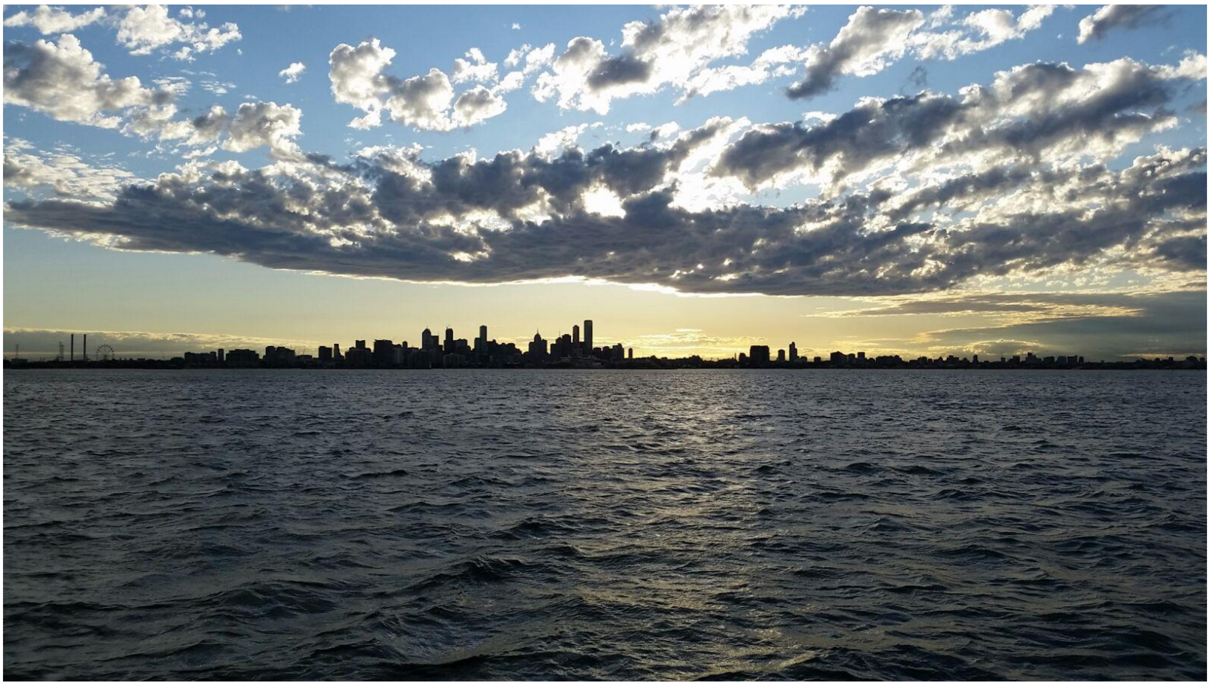
Do anthropogenic changes to marine ecosystems result in the formation of ecological traps?



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Abstract

Human activities such as overfishing, pollution and the introduction of invasive species have led to major changes in the marine environment. One of these anthropogenic impacts is the global proliferation of artificial structures for a variety of purposes, such as shoreline protection, wave and wind power stations, oil and gas platforms, and marinas. All of these structures have a secondary function: as habitat for marine organisms. Moreover, for generations, a large array of various types of purposely and accidently deployed artificial reefs have been used for the enhancement of recreational fisheries. More recently, planned and specially designed artificial reefs have also been used for management and conservation purposes, such as fish species protection, mediation of fisheries impacts, the redirection of fishing effort and habitat restoration. Regardless of the purposes of artificial reef deployment, all artificial reefs function as a habitat for marine species.

Habitats play an important role in structuring animal communities, and poor habitat quality can be detrimental to the survival of animal populations. Therefore, for artificial reefs to be successful, it is vitally important that they mimic natural reef structure and community composition as closely as possible. Many artificial reefs have failed to achieve their goals, potentially due to inappropriate size, placing and design. Despite short coming in artificial reef design or placement they may still be selected as habitat by many marine fishes.

The majority of marine fishes exhibit a pelagic larval stage that persists in the water column before settling onto a suitable habitat. Fish larvae use a combination of environmental cues to determine habitat suitability. Artificial reefs may mimic the habitat cues of a natural habitat but fail to provide adequate habitat diversity, complexity or the variety of other resources required for growth, reproduction, and survival. Preferential selection of an unfavourable habitat (i.e. a habitat that leads to lower fitness of individuals) is known as an "ecological trap". The ecological traps phenomenon has been relatively well documents in

terrestrial environments for a large array of species. However, despite its importance for conservation and management of marine ecosystems, ecological traps have been poorly investigated in marine environments. The introduction of an artificial structure may cause the formation of an ecological trap through the provision of a seemingly suitable habitat that provides lower fitness advantages.

Here, I investigated whether artificial reefs can act as ecological traps for fish populations and whether these effects may be reef design related. I examined temporal changes in fish community composition, recruitment rates and condition of individuals occupying different habitats (natural reefs, new design artificial reefs and Reef Ball reefs) at three locations in Port Phillip Bay, Victoria, Australia. Findings from **CHAPTER TWO**, where fish communities were compared between Reef Ball reefs and adjacent natural reefs, show that the performance of Reef Ball reefs as fish habitat greatly depends on the reef location and the type and quality of the adjacent natural reef. Generally, Reef Ball reefs supported richer fish communities than natural reefs, with the exception of one large continuous natural reef in Portarlington (Prince Georges Bank). However, Reef Ball reefs supported on average 75% lower fish abundances than natural reefs, with the exception of low-lying boulder field reefs like Altona natural reef and Portarlington Steele's Rocks reef. The community composition of all habitats across all locations were significantly different. **CHAPTER THREE**, where fish communities were monitored for two years on three habitats (Reef Ball reefs, adjacent natural reefs and new design artificial reefs) across three locations, provides further support for findings in **CHAPTER TWO**. However, it also illustrates that suitable design of the artificial reef may greatly improve its performance as fish habitat. While natural reefs supported up to thirty times higher fish abundances than both types of artificial reefs, new design artificial reefs on average supported twice as many species as natural reefs or Reef Ball reefs across all locations. Moreover, despite large dissimilarities in fish community structure between all three habitats, fish community composition was the most similar between natural reefs and new design artificial reefs, indicating that new design artificial reefs are closer mimics of the natural reefs in Port Phillip Bay, Victoria. **CHAPTER FOUR** investigates habitat preferences of three common reef fish species (*Trachinops caudimaculatus, Vincentia conspersa* and *Trinorfoklia clarkei*) through the observation of recruitment patterns to three study habitats and through laboratory based habitat choice experiments. The results of **CHAPTER FOUR** highlight differences in recruitment patterns and habitat preferences between different fish species. While some species recruit in higher numbers to natural reefs (*T. caudimaculatus*), others present no differences in recruitment patterns (*T. clarkei*) or recruit in higher numbers to Reef Ball reefs (*V. conspersa*), at least in some locations. These findings were corroborated by the laboratory experiments for *T. caudimaculatus*, as recruits selected Reef Ball reefs almost three times as often as the other two habitats, but not for *V. conspersa*, which showed no evidence for habitat preference. Finally, **CHAPTER FIVE** investigates consequences of these choices to individual performance. The results of **CHAPTER FIVE** demonstrate that responses by fishes to different types of artificial habitats are strongly species-, location- and habitat-specific. Instantaneous mortality rates obtained from fortnightly recruitment monitoring of *T. caudimaculatus* and mark-resighting experiments both indicate significantly higher mortality rates of this fish species on Reef Ball reefs and provide the first evidence of ecological trap formation in the marine environment. Generally, the higher condition of *V. conspersa* individuals on Reef Ball reefs indicates adaptive habitat selection for this fish species. In contrast, the higher condition of *T. clarkei*, combined with their lack of habitat preference, suggests, for the first time in a marine environment, the potential for the formation of a perceptual trap (when animals preferentially avoid high-quality habitat).

Artificial reefs are excellent management tools of degraded habitats, recreational fisheries and for fish species conservation. However, poorly designed or poorly placed artificial reefs may lead to insufficient positive outcomes or even significant negative impacts on marine communities. Combined with their high costs, these effects may, in turn, lead to wasted resources and a negative community attitude towards future artificial reef deployments, which in turn could impede further management and conservation efforts.

Declaration

This declaration is to certify that:

(i) The thesis comprises only my original work towards the PhD except where indicated in the Preface.

(ii) Due acknowledgement has been made in the text to all other material used.

(iii) The thesis is less than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices.

Valeriya Komyakova

April 2017

Preface

While the analysis, writing, and ideas contained in this thesis are my original work, some components were carried out in collaboration with a number of colleagues.

Professor Steve Swearer provided expert advice and guidance through the research project, including sampling design, methodologies, training in VIE tagging, ideas for the artificial reef design and editorial assistance with all of the chapters.

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Dean Chamberlain and Kevin Menzies provided extensive fieldwork assistance and assistance with artificial reef design.

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I would like to dedicate this thesis first of all to my parents, but also to my siblings, my friends and two people that have been extremely influential in my life and are dearly loved, uncle Pasha Lihobabenko and Anastasiya Ageeva. Deepest thanks to all the people that believed in my dream and believe in me.

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CHAPTER ONE:

General Introduction: artificial reefs, ecological traps and their consequences for fish populations

Frankston Reef Ball reef with a school of *Trachinops caudimaculatus* juveniles

1.1 Ecological traps and their potential relevance to marine ecosystems

Humans have had significant negative impacts on every ecosystem on the planet, especially since industrialisation (Vitousek *et al.*, 1997; Sanderson *et al.*, 2002; Halpern *et al.*, 2008; Pereira *et al.*, 2010; Sih *et al.*, 2011). Sih (2013) identified five primary human impacts that have had the most severe consequences to the natural environment: climate change, exotic species introduction, pollution, human harvesting and habitat change. These and other human impacts have led to accelerated changes in natural environments, which is referred to as Human-Induced Rapid Environmental Change (Sih, 2013; Hale and Swearer, 2016). The majority of animals use a variety of cues to detect suitable habitat, nesting sites, breeding sites, hunting grounds etc. (Jones, 2001; Kingsford *et al.*, 2002; Kristan, 2003; Stamps and Krishnan, 2005). However, changes to the environment caused by human activities may mask or alter those cues leading to inadequate choices, such as avoidance of good quality habitat or preference for poor quality habitat (Battin, 2004; Gilroy and Sutherland, 2007; Robertson *et al.*, 2013; Hale and Swearer, 2016).

The situation in which an animal preferentially selects a lower quality habitat that leads to reduced fitness outcomes has been referred to in the literature as an "ecological trap" (Kingsford *et al.*, 2002; Schlaepfer *et al.*, 2002; Kristan, 2003; Battin, 2004; Robertson *et al.*, 2013). The term was first introduced over 4 decades ago (Dwernychuk and Boag, 1972). Since then the topic has received a significant amount of attention (Schlaepfer *et al.*, 2002; Battin, 2004; Robertson and Hutto, 2006; Hale and Swearer, 2016), particularly in terrestrial ecosystems in the northern hemisphere. Some of the strongest evidence for the formation of ecological traps comes from aquatic insects. Insects use horizontally polarized light to detect water surfaces. However, many man-made materials polarize light in a similar way (e.g. plastic, some glass, oils etc.) causing insects to lay eggs on those surfaces, which leads to reduced reproductive outcomes (Horváth *et al.*, 2007; Horváth *et al.*, 2009). Another compelling example is the effects of coastal light pollution near sea turtle nesting beaches where new hatchlings are attracted by the artificial lights and travel away from the water, which consequently leads to mortality (Witherington and Martin, 2000; Schlaepfer *et al.*, 2002; Longcore and Rich, 2004). Similarly, anthropogenic changes to the natural habitat of desert lizards in Israel caused increased predatory bird activity leading to higher lizard mortality (Hawlena *et al.*, 2010).

Ecological traps may have significant negative consequences to animal communities, through increasing risk of local extinctions; and therefore, require careful attention (Battin, 2004; Hale and Swearer, 2016). While there are numerous examples of ecological traps caused by anthropogenic activities in terrestrial environments (amphibians: Suislepp *et al.* (2011); birds: Dwernychuk and Boag (1972), Misenhelter and Rotenberry (2000); insects: Horváth *et al.* (1998), Horváth *et al.* (2007), Severns (2011); mammals: Reid *et al.* (2010); reptiles: Hawlena *et al.* (2010)), only a handful of studies have investigated the potential for ecological traps to form in marine and freshwater environments (Hallier and Gaertner, 2008; Pelicice and Agostinho, 2008; Dempster *et al.*, 2011; Reubens *et al.*, 2013)

1.2 Proliferation of artificial reefs in the marine environment

Approximately half of the world's population resides in close proximity to the shore (Halpern *et al.*, 2008; Seto *et al.*, 2012). For thousands of years, humans have relied on the ocean for transport routes, energy and food resources, and these exploitations have led to major intrusions into marine environments and significant negative impacts, including overfishing, habitat fragmentation and loss, introduction of invasive species, and pollution. (Jackson *et al.*, 2001; Halpern *et al.*, 2008; Jackson, 2008; McCauley *et al.*, 2015). As the human population is predicted to double by 2025 (Bos *et al.*, 1992; Seto *et al.*, 2012), exploitation of and impacts on marine environments are expected to increase.

One of the major intrusions into the marine environment is the proliferation of a large variety of artificial structures, such as marinas and moorings, wind and wave power stations, oil and gas platforms, underwater tunnels, artificial islands, breakwater walls, groins and purposely or accidently deployed artificial reefs. This proliferation of artificial structures is commonly referred to as ocean sprawl (Duarte *et al.*, 2013; Firth *et al.*, 2016; Heery *et al.*, 2016). While all of the hard artificial structures could act as artificial reefs, their functionality as habitat for marine organisms may differ. Moreover, deployments of waste materials and wrecks is a costly endeavour, that often doesn't achieve its goals or even carries negative consequences (Bohnsack and Sutherland, 1985; Milon, 1989; Seaman Jr and Sprague, 1991; Hamilton *et al.*, 1993; Collins *et al.*, 1995; Baine, 2001; Edelist, 2006).

In recent decades, millions of dollars have been spent on the design and construction of specialised artificial reefs to improve their function (Bohnsack and Sutherland, 1985; Thierry, 1988; Seaman Jr and Sprague, 1991; Baine, 2001; Edelist, 2006; Seaman and Lindberg, 2009; Fabi *et al.*, 2011; Kheawwongjan and Kim, 2012). Moreover, artificial reefs have been used for enhancement of artesian fisheries for many decades through the attraction and potentially the production of fish biomass (Grove *et al.*, 1991; Seaman Jr and Sprague, 1991; Edelist, 2006; Seaman and Lindberg, 2009; Fabi *et al.*, 2011). More recently, specially designed artificial reefs have been used not only for recreational fisheries enhancement, for waste disposal, and the diving industry, but also for the redirection of fishing efforts, habitat restoration and species conservation (Bohnsack and Sutherland, 1985; Seaman Jr and Sprague, 1991; Baine, 2001; Edelist, 2006; Fabi *et al.*, 2011). A large variety of the designs and materials have been used to construct artificial reefs – from basic brick and car tire reefs, to ship, car and train wrecks, and elaborate concrete and metal reef designs (Seaman Jr and

Sprague, 1991; Baine, 2001; Seaman and Lindberg, 2009; Fabi *et al.*, 2011). However, many of these designs focus predominantly on material and structure durability and stability and less on the specific habitat requirements of associated marine organisms and the primary goals of their deployment, such as new biomass production, fisheries redirection or habitat restoration.

The success of an artificial reef is greatly dependent on the purpose of the reef's deployment and on the potential negative impacts associated with that deployment. In general, an effective artificial reef should 1) mimic the natural habitat as closely as possible, and support animal communities typical of the area of deployment in order to minimise any negative impacts of creating novel communities (Connell and Glasby, 1999; Connell, 2001; Simon *et al.*, 2011); 2) minimise negative impacts to the area through, for example, pollution, recruitment redirection or other means; and 3) succeed in achieving the goals of deployment. These goals of deployment may include habitat restoration, new biomass production, fisheries redirection or species conservation. A large number of artificial reefs have failed to achieve their goals, potentially due to inappropriate reef design, size and/or deployment location (Pickering and Whitmarsh, 1997; Baine, 2001; Jan *et al.*, 2003; Campbell *et al.*, 2011; Hackradt *et al.*, 2011).

