[Review]

Cryptic Processes in the Sea: A Review of Delayed Development in the Microscopic Life Stages of Marine Macroalgae

Laura T. Carney* and Matthew S. Edwards

Department of Biology, San Diego State University, San Diego, CA 92107, USA

The ability to survive long periods of unfavorable environmental conditions and to recover following severe disturbances is crucial to the persistence of populations occurring in temporally variable environments. To compensate for this variability, many species have developed life histories in which the adult life stages become dormant or exhibit reduced metabolic activity during unfavorable conditions and then re-establish activity when conditions improve (Cohen 1966; Hinton 1968; Crowe 1971; Hochachka and Guppy 1987; Edwards 2000; Kortner and Geiser 2000). Alternatively, if adult mortality is severe, some species can delay their development as more resistant immature or alternate life stages (Cohen 1966; Tauber and Tauber 1978; Venable and Lawlor 1980; Grice and Marcus 1981; Hollibaugh *et al.* 1981; Maier 1990; Pake and Venable 1996). Such cases of delayed development are often considered as temporal dispersal strategies and a trade-off with spatial dispersal strategies (Venable and Lawlor 1980; Levin *et al.* 1984; Cohen and Levin 1987; Edwards 2000).

While examples of delayed development have been observed across a wide array of taxa, the terminology used to describe them varies considerably; e.g. "cryptobiosis" for tardigrades (Nelson 2002), "dormancy" for terrestrial plant seeds (Crocker 1916), "diapause" for zooplankton (Hollibaugh *et al.* 1981), "resting states" for microalgae (Rengefors *et al.* 2004), "delayed metamorphosis" for marine invertebrate larvae (Pechenik 1990), "deceleration of vital activity" for microorganisms (Feofilova 2003), and "banks of microscopic forms" for marine macroalgae (Chapman 1986). Regardless of terminology, delayed development in juvenile or alternate life stages may be a crucial adaptation to surviving in variable environments and in establishing spatial patterns in adult stages (Swanson and Druehl 2000). In this review, we focus our attention on banks of microscopic forms (hereafter "stages") of marine macroalgae. We specifically address the kelps (Laminariales) which include the largest algae in the world, reaching up to 50 m in length (Van den Hoek *et al.* 1995), provide the primary habitat for a wide variety of species, and promote biodiversity of commercially and ecologically important fishes, invertebrates and mammals (Dayton 1985; Foster and Schiel 1985). Understanding the factors that regulate kelp forest persistence is fundamental to understanding how temperate coastal marine ecosystems are regulated. Our intent is not to provide a comprehensive review of all known information on the subject, but rather to provide a brief history of advances in the field and to suggest possible directions for future research.

Many species of marine macroalgae exhibit an alternation of heteromorphic generations in which one generation is more tolerant to unfavorable environmental conditions. For example, some species of intertidal red algae occur as diploid tetrasporic crusts during periods of increased sand abrasion (Hawkes 1983) and grazer densities (Slocum 1980), and produce upright fleshy haploid gametic blades when these pressures are reduced. Further, many marine macroalgae exhibit a time lag between peak spore production and recruitment of new juvenile stages, during which the adult life stages are absent (Klinger 1984; Blanchette 1996; Edwards 2000). For these species to persist from year to year, microscopic (or unknown heteromorphic) stages must maintain populations during periods when the macroscopic stages are absent. While studies of delayed development in alternate life stages are common for terrestrial plants, aquatic invertebrates, and phytoplankton (see references above), in situ studies for macroalgae are rare, at least in part due to the difficulties associated with their microscopic sizes (Dayton 1985). However, there has been growing evidence that many species of marine macroal-

*Corresponding author (lcarney@sciences.sdsu.edu)

gae rely on banks of microscopic stages to survive periods of environmental stress and produce new macroscopic stages when conditions improve (Kain 1964; Dayton 1985; Hoffmann *et al.* 1984; Hoffmann and Santelices 1991; Edwards 2000). As a result, these stages have now been identified in a variety of habitats, from subtidal kelp forests to intertidal boulder fields and the number of investigations into their ecology is growing (e.g. Chapman 1986; Hoffmann and Santelices 1991; Edwards 2000).

