ability continued to improve with increasing length and differed among species ( $F_{2,137} = 10.8$ ,  $p < 0.001$ , length covariate  $F_{1,137} = 164.6$ ,  $p < 0.001$ ), with splitnose swimming significantly faster at a given length than kelp and gopher, which did not significantly differ from each other (Tukey post-hoc tests). Relative  $U_{crit}$  decreased with increasing length, with no significant difference in slope of the relationships ( $F_{2,136} = 3.0$ ,  $p = 0.053$ ). There were significant differences in the elevation of the relationships ( $F_{2,137} = 10.8$ ,  $p < 0.001$ , length covariate  $F_{1,137} = 30.98$ ,  $p < 0.001$ ) with splitnose swimming at a higher relative  $U_{crit}$  for their size than kelp and gopher, which did not significantly differ from each other (Tukey post-hoc tests).

Table 2. Log-transformed linear relationship between absolute  $U_{crit}$  and TL for pre- and post-flexion stages of 5 species of rockfishes. Refer to Fig. 5a for scatterplot of data.  $p < 0.01$  for all relationships

| Rockfish species    | n   | Size range (TL mm) | Relationship                             | $r^2$ |
|---------------------|-----|--------------------|--|-------|
| <b>Pre-flexion</b>  |     |                    |  |       |
| Brown               | 146 | 5.7–9.0            | $\log(U_{crit}) = 3.38(\log TL) - 2.51$  | 0.65  |
| Gopher              | 60  | 4.5–7.5            | $\log(U_{crit}) = 2.41(\log TL) - 1.69$  | 0.56  |
| Kelp                | 57  | 4.8–6.4            | $\log(U_{crit}) = 3.32(\log TL) - 2.58$  | 0.24  |
| Yellowtail          | 110 | 4.6–6.0            | $\log(U_{crit}) = 2.45(\log TL) - 1.76$  | 0.29  |
| <b>Post-flexion</b> |     |                    |  |       |
| Brown               | 5   | 29.0–35.5          | $\log(U_{crit}) = 2.18(\log TL) - 1.85$  | 0.58  |
| Gopher              | 40  | 28.8–60.2          | $\log(U_{crit}) = 0.90(\log TL) - 0.002$ | 0.61  |
| Kelp                | 53  | 28.2–56.4          | $\log(U_{crit}) = 0.61(\log TL) - 0.50$  | 0.53  |
| Splitnose           | 90  | 18.9–53.8          | $\log(U_{crit}) = 0.96(\log TL) - 0.03$  | 0.70  |

### Ontogenetic patterns

In total, 468 lab-reared larvae and 210 wild-caught juvenile *Sebastes* spp. were swum, ranging in size from 4.5 mm to 60.2 mm TL (Fig. 5). Absolute  $U_{crit}$  ranged from 0.5 to 43.4  $\text{cm s}^{-1}$  and relative  $U_{crit}$  ranged from 0.9 to 11.8  $\text{bl s}^{-1}$ . Overall, ontogeny of log-transformed absolute  $U_{crit}$  had a positive linear relationship with log-transformed length (Fig. 5a), whereas the relationship between relative  $U_{crit}$  and TL reached a peak at 20 to 35 mm and then declined to a value of ~70% of the maximum (Fig. 5b). The linear relationship between log-transformed  $U_{crit}$  and TL was calculated separately for pre- and post-flexion fish within each species (Table 2). Regressions for post-flexion yellowtail and pre-flexion blue rockfish were not conducted due to either low sample size or limited size range.

## DISCUSSION

### Critical swimming

Information on swimming ability in young *Sebastes* adds to a comprehensive understanding of rockfish early life history. Rather than spawning free-floating eggs that drift in the current, rockfishes release developed young with the capacity for movement. At parturition, swimming speeds were generally weak and not well described by size (Fig. 3a), although species with larger larvae at parturition outperformed species with smaller larvae. High variability in individual performance was unrelated to trunk width, oil globule volume or maternal factors (size, age, condition). This variability may be explained by unmeasured morphologi-

cal traits or reflect a trade-off with inversely related traits such as growth rate (Billerbeck et al. 2001, Fuiman & Cowan 2003). The range of variability in  $U_{crit}$  at parturition is likely of minor importance to dispersal. However, if  $U_{crit}$  correlates with other performance measures related to survival (Plaut 2001, Fisher & Leis 2009), early individual differences may have consequences for survivorship (e.g. catching food and evading predators).

Post-parturition through to flexion, body size is an important factor in swimming development, with  $U_{crit}$  improving markedly with length (and associated developmental traits). In early life, rockfish larvae grow slowly at a mean rate of ~0.1  $\text{mm d}^{-1}$  (Kendall & Lenarz 1987, Sakuma & Laidig 1995, Fisher et al. 2007) and thus remain small with limited swimming capability during the first several weeks of their pelagic duration. Swimming ability improves by flexion, at 1 to 2 mo of age and 9 to 10 mm TL (Kendall & Lenarz 1987, Moser et al. 1977), reaching up to 4.7  $\text{cm s}^{-1}$  (i.e. 3.5 times faster than at parturition). Interspecific differences are small compared with differences due to body size and do not appear to be associated with adult habitat or parturition season (Table 1).