1.3 Summary of current knowledge of the impacts of artificial reefs

While artificial reefs have been the subject of interest for many decades, there are still large gaps in knowledge of their impacts on marine biota. Several studies have investigated the accumulation of individual species and fish community formation on artificial reefs (Bohnsack, 1989; Brickhill *et al.*, 2005; Langhamer and Wilhelmsson, 2009; Andersson and Öhman, 2010; Folpp *et al.*, 2011; Fowler and Booth, 2012; Folpp *et al.*, 2013). However, even more recent studies have overlooked the necessary comparisons between artificial and local natural reefs (Carr and Hixon, 1997; Rilov and Benayahu, 1998; Wilhelmsson *et al.*, 2006; Langhamer and Wilhelmsson, 2009; Langhamer *et al.*, 2009; Folpp *et al.*, 2011). Further, in some comparative studies, fish communities associated with an artificial reef were compared to the adjacent sand bottom habitat, rather than to equivalent hard substratum habitats (Alevizon and Gorham, 1989; Bortone *et al.*, 1994; Zalmon *et al.*, 2002). In those that investigated the differences in fish community structure between artificial reefs and local natural rocky or coral reefs, many reported higher abundances and diversity of fishes associated with artificial reefs (Bohnsack and Sutherland, 1985; Bohnsack, 1989; Tupper and Hunte, 1998; Hackradt *et al.*, 2011; Simon *et al.*, 2011; Folpp *et al.*, 2013), although the community composition between artificial and natural reefs reported in these studies often differed (Hackradt *et al.*, 2011; Simon *et al.*, 2011; Ford and Swearer, 2013; Simon *et al.*, 2013). These findings, however, are in stark contrast to one, if not the only, study that controlled for reef size and age, which found no differences in fish community composition between the two reef types (Carr and Hixon, 1997). This finding is important, as fish community composition associated with artificial reefs are likely to be influenced by reef size, age, material and design, distance from and quality of the nearest natural reefs, types of adjacent habitats, natural fish community structure, depth, and geographical and specific location of deployment (Milon, 1989; Carr and Hixon, 1997; Seaman and Jensen, 2000; Baine, 2001). Therefore, making generalisations among geographic locations, scales and artificial reef types is likely unhelpful, and each artificial reef should be compared with adjacent natural habitats that match the artificial reef as close as possible in size, depth and location, to determine genuine differences in fish community structure.

Although considerable research has been done on the fish community structure associated with artificial reefs, little is known about differences in habitat preferences between artificial and natural reefs. Some studies have investigated the temporal attraction potential of artificial reefs for highly mobile fish species (Bohnsack, 1989; Grossman *et al.*, 1997; Lindberg, 1997; Pickering and Whitmarsh, 1997; Scott *et al.*, 2015). However, information on small, territorial, reef-associated fish species, that are more likely to use artificial reefs as a permanent habitat, is more limited (Bohnsack, 1989; Grossman *et al.*, 1997).

Athough the “attraction-production” debate remains unresolved, most would agree that artificial reefs function as attraction devices for highly mobile, large fish species and are more likely to produce new biomass of the smaller, site-attached reef associated species (Bohnsack, 1989; Grossman *et al.*, 1997; Lindberg, 1997; Pickering and Whitmarsh, 1997). In situations where habitat is limiting, the addition of artificial reefs may lead to positive outcomes for these small reef associated species. However, with current levels of overfishing and pollution, natural habitats may not be a limiting resource in many locations and hence the question is whether artificial reefs are more attractive than natural reefs, especially for new recruits (Grossman *et al.*, 1997; Jackson *et al.*, 2001; Halpern *et al.*, 2008; Jackson, 2008). If artificial reefs are more attractive to fish species than natural reefs, artificial reefs could impact local fish communities if the performance of fishes on artificial reefs differs to fishes on natural reefs. Several previous studies have highlighted that individual condition of fish may be influenced by the quality of the occupied habitat, with better quality habitat generally leading to better fitness outcomes (Lloret and Planes, 2003; Amara *et al.*, 2009; Maceda-Veiga *et al.*, 2014; Yeung and Yang, 2017). Habitat complexity and diversity can also alter and mediate outcomes of predation and competition (Behrents, 1987; Hixon and Menge, 1991; Hixon and Beets, 1993; Stunz and Minello, 2001; Almany, 2004; Ford and Swearer, 2013). Furthermore, habitat quality may also lead to improved general fitness potentially through improved feeding outcomes or reduced stress (Lloret and Planes, 2003; Amara *et al.*, 2009; Maceda-Veiga *et al.*, 2014). Surprisingly, comparative studies of individual condition of fish from natural and artificial reefs/structures are remarkably scarce (Dempster *et al.*, 2011; Reubens *et al.*, 2013). The few studies that contrasted the condition of individuals occupying artificial and natural habitats did not report significant differences (Dempster *et al.*, 2011; Reubens *et al.*, 2013). Dempster *et al.* (2011) investigated whether fish farms in Norway may act as ecological traps for wild fish populations and proposed that fish farms may actually act as population sources for some fish species, as farm associated wild fishes demonstrated higher somatic and liver condition indexes than fish collected away from the farms. However, neither of these two studies looked at purposely-built artificial reefs. If artificial reefs are more attractive to some fish species than natural reefs and lead to lower fitness outcomes, they may act as ecological traps and have detrimental effects on fish populations, at least at the local scale.

Marine coastal hardening and the proliferation of artificial structures will continue to expand in the next several decades as human populations continue to grow and use the resources associated with the marine environment (Halpern *et al.*, 2008; Seto *et al.*, 2012; Firth *et al.*, 2016; Heery *et al.*, 2016). Therefore, understanding potential impacts, such as ecological trap formation associated with ocean sprawl, is of crucial importance for creating more environmentally friendly artificial structure designs, incorporating multi-function marine green engineering into artificial structures, such as for example wind and wave energy generators; and generating successful management strategies and conservation plans.

1.4 Thesis overview

The overall aim of this thesis is to examine whether artificial reefs can act as ecological traps for marine reef fish populations and whether these effects may be reef design related. A comparative investigation of fish community structure on commonly used artificial reefs (Reef Balls), new design artificial reefs and adjacent natural reefs (**CHAPTER TWO** and **THREE**) is presented, followed by an examination of fish habitat preferences for these three reef types (**CHAPTER FOUR**) and the consequences of these preferences for the condition and survival of individuals occupying different reef types (**CHAPTER FIVE**).

Specifically, **CHAPTER TWO** investigates differences and establishes general patterns in fish species richness, abundance and community composition between commonly used artificial reefs (Reef Balls) and adjacent natural reefs at three locations in Port Phillip Bay, Victoria, Australia.

CHAPTER THREE employs an experimental approach to examine whether changes to artificial reef design may lead to the improvement in the fish community structure artificial reef supports by bringing it closer to the local natural reef fish community structure. Therefore, it examines differences in fish community structure between Reef Ball reefs, adjacent natural reefs and new design artificial reefs and investigates the changes in the fish community structure on these three habitats at three locations in Port Phillip Bay, Victoria, Australia over a two-year period.

CHAPTER FOUR employs *in situ* observations and laboratory-based habitat choice experiments to investigate habitat preferences of three study species (*Trachinops caudimaculatus*, *Trinorfolkia clarkei* and *Vincentia conspersa*) for three reef types (Reef Ball reef, natural reef and new design artificial reef).

CHAPTER FIVE uses a mark-resighting study using visible implant elastomer (VIE) tagging and a longitudinal study to investigate differences in mortality rates of newly recruited *T. caudimaculatus* among reef types at Frankston, Port Phillip Bay, Victoria, Australia. Additionally, **CHAPTER FIVE** explores differences in condition of individuals using several measures of condition (relative weight (*W*rm), gonadosomatic index (GSI) and hepatosomatic index (HSI)) for the three reef types at Altona and Frankston. Two species (*V. conspersa* and *T. clarkei*) were studied over two years and a third species (*T. caudimaculatus*) was observed for one year.

CHAPTER SIX combines the results of the investigative studies explored in **CHAPTER TWO** through **FIVE** and analyses available evidence for the potential for ecological trap formation in the marine environment based on those results. It further examines the potential impacts of deployment of artificial reefs on fish populations and provides advice for future green-marine engineering of artificial habitats to help inform future management and conservation strategies.

1.5 References

Alevizon, W. S. and Gorham, J. C. (1989) Effects of artificial reef deployment on nearby resident fishes. *Bulletin of Marine Science*, 44(2), 646-661.

Almany, G. R. (2004) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos*, 106(2), 275-284.

Amara, R., Selleslagh, J., Billon, G. and Minier, C. (2009) Growth and condition of 0-group European flounder, *Platichthys flesus*, as indicator of estuarine habitat quality. *Hydrobiologia*, 627(1), 87.

Andersson, M. H. and Öhman, M. C. (2010) Fish and sessile assemblages associated with wind-turbine constructions in the Baltic Sea. *Marine and Freshwater Research*, 61(6), 642-650.

Baine, M. (2001) Artificial reefs: a review of their design, application, management and performance. *Ocean & Coastal Management*, 44(3–4), 241-259.

Battin, J. (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, 18(6), 1482-1491.

Behrents, K. C. (1987) The influence of shelter availability on recruitment and early juvenile survivorship of *Lythrypnus dalli* Gilbert (Pisces: Gobiidae). *Journal of Experimental Marine Biology and Ecology*, 107(1), 45-59.

Bohnsack, J. A. (1989) Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? *Bulletin of Marine Science*, 44(2), 631-645.

Bohnsack, J. A. and Sutherland, D. L. (1985) Artificial reef research: A review with recommendations for future priorities. *Bulletin of Marine Science*, 37(1), 11-39.

Bortone, S. A., Van Tassell, J., Brito, A., Falcón, J. M., Mena, J. and Bundrick, C. M. (1994) Enhancement of the nearshore fish assemblage in the Canary Islands with artificial habitats. *Bulletin of Marine Science*, 55(2-3), 602-608.

Bos, E., Vu, M. T., Levin, A. and Bulatao, R. A. (1992) World population projections 1992-Estimates and projections with related demographic statistics. Baltimore, Maryland, Johns Hopkins University Press, VII, 515 p.

Brickhill, M. J., Lee, S. Y. and Connolly, R. M. (2005) Fishes associated with artificial reefs: attributing changes to attraction or production using novel approaches. *Journal of Fish Biology*, 67, 53-71.

Campbell, M. D., Rose, K., Boswell, K. and Cowan, J. (2011) Individual-based modeling of an artificial reef fish community: Effects of habitat quantity and degree of refuge. *Ecological Modelling*, 222(23–24), 3895-3909.

Carr, M. H. and Hixon, M. A. (1997) Artificial reefs: the importance of comparisons with natural reefs. *Fisheries*, 22(4), 28-33.

Collins, K. J., Jensen, A. C. and Albert, S. (1995) A review of waste tyre utilisation in the marine environment. *Chemistry and Ecology*, 10(3-4), 205-216.

Connell, S. D. (2001) Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs. *Marine Environmental Research*, 52(2), 115-125.

Connell, S. D. and Glasby, T. M. (1999) Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. *Marine Environmental Research*, 47(4), 373-387.

Dempster, T., Sanchez-Jerez, P., Fernandez-Jover, D., Bayle-Sempere, J., Nilsen, R., Bjørn, P.-A. and Uglem, I. (2011) Proxy Measures of Fitness Suggest Coastal Fish Farms Can Act as Population Sources and Not Ecological Traps for Wild Gadoid Fish. *PLoS ONE*, 6(1), e15646.

Duarte, C. M., Pitt, K. A., Lucas, C. H., Purcell, J. E., Uye, S.-i., Robinson, K., Brotz, L., Decker, M. B., Sutherland, K. R. and Malej, A. (2013) Is global ocean sprawl a cause of jellyfish blooms? *Frontiers in Ecology and the Environment*, 11(2), 91-97.

Dwernychuk, L. and Boag, D. (1972) Ducks nesting in association with gulls—An ecological trap? *Canadian Journal of Zoology*, 50(5), 559-563.

Edelist, D. (2006) Influence of Levantine artificial reefs on the fish assemblages of the surrounding seabed and global history and evolution of artificial reefs, University of Haifa.

Fabi, G., Spagnolo, A., Bellan-Santini, D., Charbonnel, E., Çiçek, B. A., García, J. J. G., Jensen, A. C., Kallianiotis, A. and Santos, M. N. d. (2011) Overview on artificial reefs in Europe. *Brazilian Journal of Oceanography*, 59, 155-166.

Firth, L. B., Knights, A. M., Thompson, R., Mieszkowska, N., Bridger, D., Evans, A., Moore, P., O'Connor, N., Sheehan, E. and Hawkins, S. (2016) Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. *Oceanogr. Mar. Biol. Ann. Rev*.

Folpp, H., Lowry, M., Gregson, M. and Suthers, I. M. (2011) Colonization and community development of fish assemblages associated with estuarine artificial reefs. *Brazilian Journal of Oceanography*, 59, 55-67.

Folpp, H., Lowry, M., Gregson, M. and Suthers, I. M. (2013) Fish assemblages on estuarine artificial reefs: natural rocky-reef mimics or discrete assemblages? *PLoS ONE*, 8(6), e63505.

Ford, J. R. and Swearer, S. E. (2013) Two's company, three's a crowd: Food and shelter limitation outweigh the benefits of group living in a shoaling fish. *Ecology*, 94(5), 1069-1077.

Fowler, A. M. and Booth, D. J. (2012) How well do sunken vessels approximate fish assemblages on coral reefs? Conservation implications of vessel-reef deployments. *Marine Biology*, 159(12), 2787-2796.

Gilroy, J. J. and Sutherland, W. J. (2007) Beyond ecological traps: perceptual errors and undervalued resources. *Trends in Ecology & Evolution*, 22(7), 351-356.

Grossman, G. D., Jones, G. P. and Seaman Jr, W. J. (1997) Do artificial reefs increase regional fish production? A review of existing data. *Fisheries*, 22(4), 17-23.

Grove, R. S., Sonu, C. J. and Nakamura, M. (1991) 4 - Design and engineering of manufactured habitats for fisheries enhancement A2 - Seaman, William. In *Artificial habitats for marine and freshwater fisheries* (Ed. L. M. Sprague), Academic Press, San Diego, pp. 109-152.

Hackradt, C. W., Félix-Hackradt, F. C. and García-Charton, J. A. (2011) Influence of habitat structure on fish assemblage of an artificial reef in southern Brazil. *Marine Environmental Research*, 72(5), 235-247.

Hale, R. and Swearer, S. E. (2016) Ecological traps: current evidence and future directions. *Proceedings of the Royal Society B: Biological Sciences*, 283(1824).

Hallier, J. and Gaertner, D. (2008) Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Marine Ecology Progress Series*, 353, 255-264.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R. and Watson, R. (2008) A global map of human impact on marine ecosystems. *Science*, 319(5865), 948-952.

Hamilton, K. L., Nelson, W. G. and Curley, J. L. (1993) Toxicological evaluation of the effects of waste-to-energy ash-concrete on two marine species. *Environmental Toxicology and Chemistry*, 12(10), 1919-1930.

Hawlena, D., Saltz, D., Abramsky, Z. and Bouskila, A. (2010) Ecological trap for desert lizards caused by anthropogenic changes in habitat structure that favor predator activity. *Conservation Biology*, 24(3), 803-809.

Heery, E., Bishop, M., Critchley, L., Bugnot, A., Airoldi, L., Mayer-Pinto, M., Sheehan, E., Coleman, R., Loke, L. and Johnston, E. (2016) Identifying the consequences of ocean sprawl for sedimentary habitats. *Journal of Experimental Marine Biology and Ecology*.

Hixon, M. A. and Beets, J. P. (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs*, 63(1), 77-101.

Hixon, M. A. and Menge, B. A. (1991) Species diversity: prey refuges modify the interactive effects of predation and competition. *Theoretical Population Biology*, 39(2), 178-200.

Horváth, G., Bernáth, B. and Molnár, G. (1998) Dragonflies find crude oil visually more attractive than water: multiple-choice experiments on dragonfly polarotaxis. *Naturwissenschaften*, 85(6), 292-297.

Horváth, G., Kriska, G., Malik, P. and Robertson, B. (2009) Polarized light pollution: a new kind of ecological photopollution. *Frontiers in Ecology and the Environment*, 7(6), 317-325.

Horváth, G., Malik, P., Kriska, G. and Wildermuth, H. (2007) Ecological traps for dragonflies in a cemetery: the attraction of Sympetrum species (Odonata: Libellulidae) by horizontally polarizing black gravestones. *Freshwater biology*, 52(9), 1700-1709.

Jackson, J. B. C. (2008) Ecological extinction and evolution in the brave new ocean. *Proceedings of the National Academy of Sciences*, 105(Supplement 1), 11458-11465.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. and Warner, R. R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293(5530), 629-637.

Jan, R.-Q., Liu, Y.-H., Chen, C.-Y., Wang, M.-C., Song, G.-S., Lin, H.-C. and Shao, K.-T. (2003) Effects of pile size of artificial reefs on the standing stocks of fishes. *Fisheries Research*, 63(3), 327-337.

Jones, J. (2001) Habitat selection studies in avian ecology: a critical review. *The auk*, 118(2), 557-562.

Kheawwongjan, A. and Kim, D.-S. (2012) Present status and prospects of artificial reefs in Thailand. *Ocean & Coastal Management*, 57, 21-33.