An important condition for macroalgal microscopic stages to survive when macroscopic forms are absent is that microscopic stages tend to be more tolerant to unfavorable light, temperature and nutrient conditions (Chapman and Burrows 1971; Nakahara 1984; Wienke and Dieck 1989, 1990; Hoffmann and Santelices 1991). However, these stages are very sensitive to other factors such as sedimentation (Devinny and Volse 1978; Deysher and Dean 1984), invertebrate grazing (Dean *et al.* 1988; Leonard 1994) and exposure to toxic effluents (Anderson *et al.* 1990; Reed and Lewis 1994). As a consequence, there has been some debate about how long these stages can survive in the field and on their relative contribution to recruitment of macroscopic stages following extended periods. In laboratory cultures, gametophytes of the giant kelp, *Macrocystis pyrifera*, survive for decades (Druehl personal communication) while in the field they may only survive for weeks to months (Deysher and Dean 1984). In contrast, studies on other macroalgae, e.g. *Desmarestia ligulata*, indicate their microscopic stages can survive in the field for at least two years (Edwards 2000). It is now widely hypothesized that microscopic stages of at least some brown algae can persist extended periods of adult absence and promote rapid recruitment once resources have been renewed (Kain 1964; Dayton 1985; Lüning 1980; Foster 1982; Klinger 1984; Pierce and Cowling 1991; Blanchette 1996; Ladah *et al.* 1999; Edwards 2000). However, studies directed at assessing the longevity of these stages and their contribution to population persistence under a variety of environmental conditions remains sorely needed to resolve these issues.

Although there is growing evidence for the occurrence of banks of microscopic stages in marine macroalgae, in situ development and survival of these stages has only rarely been investigated (Hsiao and Druehl 1973; Santelices *et al.* 1995; Edwards 2000; Worm *et al.* 2001) and it is not fully understood which factors regulate it. This has prevented a complete understanding of the full macroalgal life history and the ecological importance of their microscopic stages. Hoffmann and Santelices (1991), however, identified several key concepts understood for terrestrial systems that are necessary to investigate for macroalgae, including 1) the environmental factors regulating the delay and resumption of microscopic development 2) species-specific information on the relative longevity of microscopic and macroscopic stages 3) if a bank of microscopic stages allows the exchange of genetic material between plants of different ages and, 4) how predation (pathogens, herbivores, bacteria and fungi) affects the microscopic stages. Resolving these concepts will greatly enhance our understanding of the full macroalgal life history. In the following paragraphs we explore what is known and unknown about these four concepts.

Addressing the above questions has thus far provided crucial information into the ecology of these stages and the environmental cues that cause them to delay development. For example, in various combinations that differ by region and species, latitudinal and seasonal changes in photoperiod, irradiance, temperature and nutrients have been shown to induce delayed development in macroalgae, with irradiance and photoperiod being the most common environmental cues identified. Hsiao and Druehl (1973) reported that in situ gametogenesis in *Laminaria saccharina* is controlled by irradiance and day length. Blue light in particular has been shown to be a necessary factor for sexual reproduction in *Laminaria* gametophytes, without which the gametophytes delay in a vegetative state (Lüning 1981). Hoffmann and Santelices (1991) reviewed some early, and often accidental, accounts of delay (3-8 months duration) and resumption of development in macroalgae largely due to changing levels of irradiance and temperature. Under laboratory conditions, Santelices *et al.* (2002) tested the microscopic stages of 15 algal species from the three primary divisions of macroalgae (Chlorophyta, Phaeophyta and Rhodophyta) from tide pools in central Chile and found that most were able to delay development for at least 60 days and resume growth due to increasing irradiance and day-length. Under laboratory conditions, Kinlan *et al.* (2003) reported that embryonic sporophytes of *Macrocystis* delay development under conditions of limiting irradiance (2-3 μmol photons m^{-2} s^{-1}) and then resume growth when switched to non-limiting irradiance (30-70 μmol photons m^{-2} s^{-1}) and nitrate (9 μM) levels. The only invasive kelp in California, *Undaria pinnatifida*, delays gametophyte development when temperatures are high (Saito 1975) and recruits once tempera-

tures decrease (Thornber *et al.* 2004). Similarly, Edwards (1998) found that the timing for recruitment of *Desmarestia* in central California is closely tied to changes in photoperiod and a dramatic decline in ocean temperature coincident with the onset of spring upwelling. Laboratory studies on *Desmarestia* gametophytes indicate they can delay growth under low light levels (< 4 μmol photons m^{-2} s^{-1}) and short day photoperiods (8:16 L:D), but resume growth when transferred to higher light and longer photoperiods (Edwards 2000). It is likely that the temperature effect, reported above, is due to the strong inverse correlation between temperature and nitrate levels along large portions of the northeastern Pacific coast (Hernández-Carmona *et al.* 2001, Edwards and Estes *in press*).