After reaching 10 mm TL the growth rate of *Sebastes* spp. increases rapidly (Kendall & Lenarz 1987, Sakuma & Laidig 1995), with swimming ability increasing 7 to 61 times by the end of their PLD relative to parturition (Table 1). There is a high degree of variability within a given size range, as also found in studies of  $U_{crit}$  in other species (Fisher & Leis 2009). As pelagic juveniles, when rockfishes must find settlement habitat, their  $U_{crit}$  is comparable with speeds of tidal and wind-driven currents (Fig. 5a).

As a measure of the upper bounds of prolonged swimming speed,  $U_{crit}$  provides an estimate of maximum aerobic capacity, not a measure of sustainable or *in situ* swimming speed (Beamish 1978, Leis 2010). Although tests were performed in a laboratory setting where fishes are forced to swim continuously in a controlled laminar or weakly turbulent flow, a situation rarely encountered in nature where flows may be more turbulent and locomotion is intermittent,  $U_{crit}$  is typically correlated with ecologically relevant measures such as sustainable and routine swimming (Plaut 2001, Fisher & Bellwood 2003, Fisher & Wilson 2004). At parturition, rockfish larvae have routine swimming speeds of 0.15 to 0.75  $\text{cm s}^{-1}$  (Fisher et al. 2007), which are 30 to 42% of  $U_{crit}$  as measured in this study.

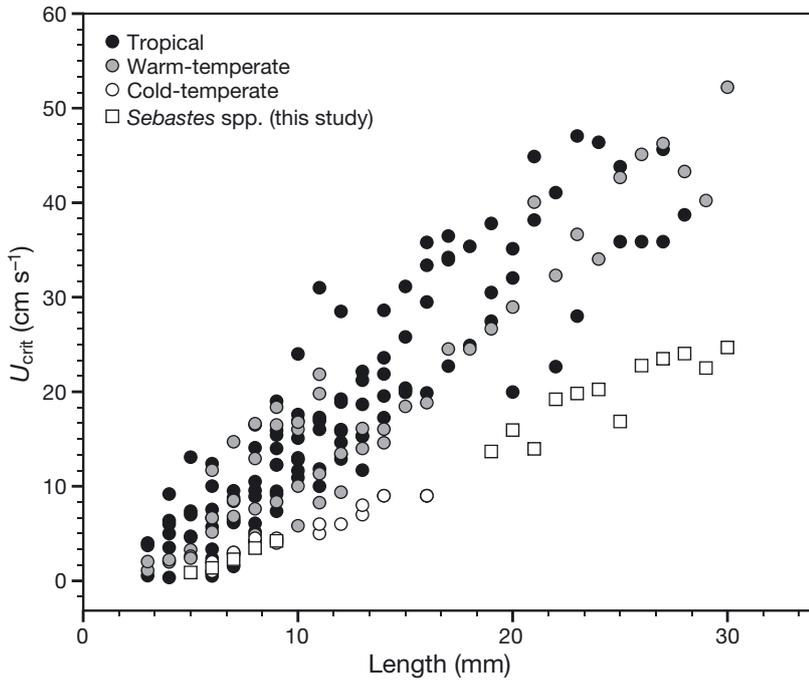


Fig. 6. Ontogeny of absolute  $U_{crit}$  of *Sebastes* spp. from this study in comparison to published values for tropical and warm- and cold-temperate species other than *Sebastes* (Fisher & Leis 2009, Leis et al. 2012a,b). Each point represents the average for a family except where data on only one species was available. Rockfishes are averaged by genus

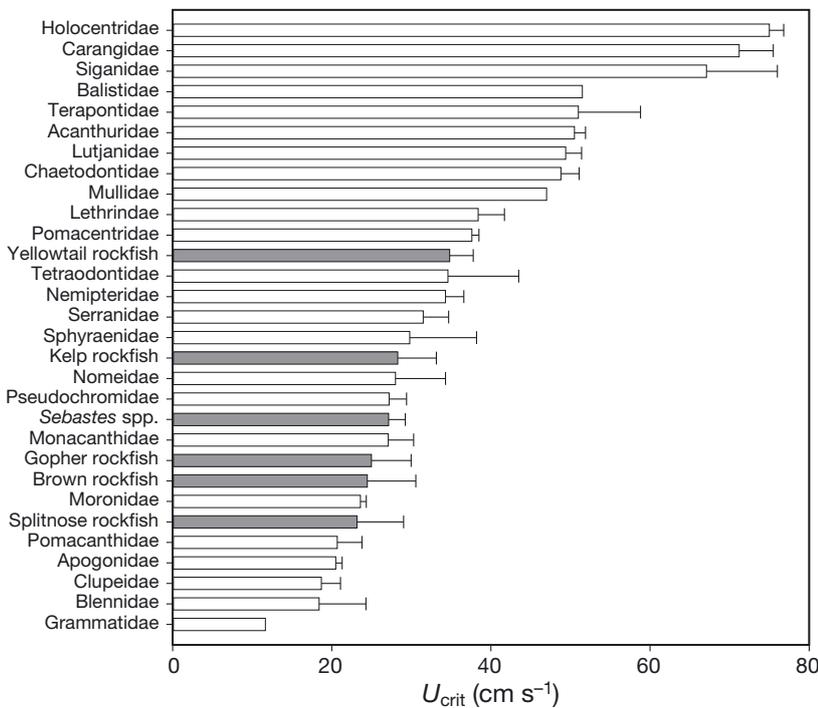


Fig. 7. Absolute  $U_{crit}$  at settlement stage, including published values for tropical and warm-temperate species (white bars; Fisher et al. 2005, Leis et al. 2012a,b) as well as cold-temperate *Sebastes* spp. (grey bars; this study). Error bars are standard error for multiple species in tropical families and *Sebastes* spp. and multiple individuals in each rockfish species. The *Sebastes* spp. bar represents the genus mean of the 5 plotted species