Kingsford, M. J., Leis, J. M., Shanks, A., Lindeman, K. C., Morgan, S. G. and Pineda, J. (2002) Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science*, 70(1), 309-340.

Kristan, I. I. I. W. B. (2003) The role of habitat selection behavior in population dynamics: source–sink systems and ecological traps. *Oikos*, 103(3), 457-468.

Langhamer, O. and Wilhelmsson, D. (2009) Colonisation of fish and crabs of wave energy foundations and the effects of manufactured holes – A field experiment. *Marine Environmental Research*, 68(4), 151-157.

Langhamer, O., Wilhelmsson, D. and Engström, J. (2009) Artificial reef effect and fouling impacts on offshore wave power foundations and buoys – a pilot study. *Estuarine, Coastal and Shelf Science*, 82(3), 426-432.

Lindberg, W. J. (1997) Can science resolve the attraction - production issue? *Fisheries*, 22(4), 10-13.

Lloret, J. and Planes, S. (2003) Condition, feeding and reproductive potential of white seabream Diplodus sargus as indicators of habitat quality and the effect of reserve protection in the northwestern Mediterranean. *Marine Ecology Progress Series*, 248, 197-208.

Longcore, T. and Rich, C. (2004) Ecological light pollution. *Frontiers in Ecology and the Environment*, 2(4), 191-198.

Maceda-Veiga, A., Green, A. J. and De Sostoa, A. (2014) Scaled body-mass index shows how habitat quality influences the condition of four fish taxa in north-eastern Spain and provides a novel indicator of ecosystem health. *Freshwater biology*, 59(6), 1145-1160.

McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H. and Warner, R. R. (2015) Marine defaunation: animal loss in the global ocean. *Science*, 347(6219).

Milon, J. W. (1989) Economic evaluation of artificial habitat for fisheries: progress and challenges. *Bulletin of Marine Science*, 44(2), 831-843.

Misenhelter, M. D. and Rotenberry, J. T. (2000) Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology*, 81(10), 2892-2901.

Pelicice, F. and Agostinho, A. A. (2008) Fish-passage facilities as ecological traps in large neotropical rivers. *Conservation Biology*, 22(1), 180-188.

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P., Fernandez-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R. and Cheung, W. W. (2010) Scenarios for global biodiversity in the 21st century. *Science*, 330(6010), 1496-1501.

Pickering, H. and Whitmarsh, D. (1997) Artificial reefs and fisheries exploitation: a review of the 'attraction versus production' debate, the influence of design and its significance for policy. *Fisheries Research*, 31(1), 39-59.

Reid, N., McDonald, R. A. and Montgomery, W. I. (2010) Homogeneous habitat can meet the discrete and varied resource requirements of hares but may set an ecological trap. *Biological Conservation*, 143(7), 1701-1706.

Reubens, J. T., Vandendriessche, S., Zenner, A. N., Degraer, S. and Vincx, M. (2013) Offshore wind farms as productive sites or ecological traps for gadoid fishes? – Impact on growth, condition index and diet composition. *Marine Environmental Research*, 90, 66-74.

Rilov, G. and Benayahu, Y. (1998) Vertical artificial structures as an alternative habitat for coral reef fishes in disturbed environments. *Marine Environmental Research*, 45(4–5), 431-451.

Robertson, B. A. and Hutto, R. L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, 87(5), 1075-1085.

Robertson, B. A., Rehage, J. S. and Sih, A. (2013) Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology & Evolution*, 28(9), 552-560.

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V. and Woolmer, G. (2002) The human footprint and the last of the wild: the human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. *BioScience*, 52(10), 891-904.

Schlaepfer, M. A., Runge, M. C. and Sherman, P. W. (2002) Ecological and evolutionary traps. *Trends in Ecology & Evolution*, 17(10), 474-480.

Scott, M. E., Smith, J. A., Lowry, M. B., Taylor, M. D. and Suthers, I. M. (2015) The influence of an offshore artificial reef on the abundance of fish in the surrounding pelagic environment. *Marine and Freshwater Research*, 66(5), 429-437.

Seaman Jr, W. and Sprague, L. M. (1991) 1 - Artificial habitat practices in aquatic systems. In *Artificial habitats for marine and freshwater fisheries*, Academic Press, San Diego, pp. 1-29.

Seaman, W. and Jensen, A. C. (2000) *Purposes and practices of artificial reef evaluation*, Boca Raton, FL: CRC Press LLC.

Seaman, W. and Lindberg, W. J. (2009) Artificial Reefs A2 - Steele, John H. In *Encyclopedia of Ocean Sciences (Second Edition)*, Academic Press, Oxford, pp. 226-233.

Seto, K. C., Güneralp, B. and Hutyra, L. R. (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, 109(40), 16083-16088.

Severns, P. M. (2011) Habitat restoration facilitates an ecological trap for a locally rare, wetland-restricted butterfly. *Insect Conservation and Diversity*, 4(3), 184-191.

Sih, A. (2013) Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour*, 85(5), 1077-1088.

Sih, A., Ferrari, M. C. O. and Harris, D. J. (2011) Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, 4(2), 367-387.

Simon, T., Joyeux, J.-C. and Pinheiro, H. T. (2013) Fish assemblages on shipwrecks and natural rocky reefs strongly differ in trophic structure. *Marine Environmental Research*, 90, 55-65.

Simon, T., Pinheiro, H. T. and Joyeux, J.-C. (2011) Target fishes on artificial reefs: Evidences of impacts over nearby natural environments. *Science of The Total Environment*, 409(21), 4579-4584.

Stamps, J. and Krishnan, V. (2005) Nonintuitive cue use in habitat selection. *Ecology*, 86(11), 2860-2867.

Stunz, G. W. and Minello, T. J. (2001) Habitat-related predation on juvenile wild-caught and hatchery-reared red drum Sciaenops ocellatus (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, 260(1), 13-25.

Suislepp, K., Rannap, R. and Lõhmus, A. (2011) Impacts of artificial drainage on amphibian breeding sites in hemiboreal forests. *Forest Ecology and Management*, 262(6), 1078-1083.

Thierry, J.-M. (1988) Artificial reefs in Japan — A general outline. *Aquacultural Engineering*, 7(5), 321-348.

Tupper, M. and Hunte, W. (1998) Predictability of fish assemblages on artificial and natural reefs in Barbados. *Bulletin of Marine Science*, 62(3), 919-935.

Vitousek, P. M., Mooney, H. A., Lubchenco, J. and Melillo, J. M. (1997) Human domination of Earth's ecosystems. *Science*, 277(5325), 494-499.

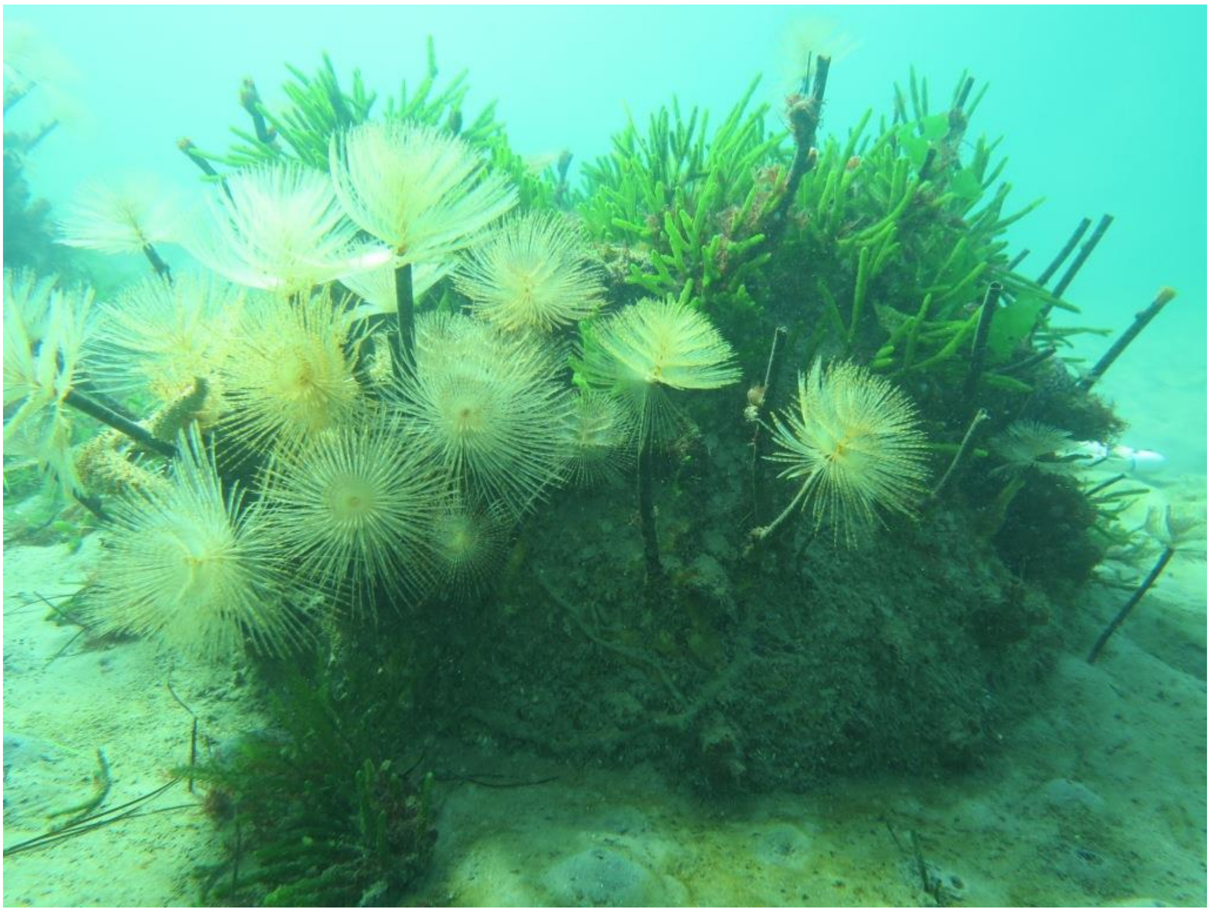
Wilhelmsson, D., Yahya, S. A. S. and Öhman, M. C. (2006) Effects of high-relief structures on cold temperate fish assemblages: a field experiment. *Marine Biology Research*, 2(2), 136-147.

Witherington, B. E. and Martin, R. E. (2000) Understanding, assessing, and resolving light-pollution problems on sea turtle nesting beaches. St. Petersburg, FL, Florida Marine Research Institute, (Florida Marine Research Institute. Technical Report, TR-2). <http://aquaticcommons.org/115/>.

Yeung, C. and Yang, M.-S. (2017) Habitat quality of the coastal southeastern Bering Sea for juvenile flatfishes from the relationships between diet, body condition and prey availability. *Journal of Sea Research*, 119, 17-27.

Zalmon, I. R., Novelli, R., Gomes, M. P. and Faria, V. V. (2002) Experimental results of an artificial reef programme on the Brazilian coast north of Rio de Janeiro. *ICES Journal of Marine Science*, 59(suppl), S83-S87.

CHAPTER TWO:
Comparative investigation of the fish assemblages formed on commonly used artificial reefs and adjacent natural reefs



Reef Ball reef at Altona

2.1 Abstract

Human activities such as overfishing, pollution and introduction of invasive species have led to major changes in the marine environment. One of these anthropogenic impacts is the global proliferation of artificial structures for a variety of purposes, such as shoreline protection, wave and wind power stations, oil and gas platforms, marinas etc. All of these structures have a secondary function, as habitat for marine organisms. Moreover, for hundreds of years humans have deliberately constructed and deployed artificial reefs for the purposes of artesian fisheries enhancement. Over the past half century, these deployments have become more planned and more effort has been put into the design and construction of artificial reefs, which are now not only used for recreational fisheries enhancement, but also as a tool for fisheries management, habitat restoration and fish species conservation. A large variety of artificial reef designs have been deployed all around the world, with a few studies investigating the "attraction – production" hypothesis, rates of fish accumulation on artificial structures and how the design or the material of artificial reef influences fish community composition. However, the performance of artificial reefs as a suitable habitat restoration tool is defined by how well it mimics the local natural community. Several studies on the fish community of artificial reefs have failed to compare community composition with the local natural reefs. Moreover, each reef design and location can exert a strong influence on the community of animals it supports and hence has to be investigated and monitored individually. Reef Ball reefs have become one of the most commonly used artificial reef designs; however, little is known about the fish community such reefs support, particularly in temperate waters.

Here, I investigated the difference in fish abundance, species richness and community structure on Reef Ball reefs in comparison to adjacent natural reefs at three locations in Port

Philips Bay, Victoria, Australia. The results showed that Reef Ball reefs generally support richer fish communities than natural reefs, with the exception of one large continuous natural reef in Portarlington (Prince Georges Bank). However, Reef Ball reefs supported on average 75% lower fish abundances than natural reefs, with the exception of low-lying boulder field reefs like Altona natural reef and Portarlington Steele's Rocks reef. Fish community composition was significantly different between all habitats across all locations; however, the lowest dissimilarities in fish community composition were observed between Reef Ball reefs and low-lying boulder field reefs. Reef Ball reefs may appear attractive to some species; however, they may fail to provide the habitat complexity or diversity found on natural reefs. If some fish species are attracted to Reef Ball reefs but suffer lower fitness, such as increased mortality, then Reef Ball reefs may function as ecological traps and carry negative consequences to reef fish communities in Port Philip Bay, particularly in further Reef Ball reefs deployments occur in the future and they become a greater percentage of available reef habitat. Further investigation into the effects of fish communities formed on Reef Ball reefs on the natural environment and whether the performance of artificial reefs as fish habitat can be improved through changing reef design is essential for future habitat restoration and fish conservation efforts.

2.2 Introduction

Human activities, such as overfishing, pollution and the introduction of invasive species, have led to major changes in the marine environment (McCauley *et al.*, 2015). Although there have been few anthropogenic global marine extinctions, many local marine extinctions and severe stock collapses have been reported all around the world (Jackson *et al.*, 2001; Jackson, 2008; McCauley *et al.*, 2015). The worldwide spread of marine infrastructure, commonly known as ocean sprawl, is one of the most common human activities that leads to habitat degradation, habitat loss and potential loss of marine species (Sih *et al.*, 2011; Sih, 2013; Firth *et al.*, 2016). Although much of marine construction leads to habitat loss and increases in pollution and sedimentation, the majority of artificial structures placed in marine environments also function as habitats themselves (Soldal *et al.*, 2002; Langhamer and Wilhelmsson, 2007; Macreadie *et al.*, 2011; Burt *et al.*, 2013). Moreover, artificial reefs, a common type of habitat modification, have been used globally for economy-based (e.g. tourism facilitation and shore protection) and conservation-based purposes (e.g. habitat restoration, species conservation, redistribution of fishing effort, and in some cases prevention of some types of fishing such as destructive bottom trawling) (Thierry, 1988; Seaman Jr and Sprague, 1991; Branden *et al.*, 1994; Baine, 2001; Fabi *et al.*, 2011; Langhamer, 2012). However, one of the main objectives of artificial reefs is for the enhancement of small-scale fisheries (Thierry, 1988; Seaman Jr and Sprague, 1991; Baine, 2001; Fabi *et al.*, 2011).

The long-standing debate over whether artificial reefs produce or simply redistribute fish biomass from nearby natural environments remains largely unresolved despite more than three decades of research (Bohnsack, 1989; Lindberg, 1997; Powers *et al.*, 2003; Brickhill *et al.*, 2005; Simon *et al.*, 2011). Artificial reefs have often been reported to support diverse and abundant fish communities, which has been used as evidence for biomass production (Bohnsack and Sutherland, 1985; Bohnsack, 1989; Tupper and Hunte, 1998; Hackradt *et al.*, 2011; Simon *et al.*, 2011; Folpp *et al.*, 2013). However, it is likely that the performance of artificial reefs along the production-attraction continuum depends on the species in question. Many artificial reefs likely function as fish attraction devices (FADs) for large, highly mobile fish species, especially for their adult stages, but potentially produce new biomass of small, highly site-attached fishes, while also functioning as nurseries for juveniles of some pelagic species (Bohnsack, 1989).