Thallus abrasion may be another mechanism of inducing sexual reproduction in kelp gametophytes and is commonly used to induce gamete production in the laboratory. It is possible that abrasion by natural process like sand scour and grazing may have the same affect in situ. Sand scour is a common phenomenon in kelp forest ecosystems where hard bottom kelp forest communities are intermixed with sandy patches. Microscopic and juvenile sporophytes and zoospores, however, are detrimentally affected by abrasion (Devinny and Volse 1978; Leonard 1994; Duggins *et al.* 2001) and any difference in the response to abrasion between these stages may be due to their different tissue regeneration abilities. A small amount of work has been done concerning predation on the microscopic stages of algae by marine invertebrates (e.g. Dean *et al.* 1988; Leonard 1994; Lotze *et al.* 1999; Lotze and Worm 2000; Sala and Graham 2002) but none of these adequately tested the differential effects of grazing on different life-history stages of the microscopic forms (e.g. gametophytes and/or embryonic sporophytes). Investigations are needed to determine if both the delayed gametophyte and delayed sporophyte are equally susceptible to abrasion damage.

In addition to environmental control over reproduction in the microscopic stages, biological control from neighboring conspecifics may also be important. Just as ethylene released by ripening fruit induces neighboring fruit to mature in fruiting trees (Abeles *et al.* 1992), cues from individuals may also induce neighboring microscopic stages to resume development. For example, though not limited to kelps, laboratory studies have shown that female kelp gametophytes release the pheromone Lamoxirene to induce sperm release from mature antheridia on nearby male gametophytes (reviewed by Maier *et al.* 2001). It is possible that a similar cue from developing neighbors may induce mature but delayed gametophytes to begin gamete production. Gametophytes, then, may potentially mate with younger individuals once they have resumed development. This could occur with either propagules from unrelated individuals which are given time to arrive near the delayed stages or, because some adult kelps release propagules over multiple years, with younger siblings. Raimondi *et al.* (2004) showed that self-fertilization in *Macrocystis* causes decreased sporophyte production and adult fecundity and may help promote the oscillating kelp abundance we have observed along our coastline. Since out-crossing is generally advantageous over selfing (Maynard Smith 1978), delayed gametophytes may increase overall population success by surviving long enough to encounter unrelated individuals or delaying long enough to ensure increased genetic differentiation between sibling cohorts.

Unlike the alternate life stages of many organisms that are truly dormant, banks of microscopic stages for marine algae likely remain physiologically active and highly sensitive to changes in environmental quality. Evidence from laboratory studies suggests that the microscopic stages of some macroalgae remain sensitive to environmental quality (e.g. Chapman and Burrows 1971; Nakahara 1984; Wienke and Dieck 1989, 1990; Hoffmann and Santelices 1991; Edwards 2000), and may be subject to strong competitive forces (Reed 1990). This has important consequences for the recovery of populations following disturbances, especially if these microscopic stages are also impacted by the disturbance (e.g. Hernández *et al.* 2001). Recovery may be further complicated if these stages exhibit ecotypic variability in their response to environmental stress (Swanson and Druehl 2000) as do some adult stages (e.g. Kpoczak et al 1991).

Unlike the resting stages of most organisms that delay development as post-reproductive diploid zygotes, algal resting stages delay development as either diploid (post-sexual reproduction) or haploid (pre-sexual reproduction) stages. The identity of the particular life stage(s) that make up these resting stages has recently come into question for some large brown seaweeds such as kelps and, in fact, may vary among species (e.g. Hsiao and Druehl 1973; Klinger 1984; Kinlan *et al.* 2003). For the kepls, the gametophyte is most often reported as the delayed algal stage (Hsiao and Druehl 1973; Dayton 1985; Klinger 1984; Blanchette 1996; Ladah *et al.* 1999; Edwards 2000), although some reports suggest that

embryonic sporophytes may serve as the delayed stage (Kinlan *et al.* 2003). If kelps delay as haploid gametophytes instead of diploid sporophytes, once they resume development they may potentially reproduce with unrelated individuals that accrue over time, thus decreasing the chance of self-fertilization. In contrast, given that male and female gametophytes must be in close proximity for sexual reproduction to occur (e.g. ~1 mm, Reed 1990; Reed *et al.* 1991), delaying development as diploid sporophytes may increase the chance of successful recruitment by removing the constraint that both sexual stages must survive the extended periods or that the stages must be reproductive when a new propagule arrives. In addition, diploid stages may be more adapted to a broader range of environmental conditions than their haploid counterparts (reviewed by Thornber and Gaines 2004).