### Tropical and temperate comparisons

$U_{crit}$  for a given size in rockfishes is only as fast as the slowest tropical species pre-flexion but similar to other cold-temperate fish larvae (as compared to Fisher & Leis 2009, Leis et al. 2012a,b; Fig. 6). Post-flexion rockfishes have lower  $U_{crit}$  than tropical and warm-temperate marine species at similar sizes. This could be due to differences in environmental temperature (influencing water viscosity, muscle contractility and efficiency; Hunt von Herbing 2002), or species-level differences in physiology, morphology and development (flexion occurs at younger ages and smaller sizes for tropical species). In general, it is thought that fishes swim more efficiently and thus have a greater behavioral influence on dispersal in tropical waters than in temperate waters (Hunt von Herbing 2002, Leis 2007). However, the much longer PLD of rockfishes (months) compared to tropical species (weeks) results in a larger size at settlement compared to most tropical species (Thresher & Brothers 1989, Love et al. 2002). Consequently, by the time of settlement the  $U_{crit}$  of rockfishes (10 to 42  $\text{cm s}^{-1}$ ) matches that of some tropical species (Fig. 7). Further, the pelagic period of post-flexion rockfishes is longer and thus increases opportunities to influence transport.

### Influence of swimming on dispersal

The transport of swimming larvae and pelagic juveniles depends on the interaction of currents and swimming behavior, with both velocity vectors changing in speed and direction on diverse time scales. Without further information on how these fishes behave in the environment, one can only speculate on how they may influence dispersal outcomes. However, the importance of swimming is strongly suggested by the fact that post-flexion rockfishes can swim at speeds similar

to ambient currents off California. The strongest currents off central California are wind-driven, with nearshore tidal/diurnal currents, and occasionally a mesoscale eddy that may impinge over the shelf (Largier et al. 1993). While currents vary in space and time, and on a variety of scales, speeds are typically less than  $30 \text{ cm s}^{-1}$ , comparable with swimming speeds of pelagic juvenile rockfishes. Maximum values are short-lived and are due to a concurrence of tidal, diurnal, and wind forcing.

A number of field studies indicate that rockfishes behaviorally influence dispersal. For example, Miller & Shanks (2004) and Buonaccorsi et al. (2005) have found that rockfishes disperse shorter distances than would be expected through passive advection—a result that may be explained by swimming. Further, high concentrations of late-stage larval and pelagic juvenile rockfishes have been observed in eddies, where they were found in larger numbers in the center than could be explained by passive advection alone (Nishimoto & Washburn 2002). Azimuthal eddy speeds were  $20$  to  $30 \text{ cm s}^{-1}$ , within the swimming ability of pelagic juvenile rockfishes. Also, Larson et al. (1994) found that cross-shore distribution varies with ontogenetic stage: smallest rockfishes occurred offshore of an upwelling front, whereas larger pelagic juveniles were present nearshore even during active upwelling. The authors infer that larger fish undergo unknown behavioral changes that allow them to maintain position nearshore or move toward shore. Our results suggest that the change is the development of greater swimming ability. However, Larson et al. (1994) also found offshore transport of larger fish in upwelling plumes, suggesting quasi-passive transport of pelagic juveniles in the core of upwelling jets, where speeds of  $50 \text{ cm s}^{-1}$  or greater are observed (Kaplan et al. 2009, Bjorkstedt et al. 2012), exceeding the swimming ability of all pelagic juveniles. Evidence for swimming of pre- and post-flexion rockfishes is found in the observation of higher catches at night, suggesting larvae are able to actively avoid nets that are visible during light hours (Sakuma et al. 1999, Bjorkstedt et al. 2002, Sakuma et al. 2007).

In addition to questions about navigation and in which direction fish choose to swim, an equally important question is the persistence of swimming. This is illustrated in Fig. 8, where 2 min depth-averaged alongshore currents off Terrace Point are plotted (i.e. the same period as laboratory swimming tests). These currents show strong tidal/diurnal variability plus high-frequency fluctuations in speed. The strongest currents are short-lived and exhibit

shorter tidal/diurnal time scales. Persistent currents are weaker and associated with wind forcing. Data are also plotted with only subtidal fluctuations (33 h low-pass filter), which show wind-driven acceleration of alongshore geostrophic current from one day to the next. The 3 wk mean flow is also shown. Although instantaneous speeds of  $20$  to  $30 \text{ cm s}^{-1}$  are common, these flows are primarily tidal/diurnal, and carry passive organisms back and forth. However, the subtidal southward flow of order  $10 \text{ cm s}^{-1}$  will carry away pelagic larvae or juveniles if they do not exhibit persistent swimming at a similar speed (or know to swim cross-current to escape from a narrow jet). Directed and persistent swimming at speeds on the order of  $10 \text{ cm s}^{-1}$  can be used to counter or enhance the effect of currents. For reference, persistent motion at  $10 \text{ cm s}^{-1}$  for a month results in a potential displacement of  $260 \text{ km}$ , exceeding dispersal distances ascribed to rockfishes (e.g. Miller & Shanks 2004, Buonaccorsi et al. 2005, Gharrett et al. 2012). At longer time scales (3 wk), mean current speed is only  $5.8 \text{ cm s}^{-1}$ , a speed that can be matched by all post-flexion fishes if they were to swim persistently and in the right direction.