Apart from the lack of a comprehensive understanding of the production-attraction function of artificial reefs, the data on the compositional distinctness of fish communities associated with them is patchy and variable (Carr and Hixon, 1997; Hackradt *et al.*, 2011; Folpp *et al.*, 2013; Simon *et al.*, 2013). One of the major reasons for this, despite a large body of research available, is the limited number of comparisons of fish communities supported by artificial reefs versus nearby local natural reefs (Rilov and Benayahu, 1998; Wilhelmsson *et al.*, 2006; Langhamer and Wilhelmsson, 2009; Langhamer *et al.*, 2009; Folpp *et al.*, 2011). Many research papers on artificial reefs focus on rates of initial colonisation, effects of artificial reef designs, construction materials, distances between modules and distance from natural reef (Kellison and Sedberry, 1998; Vose and Nelson, 1998; Collins *et al.*, 2002; Jan *et al.*, 2003; Jordan *et al.*, 2005; Wilhelmsson *et al.*, 2006; dos Santos *et al.*, 2010; Folpp *et al.*, 2011). Several studies that did perform fish community comparisons between artificial reefs and natural habitats used soft-bottom habitats as their control sites and failed to run contrasts with more equivalent natural habitats, such as natural rocky or coral reefs (Alevizon and Gorham, 1989; Bortone *et al.*, 1994; Zalmon *et al.*, 2002). Moreover, many studies that do compare fish community structure on natural and artificial reefs usually focus on ship wrecks (e.g. Diamant *et al.*, 1986; Wilhelmsson *et al.*, 1998; Simon *et al.*, 2011; Fowler and Booth, 2012; Simon *et al.*, 2013).

Among the limited studies that have compared fish communities associated with purposely designed artificial reefs and natural reefs, results have been inconsistent, with some reporting differences in fish abundance, species richness, trophic and community structure between natural and artificial reefs (Hackradt *et al.*, 2011; Simon *et al.*, 2011; Folpp *et al.*, 2013; Simon *et al.*, 2013) whereas others have not (Carr and Hixon, 1997). These discrepancies may be attributed to differences in reef size, age and distance from natural reef (Milon, 1989; Carr and Hixon, 1997; Seaman and Jensen, 2000; Baine, 2001). However, artificial reef design and material are likely to also play an important role. If artificial reefs host fish communities distinct from natural ones, they may cause changes in local fish community structure, alter overall local diversity or abundance, lead to higher mortality rates of newly recruited or attracted individuals and cause changes to soft sediment communities (Bohnsack and Sutherland, 1985; Connell and Glasby, 1999; Connell, 2001; Simon *et al.*, 2011). Therefore, one of the primary objectives of artificial reef performance should be its ability to mimic natural reefs in fish community assemblage as closely as possible. Due to the potential for significant effects of artificial reef design and deployment location on fish community structure, each new artificial reef should be investigated independently.

Reef Ball reefs have become one of the most popular artificial reef designs around the world. They have been used for shore protection, habitat restoration and enhancement of recreational fisheries (Thierry, 1988; Grove *et al.*, 1991; Fabi *et al.*, 2011). They have also been considered as a tool with the combined benefits of scour protection and the provision of new habitat (Langhamer, 2012). According to Reef Ball Australia web site <http://www.reefballaustralia.com.au/default.htm>, over 3500 Reef Ball modules have been deployed in the coastal waters of most Australian states. However, the research on the performance of these reefs is relatively limited. A few studies have investigated fish community formation on Reef Ball reefs in the tropics (e.g. dos Santos *et al.,* 2010; Hackradt *et al.*, 2011) while comparable studies from temperate environments, particularly in comparison to natural reefs, are more scarce (but see Folpp *et al.*, 2013).

To assess whether Reef Ball reefs develop temperate reef fish assemblages similar to natural reefs, I examine fish abundance, species richness and community structure on natural reefs and adjacent three Reef Ball reefs deployed in Port Phillip Bay, Victoria, Australia for recreational fisheries enhancement.

2.3 Materials and Methods

Study area

The study was conducted in Port Phillip Bay, Victoria, Australia, which is one of the largest natural embayments in Australia, covering an area ~ 1,930 km^2 (Figure 2.1). The bay is adjacent to the city of Melbourne, Australia's second largest city and is connected to the ocean by a very narrow entrance (~3 km wide). The majority of the bay is quite shallow (> 8 m deep) with extensive areas of sandy bottom and relatively small patches of rocky reef (Harris *et al.*, 1996). Three locations within the bay, Frankston, Altona and Portarlington, had Reef Ball reefs that were constructed in 2012 to enhance recreational fishing through the provision of artificial fish habitat. All Reef Ball reefs were deployed in 3-5 m depth, 40-70 m offshore from piers (Agriculture Victoria State Government, 2016). At each location adjacent natural reefs were selected: one at Frankston and Altona and two at Portarlington (two reefs were sampled at Portarlington because the closest natural reef to the Reef Ball reef was a very shallow, poor quality natural reef). Natural reefs sampled lay in 2-5.5 m depth. The reefs in each location were within 2 km of each other.

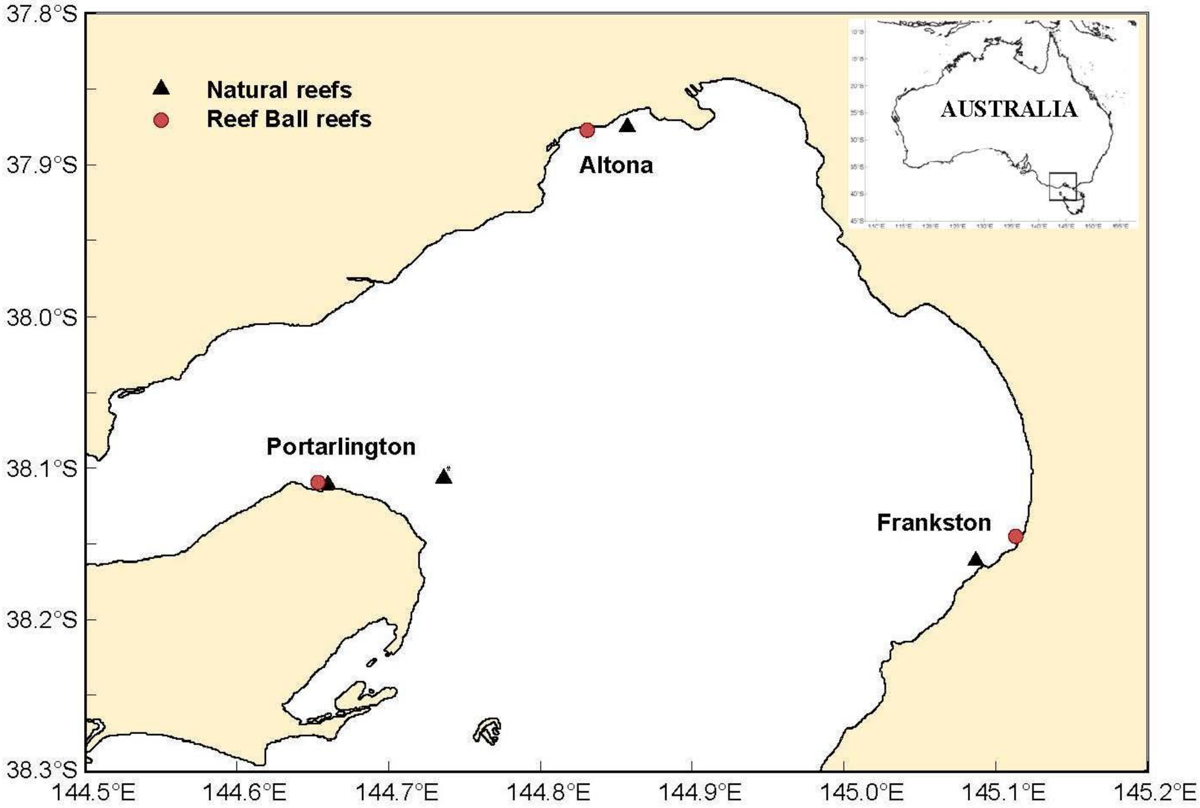


Fig. 2.1 Study area of Port Phillip Bay, Victoria, Australia. Black triangles identify the location of natural reefs at each site. For Portarlington, the asterisk indicates Prince George Bank natural reef (Natural reef), while the black triangle without asterisk indicates Steele's Rocks natural reef (Natural 2). Red circles identify the position of Reef Ball reefs at each site. The coastline was derived from the full resolution version of the Global Self-consistent, Hierarchical, High-resolution Geography (GSHHS) database (Wessel and Smith, 1996).

Natural reefs

Pelican reef (Frankston natural reef) is an average quality reef, with some good relief and high rugosity areas. It is separated from the Frankston Reef Ball reef by sand. These reefs are located approximately 2.7 km from each other. In comparison, natural reef at Altona is a low-lying shallow boulder field with little vertical relief and low macroalgal cover. At Altona the reefs are separated from each other by 2.5 km of sand and a few poor quality, small reef patches. Finally, at Portarlington, Prince George Bank natural reef is a low-lying reef with many small caves and dense macroalgal cover. It is the deepest natural reef sampled with an average depth of 5.5 m. Steele's Rocks natural reef is a shallow low-lying reef with several overhangs and caves. In general, it has relatively low macroalgal cover and is broken up by small patches of sand. It is the shallowest natural reef sampled with an average depth of 2.3 m. The distance between Prince George Bank and the Reef Ball reef is approximately 7.2 km, and between Steele's Rock and the Reef Ball reef is 0.6 km.

Reef Ball reefs

Reef Ball reefs consist predominantly of two types of hollow dome shaped modules: Mini-Bay Ball (~50 cm tall) and Bay Ball (~60 cm tall) of 2 primary designs (Figure 2.2). The modules have various sized openings, allowing fish movement. One design has predominantly large but different sized holes leading to a completely hollow large interior space (Figure 2.2 a), while the other design (less used) has smaller but similar sized holes leading to a narrower interior space (Figure 2.2 b). The modules are constructed from marine concrete with a relatively rough surface. Most Reef Balls are positioned in arrangements, as on a dice for five points, with 5-Reef-Ball units in close proximity to each other (between 0.5-1 m). Each 5-Reef-Ball unit arrangement covers an area of ~2.5 m in diameter and each 5-Reef-Ball unit arrangement lays approximately 5 m away from the next Reef- Ball unit arrangement. Each reef at each location consists of 18 5-Reef-Ball unit arrangements and three 3-Reef-Ball unit arrangements. Only 5-Reef-Ball unit arrangements were sampled here.

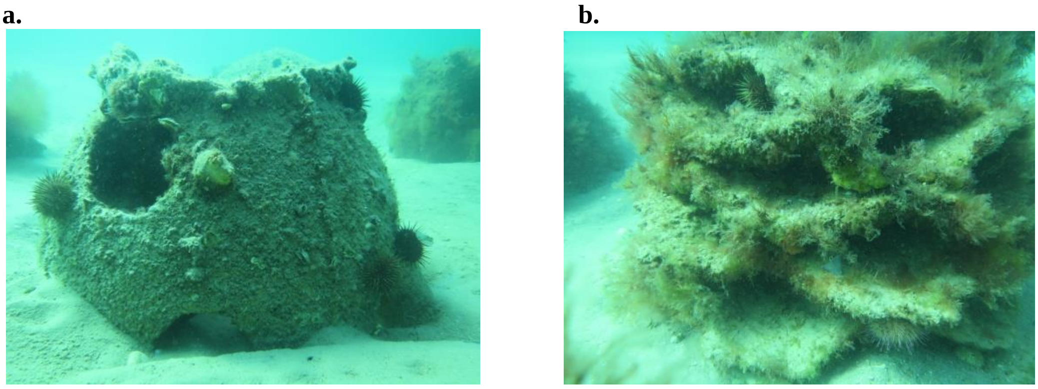


Fig. 2.2 Typical designs of Reef Ball reefs for shore based reefs in Port Phillip Bay, Victoria, Australia. a. Most common "cave-like" design. b. Less common "bee-hive" design.

Sampling design

To investigate the differences in fish density, species richness and community structure between natural and artificial (Reef Balls) reefs, I sampled fish communities on each habitat at each of the three locations using underwater visual surveys between January and May during the 2013/2014 field season. Fish were identified to species and their ontogenetic stage recorded. Fish counts were performed in two stages; first an observer recorded all mobile species associated with the habitat in the sampled area from a distance of ~ 2 m for a maximum of 5 min, then the sampled area was carefully checked for approximately another 3 min for any small individuals and cryptic species. A high power LED torch was used to examine cracks and crevices.

On the Reef Ball reefs each of 5-Reef-Ball unit arrangements was treated as a replicate (Figure 2.3). To match the area taken up by a 5-Reef-Ball unit arrangement, an area of 2.5 m in diameter was sampled on natural reef. When possible all 18 5-Reef-Ball unit arrangements were sampled on Reef Ball reefs and 18 point counts were conducted on natural reefs. Due to weather constraints it was not possible to sample all arrangements at some locations; and therefore, a minimum of 14 5-Reef-Ball unit arrangements on Reef Ball reefs and 14 2.5 m point counts on natural reef were sampled. On a natural reef, point counts were selected randomly for each sampling round and a minimum of 5 m distance was maintained between each sampling point.

On natural reefs chain method was used to estimate the new radius based on the ratio of actual surface distance relative to linear distance along diagonal transects (Risk 1972). Two tape measures were placed crossing each other within each 2.5 m sampling area conforming as closely as possible to all contours and crevices. The mean of the two estimates for each sampling area was calculated and used in subsequent calculations of surface area. Estimated average surface area did not differ greatly between reefs (5.1 – 5.3 m^2) and therefore was averaged for all further density calculations. The dimensions of Reef Balls were known and the distance between modules within each arrangement was measured and averaged for all further calculations. These data facilitated average surface area estimates for Reef Balls reefs, which was used in density calculations.

Statistical analysis

Univariate and multivariate analyses were performed using PRIMER-E v6 with the PERMANOVA (Permutational Multivariate Analysis of Variance) add-on (McArdle and Anderson, 2001). Clarke and Gorley (2006) and Anderson *et al.* (2008) state that the use of PERMANOVA is appropriate for univariate analysis. Univariate Permanova is an approach similar to parametric ANOVA; however, it is not restricted by as many assumptions and is better suited for unbalanced designs.

Fig. 2.3 Illustration of a typical 5-Reef-Ball unit arrangement at Port Phillip Bay, Victoria, Australia, that was treated as a replicate.

Fish species richness

To determine the effects of location and habitat on fish species richness I used PERMANOVA. A univariate PERMANOVA test, with fish species richness as the dependent variable, was run on Euclidean distance matrices with 9999 permutations. For this analysis the data from the two natural reefs at Portarlington were pooled together. Location (3 levels) and habitat (2 levels) were identified as fixed factors. Due to the complexity of the design I used permutation of residuals under a reduced model permutation method with Type III sum of squares. Pair-wise PERMANOVA tests were conducted as a post-hoc test to identify which locations and habitats were significantly different from each other in fish species richness. For this analysis the data from the two natural reefs at Portarlington were treated separately. Due to the low numbers of permutations possible, Monte Carlo adjustments were used and are reported as p values.

Fish density

To determine the effects of location and habitat on fish density I also used univariate PERMANOVA. Fish density was log+1 transformed. While PERMANOVA is more robust to the violations of the assumptions of parametric tests, the overall model fit the log+1 transformed data better than the raw data. A univariate PERMANOVA test, with fish density as the dependent variable, was run on Euclidean distance matrices with 9999 permutations. The model design and methodology were identical to that described above for species richness.

Fish community structure

To determine the effects of location and habitat on the fish community structure, a multivariate PERMANOVA analysis using a Bray-Curtis similarity matrix of fourth root transformed density data with 9999 permutations was conducted. Fourth root transformation was applied to reduce the influence of species that occurred in extremely high densities. Due to the complexity of the design I used permutation of residuals under a reduced model permutation method with Type III sum of squares. The community data included individual species and, when recorded, life stage (recruits, juveniles, and adults). Only the species with raw abundances over 10 individuals across all samples were included in the analysis. Several of the species were pooled together to create generic taxonomic groups with sufficient numbers for inclusion: other leather jacket. A total of 21 dependent variables were used in the analysis. Because Bray-Curtis coefficients cannot deal with multiple blank samples (samples containing no species), all zero value samples were removed as recommended by Clarke and Gorley (2006). The model structure and methodology were as described for the two univariate PERMANOVA tests. For this analysis the data from all natural reefs at Portarlington was pooled together.

Due to a significant Location x Habitat interaction, I conducted separate PERMANOVA tests for each Location and a Bonferroni-adjusted alpha was used to account for multiple non-independent tests. For this analysis the data from all natural reefs at Portarlington was treated separately. Due to the simplified design I used unrestricted permutation of raw data with Type III sum of squares for these analyses. For Portarlington additional pair-wise PERMANOVA tests were conducted as a post hoc test to identify which habitats were significantly different from each other in community structure.

Community composition for each Location was visualised using a principal coordinates analysis (PCO) plot, which is a recommended approach for the data with "within-group" dissimilarities that are smaller than "between-group" dissimilarities (Anderson *et al.*, 2008). The vectors overlying the plot represent the correlations (Spearman correlation coefficients) between taxa and PCO axes. Spearman correlations were chosen as they are better suited to deal with non-linear relationships that are common in ecological data sets. The 'similarity percentage' routine (SIMPER) was used to identify the contribution of each taxon to a significant community change between habitats within each location. The consistency of the contribution of each taxon to the community variance is represented by the ratio of each taxon's average dissimilarity to the standard deviation of dissimilarities (Diss/SD), with values greater than 1 representing taxa which consistently contribute to community change among habitats.