Unlike terrestrial plant seed banks, which generally reside under a sediment layer, macroalgal microscopic stages reside on the rocky substrate below the adults, which may facilitate our ability to find and study them in the field (Edwards 1999). Exceptions to this have been noted by Dube and Ball (1971), who found and were able to produce sporophytes from *Desmarestia viridis* gametophytes growing in the tissues of the sea pen *Ptilosarcus gurneyi*, and Garbary *et al.* (1999) who found several species of kelp gametophytes growing endophytically in the tissues of red algae along the northwest coast of the Unites States. Hsiao and Druehl (1973) and Edwards (1999) have applied fluorescent labeling techniques to study the ecology of microscopic gametophytes in situ. Here, microscopic stages can be labeled (e.g. with Calcifluor White), outplanted to the field, and later retrieved for examination with epifluorescent microscopy. This can allow researchers to study growth and development under natural field conditions. Further, evaluation of the relative importance of these stages to recruitment of macroscopic forms have largely been done by collecting pieces of substrate (e.g. boulders), placing them in sunlight to kill all algal forms, transplanting them back in the field, and then monitoring them for recruitment (Hoffmann and Santelices 1991; Reed *et al.* 1997; Edwards 2000). Similar to soil sterilization techniques developed for terrestrial seed banks (e.g. Bullock *et al.* 1994; Edwards and Crawley 1999; Rogers and Hartnett 2001), Edwards (1999) developed a method for chemically sterilizing (e.g. with bleach) the substrate in situ using watertight tents, thereby allowing for the study of microscopic stages on solid rocky reefs. While

these methods, coupled with laboratory experiments, have increased our ability to study the ecology and importance of banks of microscopic stages of marine macroalgae to the persistence of macroscopic populations, they are still limiting in their ability to identify and/or quantify these stages in situ. One solution may be found using molecular techniques in which microscopic stages are identified and quantified using microbial genomics (Swanson and Druehl 2000). Integration of all these approaches may yield our best opportunity to finally comprehensively study the ecology of microscopic life stages in the field.

Recent declines in north Pacific kelp forests have been linked to large-scale oceanographic disturbances (Dayton and Tegner 1990; Edwards 2004), changes in grazing intensity, and changes in the abundance and distribution of species reliant on kelp forest habitat (Dayton and Tegner 1990; Anderson 1994; Carr 1994; Edwards 2004). Recovery of *Macrocystis* from large-scale disturbances such as El Nino has been geographically variable (Edwards 2004; Edwards and Estes in press), with some locations (e.g. near their southern range limit in Baja California, México), delayed for years to decades (Hernández *et al.* 2001). One mechanism for this delayed recovery has been the rapid recruitment of subsurface kelps that competitively exclude the otherwise dominant *Macrocystis* (Dayton *et al.* 1992; Edwards and Hernández 2005). Consequently, the timing of recruitment may play an integral role in determining which species recover following disturbances and thus persist year to year. Ladah *et al.* (1999) suggested that rapid recovery of *Macrocystis* at one location along Baja California, México came from a bank of microscopic stages that survived the El Niño, while Hernández *et al.* (2001) suggested that a complete mortality of the miocroscopic stages ~70 km to the south completely prevented *Macrocystis* recovery. Further, reliance on a 'seed bank' may differ within a kelp forest between edge and interior where zoospore dispersal is largely constrained by dampened water motion (Graham 2003), but this has yet to be studied. Thus, it appears that the importance of delayed development in kelp microscopic stages to population persistence may be both context and scale dependent.

Populations in regions where adult disappearance and prolonged absences are common would benefit from having long-lived stages. It may be that when environmental variability is seasonally predictable, delaying development of immature life stages allows a population to exhibit an annual life history (Tauber and Tauber

1978;Venable and Lawlor 1980; Klinger 1984; Edwards 2000), but when environmental variability is stochastic and/or seasonally unpredictable, delaying development of immature stages may promote opportunistic life histories and allow populations to rapidly recruit following resource-renewing disturbances (Keeley 1987; Ladah *et al.* 1999; Edwards 2000). Alternatively, Reed *et al.* (1997) reported that newly settled zoospores dispersed from distant populations are the primary contributors to recovery in some California, USA *Macrocystis* forests following losses of the adults. It is possible that kelp populations in environments that regularly maintain a portion of reproductive adults during disturbance events may invest less in seed bank development than do populations where total regional loss of reproductive adults is more common. This may not apply to purely annual algae like *Desmarestia ligulata*, *Postelsia palmaeformis*, and *Nereocystis luetkeana* in central California, USA, or *Alaria fistulosa* in Alaska, USA which recruit in the spring following several months of adult sporophyte absence. It has been well established for terrestrial plant communities that annual species tend to invest more energy in seed bank formation and have longer-lived seeds than perennial species do (Grime 1979; Venable and Brown 1993; Rees 1996). Similar questions have recently been investigated for annual and perennial algae, but so far results have been mixed and suggest variable reliance between annuals and perennials (Hoffmann and Santelices 1991; Worm *et al.* 2001; Santelices *et al.* 2002).