Our focus in comparing current speeds to  $U_{\text{crit}}$  is on alongshore currents, as they are the strongest (e.g. Largier et al. 1993). Offshore currents due to wind-driven Ekman transport are weaker but widespread, with mean speeds of about  $2 \text{ cm s}^{-1}$  and peak speeds of  $5 \text{ cm s}^{-1}$  (Dever et al. 2006). These speeds would nevertheless challenge larval rockfishes, which is consistent with observations that smaller rockfishes are found further offshore (Larson et al. 1994, Yoklavich et al. 1996, Schwing et al. 2000). Alongshore flow can be significantly faster than that shown in Fig. 8, partly because currents are weaker in the coastal boundary layer closer to shore (Nickols et al. 2012) and partly because the alongshore current forms a narrow, fast jet in upwelling areas (Rosenfeld et al. 1994, Largier et al. 1993, Kaplan et al. 2005, 2009, Halle & Largier 2011). The upwelling jet can exceed  $50 \text{ cm s}^{-1}$  and separate from the shelf (Rosenfeld et al. 1994, Largier 2004), thus exporting organisms offshore, including even fast-swimming pelagic juvenile rockfishes (as observed by Larson et al. 1994 in upwelling plumes).

Contrasting strategies in seasonality and location of parturition in *Sebastes* spp. may serve to maximize settlement success in variable oceanographic conditions. One way to avoid immediate offshore transport of larvae is to parturite in winter, as do blue and yellowtail rockfish, which live in deep nearshore to shelf habitat. By the onset of the upwelling season,