2.4 Results

Overall, a total of 5167 fish from 43 taxa were counted during the 2013/2014 field season. The highest total number of fish species was recorded from Frankston reefs, with 16 and 15 species on Reef Ball and natural reefs, respectively. Between 10 and 13 different fish species were recorded from reefs at Altona and Portarlington. The most commonly observed and relatively abundant fish species were: *Parablenius tasmanianus, Upeneichthys vlamingi, Neoodax balteatus, Trachinops caudimaculatus* and *Vincentia conspersa*.

Fish species richness

For species richness, there was a significant effect of location and habitat (Table 2.1). Frankston and Portarlington supported over 20% more species rich fish communities than Altona (Figure 2.4 a). Reef Ball reefs on average supported over 20% more species than natural reefs (Figure 2.4 a). Pair-wise PERMANOVA tests identified significant differences in fish species richness between natural and artificial habitat at Frankston, but not at Altona. At Portarlington, there was no significant difference in fish species richness between Prince George Bank natural reef and Reef Ball reef. However, fish species richness on Prince George Bank natural reef and Reef Ball reef was ~50% higher than on Steele’s Rock natural reef (Table 2.2; Figure 2.4 a).

Table 2.1 Results from univariate PERMANOVA on Euclidean distances to test for Location (Frankston, Altona, Portarlington) or Habitat (Natural reef, new design artificial reef, Reef Ball reef) differences on fish density and species richness. The test statistic (F*) is a pseudo-F value and the probability value (P†) are computed by the PERMANOVA routine with max 9,999 permutations under a reduced model. Sum of squares is Type III (partial). Fish density data was log+1 transformed. Location and Habitat were treated as fixed factors. For these analyses the data from the two natural reefs at Portarlington were pooled together.

Variable type	Source	df	SS	MS	F*	P†	Unique permutations
Fish species richness	Location	2	14.276	7.1382	3.3356	**0.0405**	9943
	Habitat	1	14.381	14.381	6.7199	**0.0113**	9843
	Location x Habitat	2	1.6802	0.8401	0.3926	0.6724	9957
	Error	109	233.26	2.14			
	Total	114	262.57				
Fish density	Location	2	23.228	11.614	11.778	**0.0001**	9938
	Habitat	1	13.112	13.112	13.298	**0.0006**	9844
	Location x Habitat	2	4.6392	2.3196	2.3524	0.1001	9945
	Error	109	107.48	0.9861			
	Total	114	149.74				

Table 2.2 Results from pair-wise tests of univariate PERMANOVA on Euclidean distances to test for Habitat (Natural reef, Reef Ball reef) differences at each Location on fish species richness. The test statistic (F*) is a pseudo-F value and the probability value (P†) are computed by the PERMANOVA routine with max 9,999 permutations under a reduced model. Sum of squares is Type III (partial). Habitat was treated as fixed factors. The data on fish species richness from all natural reefs was treated separately for this analysis. Note: at Portaringto natural reef is also known as Prince George Bank reef and natural reef 2 as Steele's Rock reef. Due to low numbers of permutations possible Monte Carlo adjustments were used and are reported as p values.

Groups	t	P (MC)	Unique permutations
Frankston			
Natural vs Reef Balls	2.0584	**0.0487**	19
Altona			
Natural vs Reef Balls	1.9516	0.0624	26
Portarlington			
Natural vs Natural 2	3.4830	**0.0018**	37
Natural vs Reef Balls	0.9766	0.3531	30
Natural 2 vs Reef Balls	3.8001	**0.0008**	13

Fish density

For fish density, there was a significant effect of location and habitat (Table 2.1). Frankston and Portarlington supported over 80% higher fish densities than Altona (Figure 2.4 b). Natural reefs on average supported over 75% higher fish densities than Reef Ball reefs (Figure 2.4 b). Pair-wise PERMANOVA tests identified significant differences in fish densities between natural and artificial reef habitat at Frankston, but not at Altona. At Portarlington, Prince George Bank natural reef had significantly higher fish densities than Steele's rock natural reef or Reef Ball reef (over 85%). However, there was no significant difference in fish densities between Steele's Rock natural reef and Reef Ball reef (Table 2.3; Figure 2.4 b).

Table 2.3 Results from pair-wise tests of univariate PERMANOVA on Euclidean distances to test for Habitat (Natural reef, Reef Ball reef) differences at each Location on fish density. The test statistic (F*) is a pseudo-F value and the probability value ($P^{\dagger}$) are computed by the PERMANOVA routine with max 9,999 permutations under a reduced model. Sum of squares is Type III (partial). Fish density data were log+1 transformed. Habitat was treated as a fixed factor. The data on fish density from all natural reefs was treated separately for this analysis. Note: at Portarington, natural reef 1 is also known as Prince George Bank reef and natural reef 2 as Steele's Rock reef.

Groups	**t**	**P**	**Unique permutations**
Frankston			
Natural vs Reef Balls	3.5501	**0.0015**	9824
Altona			
Natural vs Reef Balls	0.8123	0.4179	9853
Portarlington			
Natural vs Natural 2	5.7537	**0.0001**	9794
Natural vs Reef Balls	5.2267	**0.0001**	9829
Natural 2 vs Reef Balls	1.4623	0.1619	9687

Fish community structure

Fish community structure varied by location and habitat (Table 2.4; Figure 2.5). There was a significant effect of habitat on fish community structure for each location (Table 2.4; Figure 2.5). At Portarlington all three habitats were significantly different from each other in fish community structure (Table 2.5; Figure 2.5 c). The dissimilarities between reefs within each location were quite large, over 65% in most cases. The smallest dissimilarity calculated by SIMPER was between natural and Reef Ball reef at Altona (69.66 %). The largest dissimilarity calculated by SIMPER was between shallow natural reef (Steele's Rock) and Reef Ball reef at Portarlington (86.63%) (Table 2.6).

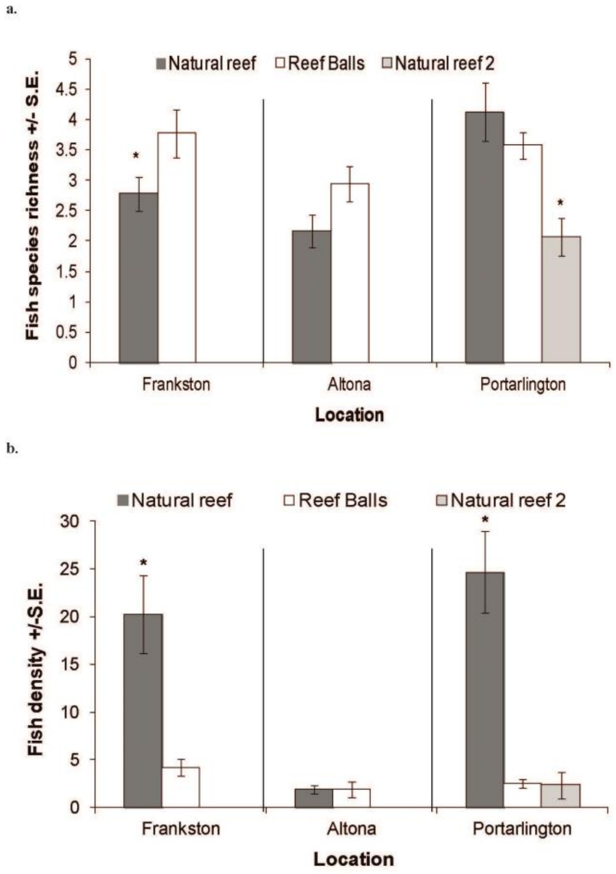


Fig. 2.4 Fish species richness and fish densities (fish / m^2) supported by Reef Ball reefs and adjacent natural reefs at three locations in Port Phillip Bay, Victoria, Australia. For pair-wise univariate PERMANOVA tests, locations were tested separately to identify which habitats were significantly different from each other *within*

each location. Habitats identified with an asterisk are significantly different from habitats without asterisk *within* each location.

Table 2.4 Results from multivariate PERMANOVA using Bray-Curtis similarity values to test for Location (Frankston, Altona, Portarlington) or Habitat (Natural reef, Reef Ball reef) differences on fish community structure. The test statistic (F*) is a pseudo-F value and the probability values ($P^{\dagger}$) are computed by the PERMANOVA routine with max of 9,999 permutations under a reduced model. Sum of squares is Type III (partial). The data was fourth root transformed. Location and Habitat were treated as fixed factors. Bonferroni correction is applied to fish community** analysis split by Location with significance level set at 0.01 and unrestricted permutations of raw data were applied for these analyses. For the multivariate PERMANOVA tests for each Location the data on fish density from all natural reefs was treated separately. Note: at Portaringto n natural reef 1 is also known as Prince George Bank reef and natural reef 2 as Steele's Rock reef.

Variable type	Source	df	SS	MS	F*	$P^{\dagger}$	Unique permutations
Fish community	Location	2	85944	42972	21.337	**0.0001**	9930
Overall	Habitat	1	46091	46091	22.886	**0.0001**	9959
	Location x Habitat	2	38343	19172	9.5194	**0.0001**	9929
	Error	107	215490	2014			
	Total	112	388320				
Fish community**	Habitat	1	37295	37295	20.834	**0.0001**	9946
Frankston	Error	33	59075	1790.2			
	Total	34	96371				
Fish community**	Habitat	1	18076	18076	10.619	**0.0001**	9951
Altona	Error	33	56175	1702.3			
	Total	34	74251				
Fish community**	Habitat	2	56575	28287	15.521	**0.0001**	9922
Portarlington	Error	40	72903	1822.6			
	Total	42	129480				

Table 2.5 Results from pair-wise multivariate tests of PERMANOVA using Bray-Curtis similarity values to test for Habitat (Natural reef, Reef Ball reef) differences at Portarlington on fish community structure. The test statistic (F*) is a pseudo-F value and the probability value (P[†]) are computed by the PERMANOVA routine with max 9,999 permutations using unrestricted permutations of raw data. Sum of squares is Type III (partial). The data was fourth root transformed. Habitat was treated as a fixed factor. The data on fish density from all natural reefs was treated separately for this analysis. Note: at Portarington natural reef is also known as Prince George Bank reef and natural reef 2 as Steele's Rock reef.

Groups	t	P	Unique permutations
Portarlington			
Natural vs Natural 2	3.7386	**0.0001**	9957
Natural vs Reef Balls	4.8412	**0.0001**	9942
Natural 2 vs Reef Balls	3.3908	**0.0001**	9960

Table 2.6 Results of SIMPER for the effects of Habitat within each Location that caused a significant change in fish community. Average dissimilarity of each pair of Habitats within each Location is presented. The data was fourth root transformed. The analysis was conducted on Bray-Curtis similarity matrices. The data on each species density from all natural reefs was treated separately for this analysis. Note: at Portarington, Natural reef 1 is also known as Prince George Bank reef and Natural reef 2 as Steele's Rock reef.

Groups	Average dissimilarity %
Frankston	
Natural vs Reef Balls	86.11
Altona	
Natural vs Reef Balls	69.66
Portarlington	
Natural vs Natural 2	85.44
Natural vs Reef Balls	82.02
Natural 2 vs Reef Balls	86.62

PCO plots of fish communities at different locations identified two main clusters at Frankston and Altona and three main clusters at Portarlington (Figure 2.5).

At Frankston and Portarlington, *Trachinops caudimaculatus* was one of the main species driving the differences between reefs, in many cases contributing over 15% to the dissimilarities. This species was predominantly associated with natural reefs (Figure 2.5 a, c; Table 2.7). *Neodax balteatus* was also a major contributor to the dissimilarities between habitats at these two sites (over 10% contribution); however, at Frankston this species was associated with the Reef Ball reef, while at Portarlington it was more common on Prince George Bank natural reef (Figure 2.5 a, c; Table 2.7). Moreover, at Frankston, *Diodon nichthemerus* was a typical species occupying Reef Ball reefs, while *Parablennius tasmanianus* was more common on natural reefs (Figure 2.5 a). At Altona and Portarlington, *Vincentia conspersa* were a major contributor to dissimilarities between reefs, predominantly being associated with Reef Ball reefs (Figure 2.5 b, c; Table 2.7).

Portarlington habitats supported the richest fish communities, with several different species associated with different reefs, in particular with Prince George Bank natural reef and Reef Ball reef. Apart of *Trachinops caudimaculatus*, other typical reef species also associated with Prince George Bank natural reef were: *Haletta semifasciata*, *Parma victoria* and predominantly adults of different species of leatherjackets. In contrast, the Reef Ball reef community was largely defined by the presence of *Upeneichthys vlamingii* and juvenile leatherjackets. *Scorpis aequipinnis* was predominantly associated with Steele's Rock natural reef (Table 2.7; Figure 2.5 c).

Table 2.7 Results of SIMPER analysis showing the Diss/SD and the percent contribution to the dissimilarity of each species at each location with Spearman correlation of 0.5 from PCO analysis (Figure 2.5) in order of: Natural reef x Reef Balls; Natural Reef 2 (Portarlington only) x Reef Balls; Natural reef 1 x Natural reef 2 (Portarlington only).

FRANKSTON		
Species	Diss/SD	% Contribution
T. caudimaculatus (Adult)	1.66	19.67
T. caudimaculatus (Juv)	1.62	19.26
N. balteatus (Juv)	1.39	13.71
D. nichthemerus	1.66	11.03
P. tasmanianus	0.75	4.81
ALTONA		
Species	Diss/SD	% Contribution
U. vlamingii (Juv)	1.10	24.66
V. conspersa	1.01	17.71

PORTARLINGTON		
Species	Diss/SD	% Contribution
T. caudimaculatus (Adult)	1.75 1.85 NA	27.24 25.24 NA
T. caudimaculatus (Juv)	1.24 1.23 NA	13.18 11.86 NA
N. balteatus (Juv)	1.21 1.04 1.34	12.74 5.08 12.90
S. aequipinnis	0.95 NA 1.13	10.54 NA 13.96
P. victoriae	1.40 1.41 NA	7.85 7 NA
Other Monacanthidae	0.90 NA NA	6.04 NA NA
Other Monacanthidae (Juv)	NA 0.95 1.03	NA 9.27 14.44
V. conspersa	NA 1.15 1.21	NA 7.82 11.62
U. vlamingii	NA 0.78 0.78	NA 5.89 8.45

U. vlamingii (Juv)	NA	NA
	0.79	6.75
	0.83	10.02
H. semifasciata	NA	NA
	0.97	5
	NA	NA
B. jacksonianus	NA	NA
	NA	NA
	0.72	6.29

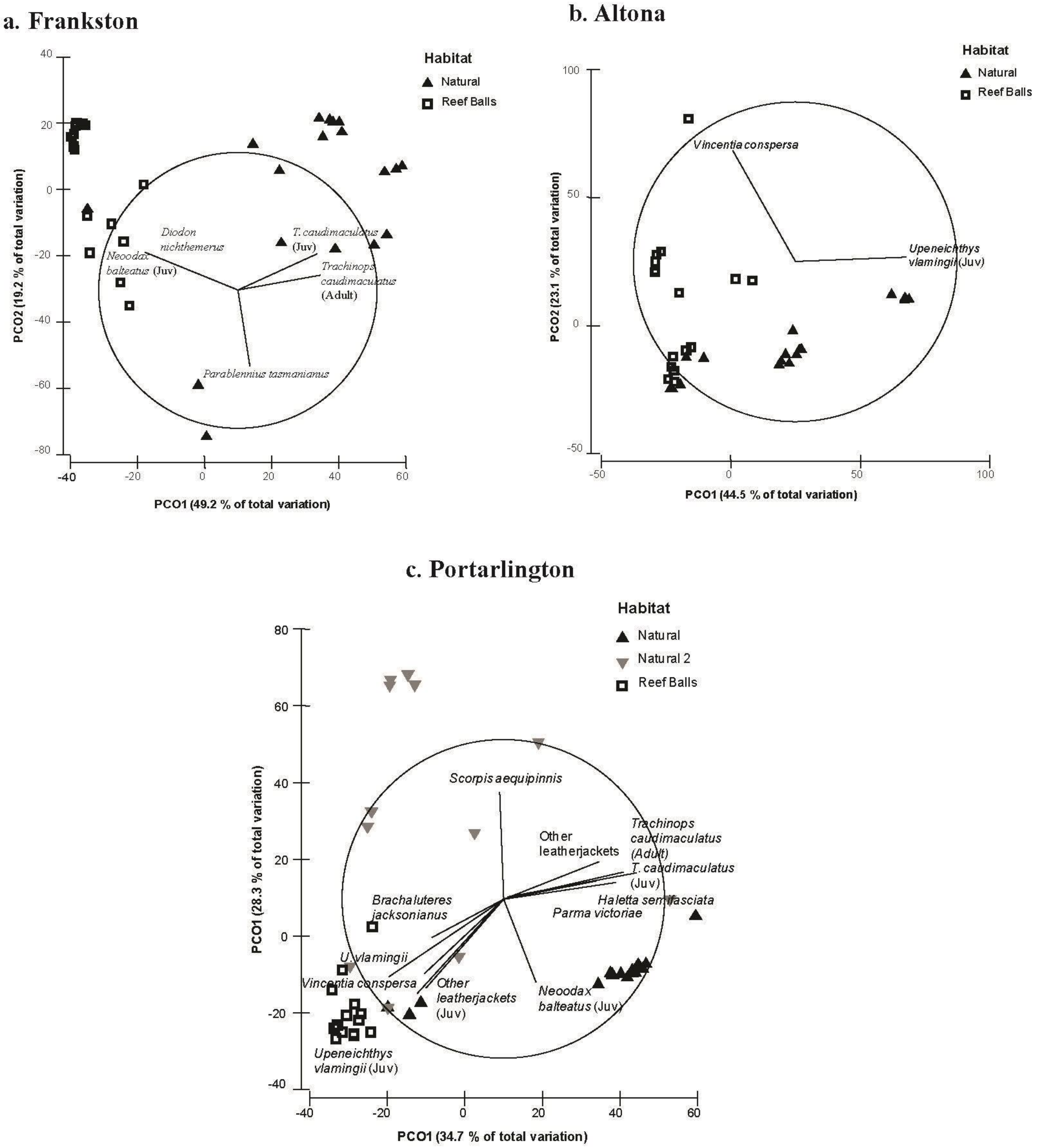


Fig. 2.5 PCO ordination based on Bray-Curtis similarity index for each fish community associated with different habitats (natural reefs, Reef Ball reefs) in Port Phillip bay, Victoria, Australia across three locations (a. Frankston; b. Altona; c. Portarlington). Projected vectors show changes in the abundance of species with Spearman correlation of 0.5 with any of the two first ordination axes.