Recognizing the entire life-cycle of marine organisms is critical to both understanding their ecology (e.g. Lotze *et al.* 1999; Morgan 2001) and implementing efficient management practices. The majority of theory on the decoupling of adult reproduction and juvenile recruitment in marine environments has been developed using fishes and invertebrates (e.g. Hixon *et al.* 2002) that disperse their larvae away from the site of release via currents. This understanding has revolutionized the way we think about designing reserves and marine protected areas and has proven invaluable to resource managers. Such recognition for many marine plants, which are key habitat providers, requires approaches that look beyond macroscopic stages and focus on how the microscopic stages may serve to decouple adult reproduction and juvenile recruitment through the process of delayed development. A population's reliance on a propagule bank rather than long distance dispersal for recovery would dictate that kelp populations be managed as separate patch populations instead of a meta-population for

which regional persistence depends on high colonization rates via dispersal. Much as our developed understanding of certain factors which break terrestrial seed bank dormancy is integral to agriculture and natural lands management practices, our understanding of microscopic macroalgal development is critical. Indeed successful maintenance of existing kelp forests, as well as currently mandated restoration efforts for those that have declined, requires this critical understanding.

ACKNOWLEDGEMENTS

REFERENCES

Abeles F.B., Morgan P.W. and Saltveit M.E. 1992. *Ethylene in Plant Biology*. Academic Press, New York.

Anderson B.S., Hunt J.W., Turpen S.L., Coulon C.A. and Martin M. 1990. Copper toxicity to microscopic stages of giant kelp *Macrocystis pyrifera*: interpopulation comparisons and temporal variability. *Mar. Ecol. Prog. Ser*. **68:** 147-156.

Anderson T.W. 1994. Role of macroalgal structure in the distribution and abundance of a temperate reef fish. *Mar. Ecol. Prog. Ser*. **113:** 279-290.

Blanchette C.A. 1996. Seasonal patterns of disturbance influence recruitment of the sea palm, *Postelsia palmaeformis. J. Exp. Mar. Biol*. **197:** 1-14.

Bullock J.M., Hill B.C., Dale M.P. and Silvertown J. 1994. An experimental study of the effects of sheep grazing on vegetation change in a species poor grassland and the role of seedlings recruitment into gaps. *J. Appl. Ecol*. **31:** 493-507.

Carr M.H. 1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology*. **75:** 1320-1333.

Chapman A.R.O. 1986. Population and community ecology of seaweeds. *Adv. Mar. Biol*. **23:** 1-161.

Chapman A.R.O. and Burrows E.M. 1971. Field and culture studies of *Desmarestia aculeata* (L.) Lamour. *Phycologia* **10:** 63-76.

Cohen D. 1966. Optimizing reproduction in a randomly varying environment. *J. Theor. Biol*. **12:** 119-232.

Cohen D. and Levin S.A. 1987. The interaction between dispersal and dormancy strategies in varying and heterogeneous environments. In: Teramato E. and Yamaguchi M. (eds), *Mathematical Topics in Population Biology, Morphogenesis and Neurosciences, Lecture Notes in Biomathematics*. Springer-Verlag, New York. pp. 110-122.

Crocker W.M. 1916. Mechanics of dormancy in seeds. *Am. J. Bot*. **3:** 99-120.

Crowe J.H. 1971. Anhydrobiosis: an unsolved problem. *Amer. Nat*. **195:** 563-573.

Dayton P.K. 1985. Ecology of kelp communities. *Ann. Rev. Ecol.*

Sys. **16:** 215-245.

Dayton P.K. and Tegner M.J. 1990. Bottoms beneath troubled waters: benthic impacts of the 1982-1984 El Niño in the temperate zone. In: Glynn P.W. (ed), *Global Consequences of the 1982-83 El Niño-Southern Oscillation.* Elsevier Science Publishers, Miami. pp. 433-472.

Dayton, P.K., Tegner M.J., Parnell E. and Edwards P.B. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.* **62:** 421-445.

Dean T.A., Jacobsen F.R., Thies K. and Lagos S.L. 1988. Differential-effects of grazing by white sea-urchins on recruitment of brown algae. *Mar. Ecol. Prog. Ser.* **48:** 99-102.

Devinny J.S. and Volse L.A. 1978. Effects of sediments on development of *Macrocystis pyrifera* gametophytes. *Mar. Biol.* **48:** 343-348.