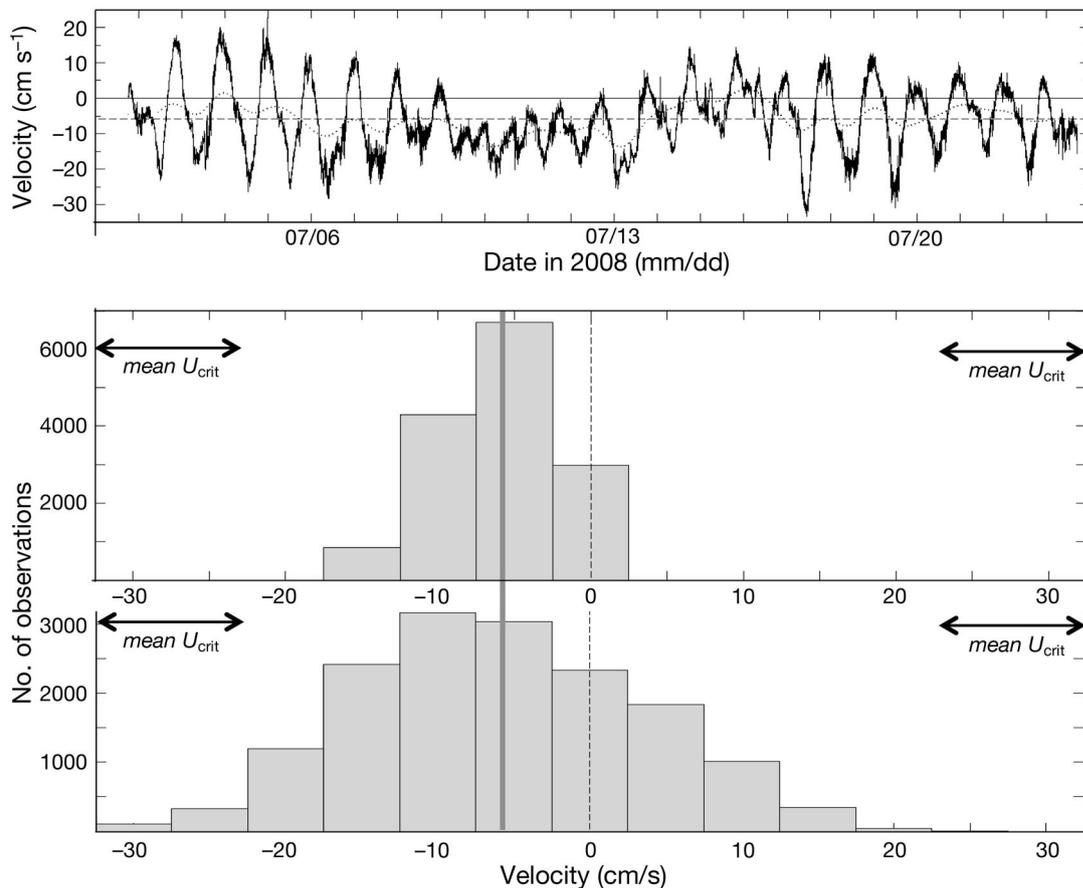


Fig. 8. Depth-averaged alongshore current observed on 25 m isobaths at Terrace Point ( $36^{\circ}56'36''\text{N}$ ,  $122^{\circ}4'50''\text{W}$ ), near Santa Cruz, CA; positive values are towards higher latitudes. Cross-shore velocities are an order of magnitude weaker (not plotted). Top: time-series plot of 2 min data (solid line), 33 h low-pass filtered data (dotted line), and 21 d mean (dashed line). Middle: histogram distribution of flow velocity for data filtered to 33 h values; 21 d mean is shown as bold gray line ( $-5.8\text{ cm s}^{-1}$ ). Bottom: histogram distribution of flow velocity for 2 min average currents. The range of mean  $U_{\text{crit}}$  speeds for rockfishes at settlement (see Fig. 7) is denoted by the double-headed arrows

larvae of winter-parturiating species have grown sufficiently that they have the muscle mass and swimming ability to overcome cross-shore currents and exert control over dispersal during spring upwelling. The extended pelagic phase of winter-parturiating species (in relation to spring-parturiating species, Table 1) may enhance opportunities for encountering suitable settlement habitat for rockfishes that release larvae further offshore. An alternative strategy is to release larvae closer to the nearshore, as do spring-parturiating species (kelp, brown and gopher rockfish), where Ekman transport is weaker (Kirincich et al. 2005, Dever et al. 2006) and upwelling jets are absent (Largier et al. 1993, Kaplan et al. 2005, Nickols et al. 2012). In addition to retention zones found nearshore in general, currents are reduced within and adjacent to kelp forests (Jackson & Winant 1983, Gaylord et al. 2007, Rosman et al. 2007), where current speed may be just a few  $\text{cm s}^{-1}$  and within the

range of swimming ability of all *Sebastes* spp. even in their first few weeks of life. Indeed, larvae appear to take advantage of the *Macrocystis pyrifera* canopy, where they have been observed in small pools of reduced flow at the surface (D. Stafford pers. comm.). The longer larvae are retained in these regions of slow flow, the less they will be exposed to strong currents over the mid/outer shelf and the stronger they will be at swimming when they do move offshore—presumably increasing their chances of settlement at a later date.

The concurrent need for food and movement back to adult habitat is well served by observations that larval and pelagic juvenile rockfishes are found in association with convergence zones (Lenarz et al. 1991, Bjorkstedt et al. 2002), where they may use their swimming abilities to remain associated with higher concentrations of zooplankton prey. Even weakly swimming larvae can take advantage of sur-

face convergences at a front by swimming vertically (e.g. Franks 1992, Shanks et al. 2000, N. Weidberg et al. unpubl.). If an upwelling front or a front associated with internal waves moves onshore, it will transport larvae and pelagic juveniles feeding at the front (Shanks 1988). Without migration of such features, fish that swim back to shore as pelagic juveniles would need a reasonable chance of finding food en-route and appropriate sensory capabilities to determine direction. For larvae, swimming may be important for reasons other than overcoming horizontal currents. Swimming enhances the probability of encountering prey and can be used to move vertically to depths at which currents are favorable. Where currents vary in speed or direction with depth, vertical positioning can have a large impact on transport and thus on dispersal pathways (Armsworth 2001, Sponaugle et al. 2002, Largier 2003). Recent studies of invertebrate dispersal have shown that planktonic larvae are retained nearshore during ongoing upwelling, presumably by maintaining vertical distribution below the surface layer (Shanks & Brink 2005, Morgan et al. 2009, Shanks & Shearman 2009, Morgan & Fisher 2010). However, this may not be the case for larval rockfishes, as field studies have shown offshore distribution of *Sebastes* larvae in years with strong upwelling (Larson et al. 1994, Yoklavich et al. 1996, Schwing et al. 2000), suggesting that young larvae remain in the surface layer, subject to offshore transport, or are entrained in upwelling jets that separate at large headlands.

In summary, larval and pelagic juvenile rockfishes may assert influence on dispersal, increase chances of settlement, and enhance population success through (1) controlling depth in a vertically sheared flow (e.g. swim downward to get below Ekman layer), (2) swimming to counter advection out of low-flow environments nearshore, or (3) by persistent swimming at speeds that exceed the mean speed of currents. It is expected that transport mechanisms vary, with some pelagic stages asserting control through behavior, while dispersal of others may be dominated by flow variability.

To ensure population persistence in a variable environment, *Sebastes* spp. have evolved a unique life history, including matrotrophic viviparity, high fecundity, and a long dispersive stage complemented with swimming ability. Larval and pelagic juvenile rockfishes are not merely passive propagules. Studies of rockfish population dynamics must consider their increasing ability to behaviorally influence dispersal throughout the pelagic stage, acting as nekton rather than plankton.

**Acknowledgements.** We thank D. Stafford, N. Parker, S. Brown, J. Garcia, S. Painter and K. Stierhoff for valuable assistance with larval husbandry. E. Sturm provided expertise in maintaining the aquarium facility. We are grateful to G. Cailliet, J. Leis and L. Allen for their advice and useful reviews of the manuscript. W. Satterthwaite and S. Munch offered beneficial statistical advice. We appreciate the generosity of the Partnership for Interdisciplinary Studies of Coastal Oceans, J. Caselle and M. Carr in providing pelagic juvenile rockfishes. We are grateful to K. Nickols for allowing us to use observations of currents at Terrace Point.