2.5 Discussion

Many previous studies have reported high species richness and fish densities associated with artificial structures (Ambrose and Swarbrick, 1989; Rilov and Benayahu, 2000; Hackradt *et al.*, 2011; Folpp *et al.*, 2013). They have also highlighted the importance of reef location in general and the proximity to local natural reefs in particular on the resulting fish community (Bohnsack, 1989; dos Santos *et al.*, 2010; Folpp *et al.*, 2013). In this study, I examined how well commonly used artificial reefs (Reef Balls) mimic natural reefs in terms of their fish communities at three locations in the temperate waters of Port Phillips Bay. The results showed that Reef Ball reefs generally support richer fish communities than natural reefs, with the exception of one natural reef at Portarlington (Prince George Bank). However, Reef Ball reefs supported on average 75% lower fish densities than natural reefs, with the exception of the low-lying boulder field reefs such as Altona natural reef and Portarlington Steele's rock reef. Similarly, while community compositions were, in general, quite distinct between natural and artificial reefs at all locations, the closest fish community compositions between habitats were observed at Altona. This indicates that apart from the reef type itself, location and the structural complexity of natural reef are influential in structuring fish communities in the Bay.

Reef fish species, like the majority of marine organisms, go through a highly dispersive planktonic larval stage (Ehrlich, 1975; Richards and Lindeman, 1987; Mapstone and Fowler, 1988). They use various olfactory, visual and auditory cues to select a suitable habitat, especially at small scales (Leis *et al.*, 1996; Kingsford *et al.*, 2002; Montgomery *et al.*, 2006). Habitat suitability may be defined by habitat complexity, benthic community structure, and the presence/absence of competitors, predators and con-specifics (Carr, 1991; Doherty *et al.*, 1996; Öhman *et al.*, 1998; Kingsford *et al.*, 2002; Morton and Shima, 2013).

For most species, low complexity, low habitat diversity, and high predator and competitor abundances can lead to habitat avoidance (MacArthur and Levins, 1964; Klopfer, 1969; Werner *et al.*, 1983; Klopfer and Ganzhorn, 1985; Pulliam and Danielson, 1991; Hugie and Dill, 1994), while the presence of conspecifics is a good indicator of quality habitat and has been shown to lead to habitat selection (Kingsford *et al.*, 2002; Lecchini *et al.*, 2007; Hunt *et al.*, 2011; Lecchini *et al.*, 2014; Fobert and Swearer, 2017). Similarly, high habitat complexity, diversity and availability of refuge sites can also lead to stronger preference for reefs with these characteristics, which can mediate the negative effects of high predator and competitor abundances (Macarthur and Levins, 1967; Hixon and Menge, 1991; Hixon and Beets, 1993; Almany, 2004; Ford and Swearer, 2013). High levels of habitat complexity and vertical relief have been previously associated with increased fish abundances (Rilov and Benayahu, 2000; Wilhelmsson *et al.*, 2006; Wilson *et al.*, 2007; Hackradt *et al.*, 2011; Komyakova *et al.*, 2013). Larger, continuous reefs with established fish and benthic communities, likely receive higher colonisation rates because they are easier to detect (Stier and Osenberg, 2010; Morton and Shima, 2013; Hale *et al.*, 2015). Moreover, larger reefs may also provide greater food resources or foraging opportunities, leading to higher abundances of some fish species, though food availability is rarely a primary limiting factor (Patton *et al.*, 1985; Lomolino, 2001; Holbrook *et al.*, 2002; Caddy, 2007).

Frankston natural reef and Prince George Bank natural reef in Portarlington are large, continuous habitats with well-established fish communities, relatively high habitat complexity and high vertical relief. In comparison, Reef Ball reefs are relatively young with less established fish communities. They are also significantly smaller than natural reefs and surrounded by sandy bottom areas that are unfavourable for reef fish, making these reefs potentially less detectable for some reef fish species and less desirable due to their low resource (e.g. refuge sites) availability. Additionally, like Altona natural reef and Steele's

Rock natural reef in Portarlington, Reef Ball reefs have visually lower habitat complexity and lower vertical relief. These factors likely contribute to the differences observed in fish abundances between locations and reef types.

Habitat diversity has been linked to high fish species richness (Messmer *et al.*, 2011; Komyakova *et al.*, 2013). Many previous studies have associated higher fish species richness with natural reefs (Carr and Hixon, 1997; Rooker *et al.*, 1997; Hackradt *et al.*, 2011), which are often assumed to have higher habitat diversity in comparison to artificial reefs (Badalamenti *et al.*, 2002; Perkol-Finkel and Benayahu, 2004; Perkol-Finkel *et al.*, 2005; Perkol-Finkel *et al.*, 2006; Burt *et al.*, 2009). Interestingly, in the present study, Prince George Bank natural reef had the highest fish species richness. However, all other natural reefs examined supported less rich fish communities than Reef Ball reefs. Similar results for Reef Ball reefs were reported by Folpp *et al.* (2013). These results may be attributable to the isolation and patchy structure of Reef Ball reefs. Highly fragmented and isolated habitats have previously been shown to support higher fish species richness, potentially due to increased edge effects (Jordan *et al.*, 2005; Macreadie *et al.*, 2009; Bonin *et al.*, 2011). Fragmented Reef Ball reefs may not only support typical reef-associated species, but also more habitat generalist species or more transient species boosting fish diversity in these habitats. Indeed, a few studies on artificial reefs have shown higher abundances of transient species, which tend to use artificial reefs for temporary foraging (Rooker *et al.*, 1997; Overholtzer-McLeod, 2004; Burt *et al.*, 2009; Folpp *et al.*, 2011; Simon *et al.*, 2011). On the other hand, some studies have suggested that small isolated artificial reefs tend to have lower predation pressure which leads to greater diversity and abundance of species (Belmaker *et al.*, 2005). More process-based research on artificial reefs is needed to determine the underlying mechanisms that may be contributing to greater numbers of species on artificial reefs.

There were large differences in fish community structure between the two habitat types at all three locations. Natural reef communities were defined by typical reef-associated species such as *Trachinops caudimaculatus*, *Scorpis aequipinnis, Neoodax balteatus* and *Parma victoriae*, in particular at Portarlington and Frankston. *Trachinops caudimaculatus* is a shoaling reef-associated fish that has high affinity for reefs with vertical relief, high habitat complexity and conspecifics (Hunt *et al.*, 2011; Fobert and Swearer, 2017). It is possible that natural reefs are more attractive to this species due to their size, age and higher resource availability, such as higher vertical relief, shelter and an established conspecific populations. *Scorpis aequipinnis* and *Neoodax balteatus* are both highly mobile reef-associated species that require large territories for foraging (Robertson and White, 1986; Jenkins and Wheatley, 1998; Edgar, 2008; Moore *et al.*, 2010). *Scorpis aequipinnis* tends to be suspended high above the hard substratum during the day, foraging over relatively large areas. Therefore, fragmented Reef Ball reefs surrounded by sandy areas may not be a suitable habitat for this species. Moreover, adult leather jackets that are relatively large, mobile predators were also common on natural reefs at Frankston and Portarlington. Conversely, the smallest leatherjacket species, *Brachaluteres jacksonianus*, and juveniles of other leatherjacket species were typical of Reef Ball reefs. Leatherjackets are very mobile species that did not appear to be resident on Reef Ball reefs, but rather were feeding on these habitats. They may have potentially travelled from nearby natural reefs. Reef Ball reef complexity might be sufficient to provide temporary shelter for smaller individuals, but may be not satisfactory for larger fish. *Upeneichthys vlamingii* and *Neoodax balteatus* were also common on Reef Balls reefs, both are also highly mobile, generalist, opportunistic species that feed on the benthos (Robertson and White, 1986; Edgar, 2008; Moore *et al.*, 2010). *Upeneichthys vlamingii* in particular tends to utilise both soft and hard substratum habitats for foraging (Edgar, 2008; Moore *et al.*, 2010). Cryptic species, such as *Vincentia conspersa,* were also typical on Reef

Ball reefs. The cave like appearance of these artificial reefs may be particularly attractive for this cave-associated, nocturnal, cryptic fish species (Baker *et al.*, 2008; Gomon *et al.*, 2008; Jenkins *et al.,* 2015). However, it is possible that due to higher cave complexity on natural reefs, these species was simply harder to detect during day diver counts. These specifics of community composition further support the suggestion that higher species richness values on Reef Balls reefs might have been boosted by edge associated species, species that are habitat generalists capable of using multiple habitat types, as well as more typical hard substratum species.

Differences in fish community structure between natural and artificial reefs have been reported in the majority of comparative studies (Rooker *et al.*, 1997; Thanner *et al.*, 2006; Burt *et al.*, 2009; Hackradt *et al.*, 2011; Folpp *et al.*, 2013; Simon *et al.*, 2013). However, many of these studies were criticised for differences in reef sizes, ages and locations (Ambrose and Swarbrick, 1989; Bohnsack *et al.*, 1994; Carr and Hixon, 1997; Perkol-Finkel *et al.*, 2006). One comparative, experimental study that controlled for these factors reported no significant differences in fish communities between natural and artificial reefs (Carr and Hixon, 1997). However, it must be kept in mind that fish community structure of each artificial reef will greatly depend on artificial reef size, age, design, condition of local community, reef location in relation to natural reefs and geographic area. Therefore, no universal conclusion on artificial reef fish communities may be drawn from one experimental study. Each artificial reef type must be examined separately. Generalisations about fish community structure on different artificial reefs may lead to false conclusions and performance expectations, with important implications for management. Moreover, the extent of community similarity on artificial versus natural reefs also depends on the natural reef in question. For Reef Ball reefs in temperate waters, fish community structures most closely resembled the natural reefs that exhibited low complexity and low natural relief. In these situations, Reef Ball reefs appeared to provide the closest mimic of natural habitats. However, communities were largely different between Reef Ball reefs and large, diverse and complex natural reefs such as Prince George Bank in Portarlington. It is thus important that any monitoring of artificial reef performance is benchmarked against natural reefs that exhibit the full range of natural variability in habitat structure and complexity.

Previous studies have suggested that artificial reef performance should be investigated in comparison to local natural reefs if the purposes of artificial reef deployment is for habitat restoration and production of animal communities that best mimic local natural reefs (Carr and Hixon, 1997; Folpp *et al.*, 2013). However, some studies have shown that, if artificial reefs harbour communities that are significantly different to natural communities or if they attract a large number of predators to the area, these artificial reefs can have significant negative effects on local natural communities by altering and modifying species composition, fish diversity and densities of the entire area (Connell and Glasby, 1999; Connell, 2001; Simon *et al.*, 2011). For that reason, one of the main objectives in designing and deploying artificial reefs, in addition to its main intended purpose - be that for shoreline or scour protection, habitat restoration, recreational fisheries enhancement etc. - should be the ability of artificial reefs to mimic natural communities as closely as possible. Therefore, assessment of reef performance should always be conducted in comparison with natural reefs to properly evaluate any potential impacts on the local ecosystem as a whole.

Artificial reefs tend to redirect fishing pressure and if they function as FADs for some fish species, that may also cause increased mortality. These issues may be small for Reef Ball reefs in Port Phillip Bay, as the reefs are too small to attract large populations of important fisheries species for extended periods of time. However, artificial reefs may provide similar cues as natural reef and appear attractive to settlement-stage reef fishes. Indeed, Reef Ball reefs in Port Phillip Bay do support communities of small territorial reef associated fishes. If Reef Ball reefs fail to provide the necessary habitat complexity, refuge diversity, space or food resources needed for survival, this could lead to higher mortality rates. Previous studies have shown that larger transient predator abundances can be associated with artificial reefs (Rooker *et al.*, 1997; Overholtzer-McLeod, 2004; Folpp *et al.*, 2011; Simon *et al.*, 2011), though predator pressure is related to the degree of reef isolation (Belmaker *et al.*, 2005). If reef habitat in Port Philip Bay is not limiting and Reef Ball reefs are more attractive to some fish species but lead to lower fitness, they may act as ecological traps. The effect of ecological traps on fish population has not been extensively researched and very little information is available (but see Hallier and Gaertner, 2008; Dempster *et al.,* 2011; Reubens *et al.,* 2013). However, if artificial reefs act as ecological traps for some fish species, they may carry additional, previously not considered negative effects on local fish populations. The performance of artificial reefs in relation to natural reefs, as well as the fitness of individuals occupying artificial habitats require further detailed attention in order to improve current management plans and to reduce the likelihood that artificial reefs create unintended negative impacts on reef fish communities.

2.6 References

Agriculture Victoria State Government (2016) Shore Based Reefs. Viewed 12th February 2017, < http://agriculture.vic.gov.au/fisheries/recreational-fishing/recreational-fishing-reefs/shore-based-reefs>

Alevizon, W. S. and Gorham, J. C. (1989) Effects of artificial reef deployment on nearby resident fishes. *Bulletin of Marine Science*, 44(2), 646-661.

Almany, G. R. (2004) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos*, 106(2), 275-284.

Ambrose, R. F. and Swarbrick, S. L. (1989) Comparison of fish assemblages on artificial and natural reefs off the coast of southern California. *Bulletin of Marine Science,* 44(2), 718-733.

Anderson, M. J., Gorley, R. N. and R, C. K. (2008) PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. *PRIMER-E Ltd: Plymouth, UK.*

Badalamenti, F., Chemello, R., D'Anna, G., Ramos, P. H. and Riggio, S. (2002) Are artificial reefs comparable to neighbouring natural rocky areas? A mollusc case study in the Gulf of Castellammare (NW Sicily). *ICES Journal of Marine Science*, 59(suppl), S127-S131.

Baine, M. (2001) Artificial reefs: a review of their design, application, management and performance. *Ocean & Coastal Management*, 44(3–4), 241-259.

Baker, J., Shepherd, S., Brown, A., Crawford, H. and Muirhead, D. (2008) Uncommon and cryptic reef fishes: results of pilot surveys along Fleurieu Peninsula, Report for Adelaide and Mt Lofty Ranges Natural Resources Management Board.

Belmaker, J., Shashar, N. and Ziv, Y. (2005) Effects of small-scale isolation and predation on fish diversity on experimental reefs. *Marine Ecology Progress Series*, 289, 273-283.

Bohnsack, J. A. (1989) Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? *Bulletin of Marine Science*, 44(2), 631-645.

Bohnsack, J. A., Harper, D. E., McClellan, D. B. and Hulsbeck, M. (1994) Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern Florida, USA. *Bulletin of Marine Science*, 55(2-3), 796-823.

Bohnsack, J. A. and Sutherland, D. L. (1985) Artificial Reef Research: A review with recommendations for future priorities. *Bulletin of Marine Science*, 37(1), 11-39.

Bonin, M. C., Almany, G. R. and Jones, G. P. (2011) Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. *Ecology*, 92(7), 1503-1512.

Bortone, S. A., Van Tassell, J., Brito, A., Falcón, J. M., Mena, J. and Bundrick, C. M. (1994) Enhancement of the nearshore fish assemblage in the Canary Islands with artificial habitats. *Bulletin of Marine Science*, 55(2-3), 602-608.