Deysher L.E. and Dean T.A. 1984. Critical irradiance levels and the interactive effects of quantum irradiance and dose on gametogenesis in the giant kelp, *Macrocystis pyrifera.* *J. Phycol.* **20:** 520-524.

Dube M.A. and Ball E. 1971. *Desmarestia* sp. associated with the sea pen *Ptilosarcus gurneyi* (Gray). *J. Phycol.* **7:** 218-220.

Duggins D.O., Eckman J.E., Siddon C.E. and Klinger T. 2001. Interactive roles of mesograzers and current flow in survival of kelps. *Mar. Ecol. Prog. Ser.* **223:** 143-155.

Edwards M.S. 1998. Effects of long-term kelp canopy exclusion on the abundance of the annual alga *Desmarestia ligulata* (light F). *J. Exp. Mar. Biol.* **228:** 309-326.

Edwards M.S. 1999. Using in situ substratum sterilization and fluorescence microscopy in studies of microscopic stages of marine macroalgae. *Hydrobiologia* **399:** 253-259.

Edwards M.S. 2000. The role of alternate life-history stages of a marine macroalga: A seed bank analogue? *Ecology* **81:** 2404-2415.

Edwards M.S. 2004. Estimating scale-dependency in disturbance impacts: El Ninos and giant kelp forests in the northeast Pacific. *Oecologia* **138:** 436-447.

Edwards M.S. and Estes J.A. 2006. Catastrophe, recovery and range limitation in giant kelp forests of the Northeast Pacific Ocean. *Mar. Ecol. Prog. Ser.* (in press)

Edwards M.S. and Hernández-Carmona G. 2005. Delayed recovery of giant kelp near its southern range limit in the North Pacific following El Niño. *Mar. Biol.* **147:** 273-279.

Edwards G.R. and Crawley M.J. 1999. Herbivores, seed banks and seedling recruitment in mesic grassland. *J. Ecol.* **87:** 423-435.

Feofilova E.P. 2003. Deceleration of vital activity as a universal biochemical mechanism ensuring adaptation of microorganisms to stress factors: A review. *Appl. Biochem. Microbiol.* **39:** 1-18.

Foster M.S. 1982. The regulation of macroalgal associations in kelp forests. In: Srivastava L. (ed.), *Synthetic and Degrative Processes in Marine Macrophytes.* Walter de Gruyter & Co, New York. pp. 185-203.

Foster M.S. and Schiel D.C. 1985. The ecology of giant kelp forests in California: a community profile. U.S. Fish and Wildlife service Biological Report. 85 (7.2).

Garbary D.J., Kim K.Y., Klinger, T. and Duggins D. 1999. Red algae as hosts for endophytic kelp gametophytes. *Mar. Biol.* **135:** 35-40.

Graham M.H. 2003. Coupling propagule output to supply at the edge and interior of a giant kelp forest. *Ecology* **84:** 1250-1264.

Grice G.D. and Marcus N.H. 1981. Dormant eggs of marine copepods. *Oceanogr. Mar. Biol. Annu. Rev.* **19:** 125-140.

Grime J.P. 1979. *Plant Strategies and Vegetation Processes.* Wiley, New York.

Hawkes M.W. 1983. *Hummbrella hydra Earle* (Rhodophyta, Gigartinales): seasonality, distribution, and development in laboratory culture. *Phycologia* **22:** 403-413.

Hernández-Carmona G., Robledo D. and Serviere-Zaragoza E. 2001. Effect of nutrient availability on *Macrocystis pyrifera* recruitment and survival near its southern limit off Baja California. *Bot. Mar.* **44:** 221-229.

Hinton, H.E. 1968. Reversible suspension of metabolism and the origin of life. *Proc. R. Soc. Lond [Biol].* **171:** 43-57.

Hixon M.A., Pacala S.W. and Sandin S.A. 2002. Population regulation: Historical context and contemporary challenges of open vs. closed systems. *Ecology* **83:** 1490-1508.

Hochachka P.W. and Guppy M. 1987. *Metabolic Arrest and the Control of Biological Time.* Harvard University Press, Cambridge.

Hoffmann A.J. and Santelices B. 1991. Banks of algal microscopic forms - hypotheses on their functioning and comparisons with seed banks. *Mar. Ecol. Prog. Ser.* **79:** 185-194.

Hoffman A.J., Avila M. and Santelices B. 1984. Interactions of nitrate and phosphate on the development of microscopic stages of *Lessonia Nigrescens* Bory (Phaeophyta). *J. Exp. Mar. Biol.* **78:** 177-186.

Hollibaugh J.T., Seibert D.L.R. and Thomas W.H. 1981. Observations on the survival and germination of resting spores of three *Chaetoceros* (Bacillariophyceae) species. *J. Phycol.* **17:** 1-9.