#### LITERATURE CITED

- Ahlstrom EH (1959) Vertical distribution of pelagic fish eggs and larvae off California and Baja California. US Fish Wildl Serv Fish Bull 60:107–146
- Ammann AJ (2004) SMURFs: standard monitoring units for the recruitment of temperate reef fishes. J Exp Mar Biol Ecol 299:135–154
- Anderson TW (1983) Identification and development of nearshore juvenile rockfishes (genus *Sebastes*) in central California kelp forests. MS Thesis, California State University, Fresno, CA
- Armsworth PR (2001) Directed motion in the sea: efficient swimming by reef fish larvae. J Theor Biol 210:81–91
- Beamish FWH (1978) Swimming capacity. In: Hoar WS, Randall DJ (eds) Fish physiology, Vol VII. Academic Press, New York, NY, p 101–187
- Bellwood DR, Fisher R (2001) Relative swimming speeds in reef fish larvae. Mar Ecol Prog Ser 211:299–303
- Billerbeck JM, Lankford TE Jr, Conover DO (2001) Evolution of intrinsic growth and energy acquisition rates. I. Trade-offs with swimming performance in *Menidia menidia*. Evolution 55:1863–1872
- Bjorkstedt EP, Rosenfeld LK, Grantham BA, Shkedy Y, Roughgarden J (2002) Distributions of larval rockfishes *Sebastes* spp. across nearshore fronts in a coastal upwelling region. Mar Ecol Prog Ser 242:215–228
- Bjorkstedt EP, Goericke R, McClatchie S, Weber E and others (2012) State of the California Current 2011–2012: ecosystems respond to local forcing as La Nina wavers and wanes. CCOFI Rep 53:41–76
- Boehlert GW (1977) Timing of the surface-to-benthic migration in juvenile rockfish, *Sebastes diploproa*, off Southern California. Fish Bull 75:887–890
- Boehlert GW, Gadamaski DM, Mundy BC (1985) Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fish Bull 83:611–622
- Breaker LC, Broenkow WW (1994) The circulation of Monterey Bay and related processes. Oceanogr Mar Biol Annu Rev 32:1–64
- Brett JR (1964) The respiratory metabolism and swimming performance of young sockeye salmon. J Fish Res Board Can 21:1183–1226
- Buonaccorsi VP, Kimbrell CA, Lynn EA, Vetter RD (2005) Limited realized dispersal and introgressive hybridization influence genetic structure and conservation strategies for brown rockfish, *Sebastes auriculatus*. Conserv Genet 6:697–713
- Dever EP, Dorman CE, Largier JL (2006) Surface boundary layer variability off northern California, USA during upwelling. Deep-Sea Res II 53:2887–2905
- Drake PT, Edwards CA, Barth JA (2011) Dispersion and con-