Branden, K. L., Pollard, D. A. and Reimers, H. A. (1994) A review of recent artificial reef developments in Australia. *Bulletin of Marine Science*, 55(2-3), 982-994.

Brickhill, M. J., Lee, S. Y. and Connolly, R. M. (2005) Fishes associated with artificial reefs: attributing changes to attraction or production using novel approaches. *Journal of Fish Biology*, 67, 53-71.

Burt, J., Bartholomew, A., Usseglio, P., Bauman, A. and Sale, P. (2009) Are artificial reefs surrogates of natural habitats for corals and fish in Dubai, United Arab Emirates? *Coral Reefs*, 28(3), 663-675.

Burt, J. A., Feary, D. A., Cavalcante, G., Bauman, A. G. and Usseglio, P. (2013) Urban breakwaters as reef fish habitat in the Persian Gulf. *Marine Pollution Bulletin*, 72(2), 342-350.

Caddy, J. F. (2007) Marine habitat and cover: their importance for productive coastal fishery resources.

Carr, M. H. (1991) Habitat selection and recruitment of an assemblage of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology*, 146(1), 113-137.

Carr, M. H. and Hixon, M. A. (1997) Artificial reefs: the importance of comparisons with natural reefs. *Fisheries*, 22(4), 28-33.

Clarke, K. R. and Gorley, R. N. (2006) *PRIMER V6: user manual-tutorial*, Plymouth Marine Laboratory.

Collins, K. J., Jensen, A. C., Mallinson, J. J., Roenelle, V. and Smith, I. P. (2002) Environmental impact assessment of a scrap tyre artificial reef. *ICES Journal of Marine Science: Journal du Conseil*, 59(suppl), S243-S249.

Connell, S. D. (2001) Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs. *Marine Environmental Research*, 52(2), 115-125.

Connell, S. D. and Glasby, T. M. (1999) Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. *Marine Environmental Research*, 47(4), 373-387.

Dempster, T., Sanchez-Jerez, P., Fernandez-Jover, D., Bayle-Sempere, J., Nilsen, R., Bjørn, P.-A. and Uglem, I. (2011) Proxy measures of fitness suggest coastal fish farms can act as population sources and not ecological traps for wild gadoid fish. *PLoS ONE*, 6(1), e15646.

Diamant, A., Tuvia, A. B., Baranes, A. and Golani, D. (1986) An analysis of rocky coastal eastern Mediterranean fish assemblages and a comparison with an adjacent small artificial reef. *Journal of Experimental Marine Biology and Ecology*, 97(3), 269-285.

Doherty, P., Kingsford, M., Booth, D. and Carleton, J. (1996) Habitat selection before settlement by *Pomacentrus coelestis*. *Marine and Freshwater Research*, 47(2), 391-399.

dos Santos, L. N., Brotto, D. S. and Zalmon, I. R. (2010) Fish responses to increasing distance from artificial reefs on the Southeastern Brazilian Coast. *Journal of Experimental Marine Biology and Ecology*, 386(1–2), 54-60.

Edgar, G. J. (2008) Australian marine life: the plants and animals of temperate waters. 2nd ed. *New Holland Publishers, Sydney*.

Ehrlich, P. R. (1975) The population biology of cral reef fishes. *Annual Review of Ecology and Systematics,* 6, 211-247.

Fabi, G., Spagnolo, A., Bellan-Santini, D., Charbonnel, E., Çiçek, B. A., García, J. J. G., Jensen, A. C., Kallianiotis, A. and Santos, M. N. d. (2011) Overview on artificial reefs in Europe. *Brazilian Journal of Oceanography,* 59, 155-166.

Firth, L. B., Knights, A. M., Thompson, R., Mieszkowska, N., Bridger, D., Evans, A., Moore, P., O'Connor, N., Sheehan, E. and Hawkins, S. (2016) Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. *Oceanogr. Mar. Biol. Ann. Rev*.

Fobert, E. K. and Swearer, S. E. (2017) The nose knows: linking sensory cue use, settlement decisions, and post-settlement survival in a temperate reef fish. *Oecologia*, 1-11.

Folpp, H., Lowry, M., Gregson, M. and Suthers, I. M. (2011) Colonization and community development of fish assemblages associated with estuarine artificial reefs. *Brazilian Journal of Oceanography,* 59, 55-67.

Folpp, H., Lowry, M., Gregson, M. and Suthers, I. M. (2013) Fish assemblages on estuarine artificial reefs: natural rocky-reef mimics or discrete assemblages? *PLoS ONE,* 8(6), e63505.

Ford, J. R. and Swearer, S. E. (2013) Two's company, three's a crowd: food and shelter limitation outweigh the benefits of group living in a shoaling fish. *Ecology*, 94(5), 1069-1077.

Fowler, A. M. and Booth, D. J. (2012) How well do sunken vessels approximate fish assemblages on coral reefs? Conservation implications of vessel-reef deployments. *Marine Biology*, 159(12), 2787-2796.

Gomon, M. F., Bray, D. J. and Kuiter, R. H. (2008) *Fishes of Australia's southern coasts. Edited by Martin Gomon, Diane Bray, Rudie Kuiter*, Reed New Holland, Musuem Victoria, Chatswood, N.S.W.

Grove, R. S., Sonu, C. J. and Nakamura, M. (1991) Design and engineering of manufactured habitats for fisheries enhancement. In *Artificial habitats for marine and freshwater fisheries* (Eds. W. J. Seaman and L. M. Sprague), Academic Press, Inc., San Diego, California, pp. 109-152.

Hackradt, C. W., Félix-Hackradt, F. C. and García-Charton, J. A. (2011) Influence of habitat structure on fish assemblage of an artificial reef in southern Brazil. *Marine Environmental Research*, 72(5), 235-247.

Hale, R., Treml, E. A. and Swearer, S. E. (2015) Evaluating the metapopulation consequences of ecological traps. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1804), 20142930.

Hallier, J. and Gaertner, D. (2008) Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Marine Ecology Progress Series*, 353, 255-264.

Harris, G., Batley, G., Fox, D., Hall, D., Jernakoff, P., Molloy, R., Murray, A., Newell, B., Parslow, J. and Skyring, G. (1996) Port Phillip Bay environmental study final report. *Canberra, Australia: CSIRO*.

Hixon, M. A. and Beets, J. P. (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs*, 63(1), 77-101.

Hixon, M. A. and Menge, B. A. (1991) Species diversity: prey refuges modify the interactive effects of predation and competition. *Theoretical Population Biology*, 39(2), 178-200.

Holbrook, S. J., Brooks, A. J. and Schmitt, R. J. (2002) Predictability of fish assemblages on coral patch reefs. *Marine and Freshwater Research*, 53(2), 181-188.

Hugie, D. M. and Dill, L. M. (1994) Fish and game: a game theoretic approach to habitat selection by predators and prey. *Journal of Fish Biology*, 45(sA), 151-169.

Hunt, T. L., Ford, J. R. and Swearer, S. E. (2011) Ecological determinants of recruitment to populations of a temperate reef fish, *Trachinops caudimaculatus* (Plesiopidae). *Marine and Freshwater Research*, 62(5), 502-509.

Jackson, J. B. C. (2008) Ecological extinction and evolution in the brave new ocean. *Proceedings of the National Academy of Sciences*, 105(Supplement 1), 11458-11465.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. and Warner, R. R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293(5530), 629-637.

Jan, R.-Q., Liu, Y.-H., Chen, C.-Y., Wang, M.-C., Song, G.-S., Lin, H.-C. and Shao, K.-T. (2003) Effects of pile size of artificial reefs on the standing stocks of fishes. *Fisheries Research*, 63(3), 327-337.

Jenkins, G. P., Kenner, T., Brown, A. and Coleman, R. (2015) Fish assemblages in locations with alternative structured habitats in an eelgrass, *Zostera*, dominated bay: Biodiversity value and potential for refuge. *Estuarine, Coastal and Shelf Science*, 161, 25-37.

Jenkins, G. P. and Wheatley, M. J. (1998) The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: comparison of shallow seagrass, reef-algal and unvegetated sand habitats, with emphasis on their importance to recruitment. *Journal of Experimental Marine Biology and Ecology*, 221(2), 147-172.

Jordan, L. K. B., Gilliam, D. S. and Spieler, R. E. (2005) Reef fish assemblage structure affected by small-scale spacing and size variations of artificial patch reefs. *Journal of Experimental Marine Biology and Ecology*, 326(2), 170-186.

Kellison, T. G. and Sedberry, G. R. (1998) The effects of artificial reef vertical profile and hole diameter on fishes off South Carolina. *Bulletin of Marine Science*, 62(3), 763-780.

Kingsford, M. J., Leis, J. M., Shanks, A., Lindeman, K. C., Morgan, S. G. and Pineda, J. (2002) Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science*, 70(1), 309-340.

Klopfer, P. H. (1969) Habitats and territories: a study of the use of space by animals. *Basic Books, Inc.* .

Klopfer, P. H. and Ganzhorn, J. U. (1985) Habitat selection: behavioral aspects. *Habitat selection in birds*, 435-453.

Komyakova, V., Munday, P. L. and Jones, G. P. (2013) Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. *PLoS ONE*, 8(12), e83178.

Langhamer, O. (2012) Artificial reef effect in relation to offshore renewable energy conversion: state of the art. *The Scientific World Journal*, 2012, 8.

Langhamer, O. and Wilhelmsson, D. (2007), Wave power devices as artificial reefs, paper presented at Proceedings of the 7th European Wave and Tidal Energy Conference.

Langhamer, O. and Wilhelmsson, D. (2009) Colonisation of fish and crabs of wave energy foundations and the effects of manufactured holes – A field experiment. *Marine Environmental Research*, 68(4), 151-157.

Langhamer, O., Wilhelmsson, D. and Engström, J. (2009) Artificial reef effect and fouling impacts on offshore wave power foundations and buoys – a pilot study. *Estuarine, Coastal and Shelf Science*, 82(3), 426-432.

Lecchini, D., Peyrusse, K., Lanyon, R. G. and Lecellier, G. (2014) Importance of visual cues of conspecifics and predators during the habitat selection of coral reef fish larvae. *Comptes Rendus Biologies*, 337(5), 345-351.

Lecchini, D., Planes, S. and Galzin, R. (2007) The influence of habitat characteristics and conspecifics on attraction and survival of coral reef fish juveniles. *Journal of Experimental Marine Biology and Ecology*, 341(1), 85-90.

Leis, J., Sweatman, H. and Reader, S. (1996) What the pelagic stages of coral reef fishes are doing out in Blue Water: daytime field observations of larval behavioural capabilities. *Marine and Freshwater Research*, 47(2), 401-411.

Lindberg, W. J. (1997) Can science resolve the attraction - production issue? . *Fisheries*, 22(4), 10-13.

Lomolino, M. V. (2001) The species-area relationship: new challenges for an old pattern. *Progress in Physical Geography*, 25(1), 1-21.

MacArthur, R. and Levins, R. (1964) Competition, habitat selection, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences,* 51(6), 1207-1210.

Macarthur, R. and Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101(921), 377-385.

Macreadie, P. I., Fowler, A. M. and Booth, D. J. (2011) Rigs-to-reefs: will the deep sea benefit from artificial habitat? *Frontiers in Ecology and the Environment*, 9(8), 455-461.

Macreadie, P. I., Hindell, J. S., Jenkins, G. P., Connolly, R. M. and Keough, M. J. (2009) Fish responses to experimental fragmentation of seagrass habitat. *Conservation Biology*, 23(3), 644-652.

Mapstone, B. D. and Fowler, A. J. (1988) Recruitment and the structure of assemblages of fish on coral reefs. *Trends in Ecology & Evolution*, 3(3), 72-77.

McArdle, B. H. and Anderson, M. J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, 82(1), 290-297.

McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H. and Warner, R. R. (2015) Marine defaunation: animal loss in the global ocean. *Science*, 347(6219).

Messmer, V., Jones, G. P., Munday, P. L., Holbrook, S. J., Schmitt, R. J. and Brooks, A. J. (2011) Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology*, 92(12), 2285-2298.

Milon, J. W. (1989) Economic evaluation of artificial habitat for fisheries: progress and challenges. *Bulletin of Marine Science*, 44(2), 831-843.

Montgomery, J. C., Jeffs, A., Simpson, S. D., Meekan, M. and Tindle, C. (2006) Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans. In *Advances in Marine Biology*, Academic Press, pp. 143-196.

Moore, C. H., Harvey, E. S. and Van Niel, K. (2010) The application of predicted habitat models to investigate the spatial ecology of demersal fish assemblages. *Marine Biology*, 157(12), 2717-2729.

Morton, D. N. and Shima, J. S. (2013) Habitat configuration and availability influences the settlement of temperate reef fishes (Tripterygiidae). *Journal of Experimental Marine Biology and Ecology*, 449, 215-220.

Öhman, M. C., Munday, P. L., Jones, G. P. and Caley, M. J. (1998) Settlement strategies and distribution patterns of coral-reef fishes. *Journal of Experimental Marine Biology and Ecology*, 225(2), 219-238.

Overholtzer-McLeod, K. L. (2004) Variance in reef spatial structure masks density dependence in coral-reef fish populations on natural versus artificial reefs. *Marine Ecology Progress Series*, 276, 269-280.

Patton, M. L., Grove, R. S. and Harman, R. F. (1985) What do natural reefs tell us about designing artificial reefs in Southern California? *Bulletin of Marine Science*, 37(1), 279-298.

Perkol-Finkel, S. and Benayahu, Y. (2004) Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs. *Coral Reefs*, 23(2), 195-205.

Perkol-Finkel, S., Shashar, N., Barneah, O., Ben-David-Zaslow, R., Oren, U., Reichart, T., Yacobovich, T., Yahel, G., Yahel, R. and Benayahu, Y. (2005) Fouling reefal communities on artificial reefs: does age matter? *Biofouling*, 21(2), 127-140.

Perkol-Finkel, S., Shashar, N. and Benayahu, Y. (2006) Can artificial reefs mimic natural reef communities? The roles of structural features and age. *Marine Environmental Research*, 61(2), 121-135.

Powers, S. P., Grabowski, J. H., Peterson, C. H. and Lindberg, W. J. (2003) Estimating enhancement of fish production by offshore artificial reefs: uncertainty exhibited by divergent scenarios. *Marine Ecology Progress Series*, 264, 265-277.

Pulliam, H. R. and Danielson, B. J. (1991) Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *The American Naturalist*, 137, S50-S66.

Reubens, J. T., Vandendriessche, S., Zenner, A. N., Degraer, S. and Vincx, M. (2013) Offshore wind farms as productive sites or ecological traps for gadoid fishes? – Impact on growth, condition index and diet composition. *Marine Environmental Research*, 90(0), 66-74.

Richards, W. J. and Lindeman, K. C. (1987) Recruitment dynamics of reef fishes: planktonic processes, settlement and demersal ecologies, and fishery analysis. *Bulletin of Marine Science*, 41(2), 392-410.

Rilov, G. and Benayahu, Y. (1998) Vertical artificial structures as an alternative habitat for coral reef fishes in disturbed environments. *Marine Environmental Research*, 45(4–5), 431-451.

Rilov, G. and Benayahu, Y. (2000) Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. *Marine Biology*, 136(5), 931-942.

Risk, M. J. (1972) Fish diversity on a coral reef in the virgin islands. *Atoll research Bulletin*, 153, 1-6.

Robertson, C. and White, R. (1986) Feeding patterns of *Nesogobius sp*., *Gymnapistes marmoratus*, *Neoodax balteatus* and *Acanthaluteres spilomelanurus* from a Tasmanian seagrass meadow. *Marine and Freshwater Research*, 37(4), 481-489.

Rooker, J., Dokken, Q., Pattengill, C. and Holt, G. (1997) Fish assemblages on artificial and natural reefs in the Flower Garden Banks National Marine Sanctuary, USA. *Coral Reefs*, 16(2), 83-92.

Seaman Jr, W. and Sprague, L. M. (1991) 1 - Artificial habitat practices in aquatic systems. In *Artificial habitats for marine and freshwater fisheries*, Academic Press, San Diego, pp. 1-29.

Seaman, W. and Jensen, A. C. (2000) *Purposes and practices of artificial reef evaluation*, Boca Raton, FL: CRC Press LLC.

Sih, A. (2013) Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour*, 85(5), 1077-1088.

Sih, A., Ferrari, M. C. O. and Harris, D. J. (2011) Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, 4(2), 367-387.

Simon, T., Joyeux, J.-C. and Pinheiro, H. T. (2013) Fish assemblages on shipwrecks and natural rocky reefs strongly differ in trophic structure. *Marine Environmental Research*, 90, 55-65.

Simon, T., Pinheiro, H. T. and Joyeux, J.-C. (2011) Target fishes on artificial reefs: evidences of impacts over nearby natural environments. *Science of The Total Environment*, 409(21), 4579-4584.