Hsiao S. and Druehl L.D. 1973. Environmental control of gametogenesis in *Laminaria saccharina.* IV. In situ development of gametophytes and young sporophytes. *J. Phycol.* **9:** 160-164.

Kain J.M. 1964. Aspects of the biology of *Laminaria* hyperborea. III. Survival and growth of gametophytes. *J. Mar. Biol. Assoc. UK.* **44:** 415-433.

Keeley J.E. 1987. Role of fire in seed germination of woody taxa in California Chaparral. *Ecology* **68:** 434-443.

Kinlan B.P., Graham M.H., Sala E. and Dayton P.K. 2003. Arrested development of giant kelp (*Macrocystis pyrifera*, Phaeophyceae) embryonic sporophytes: A mechanism for delayed recruitment in perennial kelps? *J. Phycol.* **39:** 47-57.

Klinger T. 1984. *Allocation of the blade surface area to meiospore production in the annual and perennial representatives of the genus* Laminaria. Masters Thesis, University of British Columbia.

Kopczak C.D., Zimmerman R.C. and Kremer J.N. 1991. Variation in nitrogen physiology and growth among geographically isolated populations of the giant kelp. *Macrocystis pyrifera* (Phaeophyta). *J. Phycol.* **27:** 149-158.

Kortner G. and Geiser F. 2000. The temporal organization of

daily torpor and hibernation: Circadian and circannual rhythms. *Chronobiol. Int.* **17:** 103-128.

Ladah L.B. Zertuche-Gonzalez J.A. and Hernández-Carmona G. 1999. Giant kelp (*Macrocystis pyrifera*, Phaeophyceae) recruitment near its southern limit in Baja California after mass disappearance during ENSO 1997-1998. *J. Phycol.* **35:** 1106-1112.

Leonard G.H. 1994. Effect of the bat star *Asterina miniata* on recruitment of the giant kelp *Macrocystis pyrifera*. *J. Exp. Mar. Biol.* **179:** 81-98.

Levin S.A., Cohen D. and Hastings A. 1984. Dispersal strategies in patchy environments. *Theor. Popul. Biol.* **26:** 165-191.

Lotze H.K., Schramm W., Schories D. and Worm B. 1999. Control of macroalgal blooms at early developmental stages: *Pilayella littoralis* versus *Enteromorpha* spp. *Oecologia* **119:** 46-54

Lotze H.K. and Worm B. 2000. Variable and complementary effects of herbivores on different life stages of bloom-forming macroalgae. *Mar. Ecol. Prog. Ser.* **200:** 167-175

Lüning K. 1980. Critical levels of light and temperature regulating the gametogenesis of three *Laminaria* species (Phaeophyceae). *J. Phycol.* **16:** 1-15.

Lüning K. 1981. Egg release in gametophytes of *Laminaria saccharina*: induction by blue light and U.V. *Br. J. Phycol.* **16:** 379-393.

Lüning K. 1994. When do algae grow? The third founders' lecture. *Eur. J. Phycol.* **29:** 61-67.

Lüning K. and Kadel P. 1993. Daylength range for circannual rhythmicity in *Pterygophora californica* (Alariaceae, Phaeophyta) and synchronization of seasonal growth by daylength cycles in several other brown algae. *Phycologia* **32:** 379-387.

Maier G. 1990. Spatial distribution of resting stages, rate of emergence from diapause, and times to adulthood and to the appearance of the first clutch in three species of cyclopoid copepods. *Hydrobiologia* **206:** 11-18.

Maier I., Hertweck C. and Boland W. 2001. Stereochemical specificity of Lamoxirene, the sperm-releasing pheromone in kelp (Laminariales, Phaeophyceae). *Biol. Bull.* **201:** 121-125.

Maynard Smith J. 1978. *The Evolution of Sex*. Cambridge University Press, Cambridge.

Morgan S. 2001. The larval ecology of marine communities. In: Bertness M., Gaines S. and Hay M. (eds), *Marine Community Ecology*. Sunderland Associates, Inc., Sunderland, MA. pp. 159-181.

Nakahara H. 1984. Alternation of generations in some brown algae in unialgal axenic cultures. *Sci. Pap. Inst. Algo.l Res.* **7:** 91-184.

Nelson D.R. 2002. Current status of the Tardigrada: Evolution and ecology. *Integr. Comp. Biol.* **42:** 652-659.

Pake C.E. and Venable D.L. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology* **77:** 1427-1435.

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

Pierce S.M. and Cowling R.M. 1991. Dynamics of soil-stored seed banks of six shrubs in fire-prone dune fynbos. *J. Ecol.* **79:** 731-747.