- nectivity estimates along the US west coast from a realistic numerical model. *J Mar Res* 69:1–37
- Fisher R, Bellwood DR (2003) Undisturbed swimming behavior and nocturnal activity of coral reef fish larvae. *Mar Ecol Prog Ser* 263:177–188
- Fisher R, Leis JM (2009) Swimming performance in larval fishes: from escaping predators to the potential for long distance migration. In: Domenici P, Kapoor BG (eds) *Fish locomotion: an etho-ecological perspective*. Science Publishers, Enfield, NH, p 333–373
- Fisher R, Wilson SK (2004) Maximum sustainable swimming speeds of late-stage larvae of nine species of reef fishes. *J Exp Mar Biol Ecol* 312:171–186
- Fisher R, Bellwood DR, Job SD (2000) Development of swimming abilities in reef fish larvae. *Mar Ecol Prog Ser* 202:163–173
- Fisher R, Leis JM, Clark DL, Wilson SK (2005) Critical swimming speeds of late-stage coral reef fish larvae: variation within species, among species and between locations. *Mar Biol* 147:1201–1212
- Fisher R, Sogard SM, Berkeley SA (2007) Trade-offs between size and energy reserves reflect alternative strategies for optimizing larval survival potential in rockfish. *Mar Ecol Prog Ser* 344:257–270
- Frank KT, Carscadden JE, Leggett WC (1993) Causes of spatio-temporal variation in the patchiness of larval fish distributions: differential mortality or behaviour? *Fish Oceanogr* 2:114–123
- Franks P (1992) Sink or swim: accumulation of biomass at fronts. *Mar Ecol Prog Ser* 82:1–12
- Fuiman LA, Cowan JH Jr (2003) Behavior and recruitment success in fish larvae: repeatability and covariation of survival skills. *Ecology* 84:53–67
- Garcia-Reyes M, Largier JL (2012) Seasonality of coastal upwelling off central and northern California: new insights including temporal and spatial variability. *J Geophys Res* 117:C03028, doi:10.1029/2011JC007629
- Gaylord B, Rosman JH, Reed D, Koseff JR and others (2007) Spatial patterns of flow and their modification within and around a giant kelp forest. *Limnol Oceanogr* 52:1838–1852
- Gharrett AJ, Riley RJ, Spencer PD (2012) Genetic analysis reveals restricted dispersal of northern rockfish along the continental margin of the Bering Sea and Aleutian Islands. *Trans Am Fish Soc* 141:370–382
- Gilbert EA (2000) Molecular genetic analysis of temporal recruitment pulses in juvenile kelp rockfish. MA Thesis, San Francisco State University, San Francisco, CA
- Halle CM, Largier JL (2011) Surface circulation downstream of the Point Arena upwelling center. *Cont Shelf Res* 31:1260–1272
- Hunt von Herbing I (2002) Effects of temperature on larval fish swimming performance: the importance of physics to physiology. *J Fish Biol* 61:865–876
- Jackson GA, Winant C (1983) Effect of a kelp forest on coastal currents. *Cont Shelf Res* 2:75–80
- Jorgensen SJ, Kaplan DM, Klimley AP, Morgan SG, O'Farrell MR, Botsford LW (2006) Limited movement in blue rockfish *Sebastes mystinus*: internal structure of home range. *Mar Ecol Prog Ser* 327:157–170
- Kaplan DM, Largier JL, Botsford LW (2005) HF radar observations of surface circulation off Bodega Bay (northern California, USA). *J Geophys Res* 110:C10020
- Kaplan DM, Halle C, Paduan J, Largier JL (2009) Surface currents during anomalous upwelling seasons off central California. *J Geophys Res* 114:C12026, doi:10.1029/2009JC005382
- Kendall AW Jr, Lenarz WH (1987) Status of the early life history studies of northeast Pacific rockfishes. In: *Proc Int Rockfish Symp*, Anchorage, AK. Alaska Sea Grant Rep no. 87-2, p 99–128
- Kirincich AR, Barth JA, Grantham BA, Menge BA, Lubchenco J (2005) Wind-driven inner-shelf circulation off central Oregon during summer. *J Geophys Res* 110:C10S03, doi:10.1029/2004JC002611
- Laidig TE (2010) Influence of ocean conditions on the timing of early life history events for blue rockfish (*Sebastes mystinus*) off California. *Fish Bull* 108:442–449
- Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. *Ecol Appl* 13:S71–S89
- Largier J (2004) The importance of retention zones in the dispersal of larvae. *Am Fish Soc Symp* 42:105–122
- Largier JL, Magnell BA, Winant CD (1993) Subtidal circulation over the northern California shelf. *J Geophys Res* 98(C10):18147–18179
- Larson RJ (1980a) Territorial behavior of the black and yellow rockfish and gopher rockfish (Scorpaenidae, *Sebastes*). *Mar Biol* 58:111–122
- Larson RJ (1980b) Competition, habitat selection, and the bathymetric segregation of 2 rockfish (*Sebastes*) species. *Ecol Monogr* 50:221–239
- Larson RJ, Lenarz WH, Ralston S (1994) The distribution of pelagic juvenile rockfish of the genus *Sebastes* in the upwelling region off central California. *CCOFI Rep* 35:175–221
- Lea RN, McAllister RD, VenTresca DA (1999) Biological aspects of nearshore rockfishes of the genus *Sebastes* from central California with notes on ecologically related sport fishes. *Fish Bull* 177:1–112
- Leis JM (2006) Are larvae of demersal fishes plankton or nekton? *Adv Mar Biol* 51:57–141
- Leis JM (2007) Behaviour as input for modelling dispersal of fish larvae: behaviour, biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography. *Mar Ecol Prog Ser* 347:185–193
- Leis JM (2010) Ontogeny of behavior in larvae of marine demersal fishes. *Ichthyol Res* 57:325–342
- Leis JM, Bullock S, Duday A, Guion C, Galzin R (2012a) Development of morphology and swimming in larvae of a coral-reef fish, the royal gramma, *Gramma loreto* (Grammatidae, Teleostei). *Sci Mar* 76:281–288
- Leis JM, Balma P, Ricoux R, Galzin R (2012b) Ontogeny of swimming ability in the european sea bass, *Dicentrarchus labrax* (L.) (Teleostei: Moronidae). *Mar Biol Res* 8:265–272
- Lenarz WH, Larson RJ, Ralston S (1991) Depth distributions of late larvae and pelagic juveniles of some fishes of the California Current. *CCOFI Rep* 32:41–46
- Love M, Yoklavich M, Thorsteinson L (2002) The rockfishes of the northeast Pacific. University of California Press, Berkeley, CA
- Miller JA, Shanks AL (2004) Evidence for limited larval dispersal in black rockfish (*Sebastes melanops*): implications for population structure and marine-reserve design. *Can J Fish Aquat Sci* 61:1723–1735
- Morgan SG, Fisher JL (2010) Larval behavior regulates nearshore retention and offshore migration in an upwelling shadow and along the open coast. *Mar Ecol Prog Ser* 404:109–126