Raimondi P.T., Reed D.C., Gaylord B. and Washburn L. 2004. Effects of self-fertilization in the giant kelp, *Macrocystis pyrifera*. *Ecology* **85:** 3267-3276.

Reed D.C. 1990. The effects of variable settlement and early competition on patterns of kelp recruitment. *Ecology* **71:** 776-787.

Reed D.C., Anderson T.W., Ebeling A.W. and Anghera M. 1997. The role of reproductive synchrony in the colonization potential of kelp. *Ecology* **78:** 2443-2457.

Reed D.C., Lewis R.J. and Anghera M. 1994. Effects of an open-coast oil-production outfall on patterns of giant kelp (*Macrocystis pyrifera*) recruitment. *Mar. Biol.* **120:** 25-31.

Reed D.C., Neushul M. and Ebeling A.W. 1991. Role of settlement density on gametophyte growth and reproduction in the kelps *Pterygophora californica* and *Macrocystis pyrifera* (Phaeophyceae). *J. Phycol.* **27:** 361-366.

Rees M. 1996. Evolutionary ecology of seed dormancy and seed size. *Philos. Trans. R. Soc. London [Biol].* **351:** 1299-1308.

Rengefors K., Gustafsson S. and Stahl-Delbanco A. 2004. Factors regulating the recruitment of cyanobacterial and eukaryotic phytoplankton from littoral and profundal sediments. *Aquat. Microb. Ecol.* **36:** 213-226.

Rogers W.E. and Hartnett D.C. 2001. Temporal vegetation dynamics and recolonization mechanisms of different sized soil disturbances in tallgrass prairie. *Am. J. Bot.* **88:** 1634-1642.

Saito Y. 1975. *Undaria*. In: Tokida J. and Hirose H. (eds), *Advances of Phycology in Japan*. Dr. W. Junk, The Hague. pp 304-320.

Sala E. and Graham M.H. 2002. Community-wide distribution of predator-prey interaction strength in kelp forests. *Proc. Natl. Acad. Sci.* **99:** 3678-3683.

Santelices B., Aedo D. and Hoffmann A. 2002. Banks of microscopic forms and survival to darkness of propagules and microscopic stages of macroalgae. *Rev. Chil. Hist. Nat.* **75:** 547-555.

Santelices B., Hoffmann A.J., Aedo D., Bobadilla M. and Otaiza R. 1995. A bank of microscopic forms on disturbed boulders and stones in tide pools. *Mar. Ecol. Prog. Ser.* **129:** 215-228.

Slocum C.J. 1980. Differential succeptability to grazers in two phases of an intertidal alga: advantages of heteromorphic generations. *J. Exp. Mar. Biol.* **46:** 99-110.

Swanson A.K. and Druehl L.D. 2000. Differential meiospore size and tolerance of ultraviolet light stress within and among kelp species along a depth gradient. *Mar. Biol.* **136:** 657-664

Tauber M.J. and Tauber C.A. 1978. Evolution of phenological strategies on insects: a comparative approach with eco-physical and genetic considerations. In: Dingle H. (ed.), *Evolution of Insect Migration and Diapause*. Springer-Verlag, New York. pp. 53-71.

Thornber C.S. and Gaines S.D. 2004. Population demographics in species with biphasic life cycles. *Ecology* **85:** 1661-1674.

Thorber C.S., Kinlan B.P., Graham M.H. and Stachowicz J.J. 2004. Population ecology of the invasive kelp *Undaria pinnatifida* in California: environmental and biological controls on demography. *Mar. Ecol. Prog. Ser*. **268:** 69-80.

Van den Hoek C., Mann C. and Jahns H.M. 1995. *Algae: An introduction to Phycology.* Cambridge Press, Cambridge.

Venable D. L. and Brown J.S. 1993. The population dynamic functions of seed dispersal. *Vegetatio* **108:** 31-55.

Venable D. L. and Lawlor L. 1980. Delayed germination and dispersal in desert annuals: Escape in space and time. *Oecologia* **46:** 272-282.

Wiencke C. and tom Dieck I. 1989. Temperature requirements for growth and temperature tolerance of macroalgae endemic to the Antarctic region. *Mar. Ecol. Prog. Ser*. **54:** 189-197.

Wiencke C. and tom Dieck I. 1990. Temperature requirements for growth and survival of macroalgae from Antarctica and southern Chile. *Mar. Ecol. Prog. Ser*. **59:** 157-170.

Worm B., Lotze H.K. and Sommer U. 2001. Algal propagule banks modify competition, consumer and resource control on Baltic rocky shores. *Oecologia* **128:** 281-293.