- Morgan SG, Fisher JL, Miller SH, McAfee ST, Largier JL (2009) Nearshore larval retention in a region of strong upwelling and recruitment limitation. *Ecology* 90: 3489–3502
- Moser HG (1996) Scorpaenidae: scorpionfishes and rockfishes. In: Moser HG (ed), *The early life stages of fishes in the California Current Region*. Allen Press, Lawrence, KS, p 733–795
- Moser HG, Boehlert GW (1991) Ecology of pelagic larvae and juveniles of the genus *Sebastes*. *Environ Biol Fishes* 30:203–224
- Moser HG, Ahlstrom EH, Sandknop EM (1977) Guide to the identification of scorpionfish larvae (Family Scorpaenidae) in the Eastern Pacific with comparative notes on species of *Sebastes* and *Helicolenus* from other oceans. NOAA Tech Rep NMFS Circ 402
- Muller-Feuga A, Robert R, Cahu C, Robin J, Divanach P (2007) Uses of microalgae in aquaculture. In: Støttrup JG, McEvoy LA (eds) *Live feeds in marine aquaculture*. Blackwell Science, Oxford, p 253–299
- Nickols KJ, Gaylord B, Largier JL (2012) The coastal boundary layer: predictable current structure decreases along-shore transport and alters scales of dispersal. *Mar Ecol Prog Ser* 464:17–35
- Nishimoto MM, Washburn L (2002) Patterns of coastal eddy circulation and abundance of pelagic juvenile fish in the Santa Barbara Channel, California, USA. *Mar Ecol Prog Ser* 241:183–199
- Norcross BL, Shaw RF (1984) Oceanic and estuarine transport of fish eggs and larvae: a review. *Trans Am Fish Soc* 113:153–165
- Plaut I (2001) Critical swimming speed: its ecological relevance. *Comp Biochem Physiol A* 131:41–50
- Rosenfeld LK, Schwing FB, Garfield N, Tracy DE (1994) Bifurcated flow from an upwelling center: a cold water source for Monterey Bay. *Cont Shelf Res* 14:931–964
- Rosman JH, Koseff JR, Monismith SG, Grover J (2007) A field investigation into the effects of a kelp forest (*Macrocystis pyrifera*) on coastal hydrodynamics and transport. *J Geophys Res* 112:CO2016, doi:10.1029/2005JC003430
- Ross JRM, Larson RJ (2003) Influence of water column stratification on the depth distributions of pelagic juvenile rockfishes off central California. *CCOFI Rep* 44:65–75
- Sakuma KM, Laidig TE (1995) Description of larval and pelagic juvenile chilipepper, *Sebastes goodei* (family Scorpaenidae), with an examination of larval growth. *Fish Bull* 93:721–731
- Sakuma KM, Ralston S, Roberts DA (1999) Diel vertical distribution of postflexion larval *Citharichthys* spp. and *Sebastes* spp. off Central California. *Fish Oceanogr* 8: 68–76
- Sakuma KM, Ralston S, Roberts DA (2007) High-frequency patterns in abundance of larval Pacific hake, *Merluccius productus*, and rockfish, *Sebastes* spp., at a single fixed station off central California. *Fish Oceanogr* 16:383–394
- Schwing FB, Moore CS, Ralston S, Sakuma KM (2000) Record coastal upwelling in the California Current in 1999. *CCOFI Rep* 41:148–160
- Shanks AL (1988) Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish. *Fish Bull* 86:703–714
- Shanks AL, Brink L (2005) Upwelling, downwelling, and cross-shelf transport of bivalve larvae: test of a hypothesis. *Mar Ecol Prog Ser* 302:1–12
- Shanks AL, Shearman R (2009) Paradigm lost? Cross-shelf distributions of intertidal invertebrate larvae are unaffected by upwelling or downwelling. *Mar Ecol Prog Ser* 385:189–204
- Shanks AL, Largier JL, Brink L, Brubaker J, Hooff R (2000) Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. *Limnol Oceanogr* 45:230–236
- Skogsberg T (1936) Hydrography of Monterey Bay, California. Thermal conditions, 1929–1933. *Trans Am Philos Soc* 29:1–152
- Sogard SM, Berkeley SA, Fisher R (2008) Maternal effects in rockfishes *Sebastes* spp.: a comparison among species. *Mar Ecol Prog Ser* 360:227–236
- Sponaugle S, Cowen RK, Shanks A, Morgan SG and others (2002) Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. *Bull Mar Sci* 70: 341–375
- Stobutzki IC, Bellwood DR (1994) An analysis of the sustained swimming abilities of pre- and post-settlement coral reef fishes. *J Exp Mar Biol Ecol* 175:275–286
- Thresher RE, Brothers EB (1989) Evidence of intra- and inter-oceanic regional differences in the early life history of reef-associated fishes. *Mar Ecol Prog Ser* 57:187–205
- West JE, Buckley RM, Doty DC (1994) Ecology and habitat use of juvenile rockfishes (*Sebastes* spp.) associated with artificial reefs in Puget Sound, Washington. *Bull Mar Sci* 55:344–350
- Wolanski E, Doherty P, Carleton J (1997) Directional swimming of fish larvae determines connectivity of fish populations on the Great Barrier Reef. *Naturwissenschaften* 84:262–268
- Woodson CB, McManus MA, Tyburczy JA, Barth JA and others (2012) Coastal fronts set recruitment and connectivity patterns across multiple taxa. *Limnol Oceanogr* 57: 582–596
- Yoklavich MM, Loeb VJ, Nishimoto M, Daly B (1996) Near-shore assemblages of larval rockfishes and their physical environment off Central California during an extended El Niño event, 1991–1993. *Fish Bull* 94:766–782

Editorial responsibility: Steven Morgan,  
Bodega Bay, California, USA

Submitted: July 9, 2013; Accepted: November 26, 2013  
Proofs received from author(s): February 26, 2014