Soldal, A. V., Svellingen, I., Jørgensen, T. and Løkkeborg, S. (2002) Rigs-to-reefs in the North Sea: hydroacoustic quantification of fish in the vicinity of a “semi-cold” platform. *ICES Journal of Marine Science: Journal du Conseil*, 59(suppl), S281-S287.

Stier, A. C. and Osenberg, C. W. (2010) Propagule redirection: habitat availability reduces colonization and increases recruitment in reef fishes. *Ecology*, 91(10), 2826-2832.

Thanner, S. E., McIntosh, T. L. and Blair, S. M. (2006) Development of benthic and fish assemblages on artificial reef materials compared to adjacent natural reef assemblages in Miami-Dade County, Florida. *Bulletin of Marine Science*, 78(1), 57-70.

Thierry, J.-M. (1988) Artificial reefs in Japan — A general outline. *Aquacultural Engineering*, 7(5), 321-348.

Tupper, M. and Hunte, W. (1998) Predictability of fish assemblages on artificial and natural reefs in Barbados. *Bulletin of Marine Science*, 62(3), 919-935.

Vose, F. E. and Nelson, W. G. (1998) An assessment of the use of stabilized coal and oil ash for construction of artificial fishing reefs: Comparison of fishes observed on small ash and concrete reefs. *Marine Pollution Bulletin*, 36(12), 980-988.

Werner, E. E., Gilliam, J. F., Hall, D. J. and Mittelbach, G. G. (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, 64(6), 1540-1548.

Wessel, P. and Smith, W. H. F. (1996) A global self-consistent, hierarchical, high-resolution shoreline database. *Journal of Geophysical Research, 101*, 8741-8743.

Wilhelmsson, D., Öhman, M. C., Ståhl, H. and Shlesinger, Y. (1998) Artificial reefs and dive tourism in Eilat, Israel. *Ambio*, 27(8), 764-766.

Wilhelmsson, D., Yahya, S. A. S. and Öhman, M. C. (2006) Effects of high-relief structures on cold temperate fish assemblages: A field experiment. *Marine Biology Research*, 2(2), 136-147.

Wilson, S., Graham, N. and Polunin, N. (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology*, 151(3), 1069-1076.

Zalmon, I. R., Novelli, R., Gomes, M. P. and Faria, V. V. (2002) Experimental results of an artificial reef programme on the Brazilian coast north of Rio de Janeiro. *ICES Journal of Marine Science*, 59(suppl), S83-S87.

CHAPTER THREE:

Fish habitat in a changing world: implications for artificial reef design

Mosaic leatherjacket using new design artificial reef at Frankston. Photo credit K. Menzies

3.1 Abstract

Recently, artificial reefs have become a common management tool for recreational fisheries, species conservation and habitat restoration. Hundreds of artificial reefs of various designs have been deployed all around the world with many countries spending several millions of dollars on design, construction and deployment of artificial reefs. However, a large number of reef deployments have failed to achieve their goals as a substitute for natural reefs, largely as a result of inappropriate size and design. Here I investigated the performance of new artificial reefs designed to provide shelter for a variety of fish species. As a benchmark for their success, I compared fish abundance, diversity and community composition on the new design artificial reefs with other commonly used artificial reefs (Reef Balls) and with nearby natural reefs. Fish were monitored over two recruitment seasons at three locations in Port Phillip Bay, Victoria, Australia, with each location containing replicate Reef Ball reefs, a new design artificial reef and natural reefs. There were no consistent differences on total fish density among new design artificial reefs, Reef Balls and natural reefs, although densities on both artificial reef designs were markedly lower than natural reefs at some locations. However, fish species richness on the new design artificial reefs was on average 2x higher than natural reefs or Reef Ball reefs across all locations. This effect was more pronounced during the second year of sampling. There were large dissimilarities in fish community composition among habitats across all locations and in both years. However, the dissimilarities declined over time with the new design artificial reefs becoming more similar to natural reef communities than Reef Ball reefs by the end of the experiment. *Trachinops caudimaculatus* was one of the major contributors to the similarities between fish communities on natural reef and new design artificial reef. While *Diodon nichthemerus* and monacanthid juveniles were more typically associated with Reef Ball reefs. My results suggest that the new design artificial reefs can play a role in reef fish conservation where

natural reefs are under threat, supporting a natural community structure, but enhancing local reef fish biodiversity.

With the recent focus of marine management on the deployment of artificial reefs as a tool for habitat restoration and fish species conservation, they are expected to perform as closely as possible to the local natural reefs. If artificial reefs support vastly different fish communities to natural reefs they may shift community structure in the area and cause declines in some species abundances over time. Failure to support similar fish communities to natural reef may lead to future criticism and loss of stakeholder support, as well as failure to achieve restoration or conservation goals.

3.2 Introduction

Reef habitats have been artificially constructed for centuries. Japanese records that mention the use of artificial reefs for enhancing fisheries output date back at least 300 years. The exploitation of artificial reefs for the purpose of fish attraction and improvement of catches by artisanal fishers most likely dates back even further than that (Thierry, 1988; Grove *et al.*, 1991; Fabi *et al.*, 2011). About 80 years ago in Japan, and 50 years ago in Europe, the development of artificial marine habitats for fisheries management has gained widespread attention (Thierry, 1988; Grove *et al.*, 1991; Fabi *et al.*, 2011). Initially, artificial reefs were predominantly used for fish attraction, which improved both artisanal and later, commercial fishery landings. However, the potential negative aspects of this increased fishing efficiency on the sustainability of fished stocks have been increasingly recognised (Matthews, 1985; Carr and Hixon, 1997; Baine, 2001; Claudet and Pelletier, 2004).

With the increasing pressures on marine ecosystems from pollution, habitat loss, resource extraction, invasive species, and climate change (Jackson *et al.,* 2001; Halpern *et al.,* 2008; Jackson, 2008), artificial reefs are increasingly being adopted as a management tool for marine habitat restoration, stock enhancement of recreational fisheries and species conservation through the provision of additional adult habitat, as well as juvenile nursery and spawning ground habitats (Thierry, 1988; Grove *et al.*, 1991; Baine, 2001; Halpern *et al.*, 2008; Seaman and Lindberg, 2009; Fabi *et al.*, 2011). Moreover, artificial reefs have also been used as a means to prevent bottom trawling, to enhance recreational diving experience, for coastal defence purposes and as a disposal option for hard waste (Grove *et al.*, 1991; Collins *et al.*, 1995; Baine, 2001). However, although artificial reefs can potentially provide a wide range of benefits, the extent to which they achieve their goals has received limited attention. The potential success of artificial reefs will depend to a large degree on how the materials and design emulate natural reef habitats.

Over the years, artificial reefs have been constructed from almost every conceivable material that is available. Artisanal fisheries tended to use natural objects such as rocks and wood (Thierry, 1988; Grove *et al.*, 1991; Baine, 2001; Fabi *et al.*, 2011). However, with the modern development of artificial reefs as a management tool, many artificial materials have been employed, such as the widespread use of car tyres in the late 20th century (Thierry, 1988; Collins *et al.*, 1995; Collins *et al.*, 2002; Fabi *et al.*, 2011). Car tyre artificial reefs served two purposes: the need to recycle and reuse, as well as the creation of artificial habitats. Moreover, tyres were widely available and had the required flexibility to withstand storms. However, the growing evidence for deleterious effects of toxic leachate from submerged tyres in marine and aquatic environments (Day *et al.*, 1993; Collins *et al.*, 1995; Collins *et al.*, 2002; Wik and Dave, 2009) have limited their current use. In the late 1980s and through the 1990s, there was also considerable interest in investigating the suitability of stabilised coal and oil ash for construction of artificial reefs (Collins *et al.*, 1992; Collins *et al.*, 1994; Collins and Jensen, 1995; Vose and Nelson, 1998), which also carried the twin purpose of habitat construction and waste disposal. Ash and coal waste artificial reefs appeared to be sufficiently strong in their structure and versatile in terms of possible designs but again there have been concerns over their environmental impacts (Collins *et al.*, 1992; Hamilton *et al.*, 1993; Collins *et al.*, 1995). Over the years, much creativity has been employed in terms of artificial reef construction and many other materials have been used, such as purposeful and accidental ship wrecks, car and train wrecks, construction waste, metal, and plastic (Grove *et al.*, 1991; Baine, 2001; Fabi *et al.*, 2011). Many reefs have also been constructed from a combination of these materials (Grove *et al.*, 1991; Baine, 2001; Fabi *et al.*, 2011). Recently, however, the most common material for the construction of artificial habitats is concrete, in particularly the less toxic marine concrete (Wakeman *et al.*, 1958; Baine, 2001; Spieler *et al.*, 2001). Concrete has the required strength, durability, flexibility in terms of designs and a surface structure well suited for this purpose.

There is even greater diversity in the artificial reef designs than the materials they have been constructed from. The designs of artificial reefs range from basic concrete blocks to complicated 3-D printed forms (Grove *et al.*, 1991; Baine, 2001; Fabi *et al.*, 2011; Hackradt *et al.*, 2011; Pardo, 2013; Jiang and Zhao, 2015). Some of the main factors that have been considered during the design of many artificial reefs have been: cost, durability, strength and purpose of deployment (Thierry, 1988; Grove *et al.*, 1991; Clark and Edwards, 1999; Baine, 2001; Fabi *et al.*, 2011). Unfortunately, the specific habitat requirements of the local marine flora and fauna have commonly been given insufficient attention (Baine, 2001).

Habitat complexity and diversity of refuge sites have been long recognised as some of the most important variables in structuring fish and invertebrate communities (Gratwicke and Speight, 2005; Wilson *et al.*, 2007; Hackradt *et al.*, 2011; Messmer *et al.*, 2011; Komyakova *et al.*, 2013), having been commonly shown to have strong effects at mediating biological interactions, such as predation and competition (Behrents, 1987; Hixon and Menge, 1991;

Hixon and Beets, 1993; Stunz and Minello, 2001; Almany, 2004; Ford and Swearer, 2013). Indeed, Komyakova *et al.* (2013) showed that, in general, areas with higher habitat diversity support more diverse fish communities. Similarly, when looking at artificial habitats, Hackradt *et al.* (2011) demonstrated that reefs with a higher number of holes (i.e. greater complexity) supported higher fish abundances and diversity. Several studies have also underlined the affinity of some fish species for vertical relief, which has been shown to correlate with higher fish abundances (Kellison and Sedberry, 1998; Wilhelmsson *et al.*, 2006).

Despite all of the research investigating the performance of artificial reefs, many reef deployments have been reported to fail in achieving their goals (Baine, 2001). The success of artificial reefs ultimately depends on the purpose of their deployment. As many artificial reefs are currently constructed, at least partially, as mitigation measures for habitat loss and degradation, and for fish species conservation (Baine, 2001), it is logical to assume they should function as closely as possible to natural reefs. However, many studies investigating fish communities on artificial reefs have failed to compare those structures to natural reefs (Carr and Hixon, 1997; Rilov and Benayahu, 1998; Wilhelmsson *et al.*, 2006; Langhamer and Wilhelmsson, 2009; Langhamer *et al.*, 2009; Folpp *et al.*, 2011). Several studies that made the necessary comparison have reported conflicting evidence. For example, while Bohnsack *et al.* (1994) reported high fish densities on artificial reefs in comparison to natural reefs, Lechanteur and Griffiths (2001) found the opposite. Furthermore, while a few studies have reported that natural reefs support richer fish communities (Carr and Hixon, 1997; Hackradt *et al.*, 2011), other studies only detected differences in community and trophic structure (Hackradt *et al.*, 2011; Simon *et al.*, 2013), or no differences at all (Carr and Hixon, 1997). These discrepancies among studies are most likely linked to differences in artificial reef designs, as well as other confounding factors such as distance from natural reef, differences in size between natural and artificial habitats and sampling design (Carr and Hixon, 1997; Baine, 2001; Simon *et al.*, 2013). While lower abundances on artificial reefs may be expected due to the difference in size and continuity of natural versus artificial habitats, for artificial reefs to be a tool for habitat restoration and species conservation, there needs to be a better understanding of how to engineer artificial structures in such a way that they develop communities which are similar in structure to natural reefs. Improving the designs of artificial reefs so they function as closely as possible to natural reefs is not only important for habitat restoration and species conservation measures, but also as an ecological consideration of other artificial structures placed in the marine environment that can function as artificial reefs (Langhamer and Wilhelmsson, 2009; Dafforn *et al.*, 2015).

The aim of this study was to test a new type of an artificial reef designed to maximise fish shelter. Performance was evaluated by comparing fish abundance, diversity and community structure of fish colonising the new artificial reefs, with a commonly used artificial reef design (Reef Balls) and adjacent natural reef. Fish abundance, diversity and community structure were compared among the three habitats at three different locations over a 2-year monitoring period.

3.3 Materials and Methods

Study area

The study was conducted in Port Phillip Bay, Victoria, Australia, which is one of the largest natural embayments in Australia, covering an area ~ 1,930 km^2 (Figure 3.1). Three locations were chosen, Frankston, Altona and Portarlington, where Reef Ball reefs that were constructed in 2012, two years prior to the beginning of the experiment. All the Reef Ball reefs were in depths of 3-5 m depth, 40-70 m offshore from piers.

In 2014 each site had new design artificial reefs constructed at each location. Reefs were placed at depths of 5-7 m on sandy bottoms away from natural reefs, with the exception of Altona, where the new design artificial reefs were in close proximity (a few meters) to one of the sampled natural reefs.

At each location adjacent natural reefs were selected for sampling: one at Frankston and two at Altona and Portarlington (two reefs were sampled at Altona and Portarlington because the closest natural reef to each type of artificial reef at both locations were poor-quality reefs of low complexity). All natural reefs sampled lay in 2-5.5 m depth. Most habitats within each location were on average 2 km from each other.

Natural reefs

In general, Pelican reef (Frankston natural reef) is an average quality reef, with some good relief and high rugosity areas. It is separated from the other two reef types by predominantly sand. In comparison, both natural reefs at Altona are low-lying boulder fields with little vertical relief and low macroalgal cover. At Altona most sampled habitats are separated from each other by sand and a few poor quality, small habitat patches, with the exception of the new design artificial reef and Altona natural reef (II), that lay in close proximity to each other (a few meters). Finally, at Portarlington, Prince George Bank natural reef is a low-lying reef with many small caves and usually dense macroalgal cover. Steele's Rock natural reef is a shallow low-lying reef with several overhangs and caves. In general, it has relatively low macroalgal cover and is broken up by small patches of sand. It is the shallowest natural reef sampled with an average depth of 2.3 m.

Reef Ball reefs

Reef Ball reefs consist predominantly of two types of hollow dome shaped modules: Mini-Bay Ball (~50 cm tall) and Bay Ball (~60 cm tall) of 2 primary designs (Figure 2.2). The modules have various sized openings, allowing fish movement. One design has predominantly large but different sized holes leading to a completely hollow large interior space (Figure 2.2 a), while the other design (less used) has smaller but similarly sized holes leading to a narrower interior space (Figure 2.2 b). The modules are constructed from marine concrete with a relatively rough surface. Most Reef Balls are positioned in arrangements, as on a dice for five points, with 5-Reef-Ball units in close proximity to each other (between 0.5-1 m). Each 5-Reef-Ball unit arrangement covers an area of ~2.5 m in diameter and each 5-Reef-Ball unit arrangement lays approximately 5 m away from the next Reef- Ball unit arrangement. Each reef at each location consists of 18 5-Reef-Ball unit arrangements and three 3-Reef-Ball unit arrangements. Only 5-Reef-Ball unit arrangements were sampled here.

New design artificial reef

The new artificial reefs were designed to maximise habitat complexity, the diversity of refuge sites and vertical relief. The reefs were constructed from marine concrete. Each module of a new design artificial reef consisted of two lids (600 x 500 x 80 mm) and a central piece (height 340 mm). Each lid had 8 small raised square sections (100 x 100 x 20 mm) to create an opening between the central piece and the lid, and a larger extension to allow connection between the lid and the central piece (Figure 3.2 a). The central pieces had several various sized holes cut into them and were made of three designs: large holes only, small holes only and a mixture of large and small holes (Figure 3.2 b). Some of the holes were blind and some were penetrating the reef straight through. The holes were allocated randomly for each central module. The central part of each module had 1-3 hollow caves going the entire height of the module. Each central piece also had two flat sides and two curved sides (Figure 3.2 b). Each individual reef was constructed in a pyramid shape with 6 single units at the bottom and three at the top (Figure 3.2 c). The assembled reef was approximately 1 m tall. Each reef at each location contained 3 x large hole units, 3 x small hole units and 3 x mixed units. Each reef (n = 3 per location) had a slightly variable central piece arrangement: flat sides facing each other, curved sides facing each other and a mixture of flat to curved sides facing each other. The reefs were positioned on sandy bottom approximately 5-10 m away from each other.

Sampling design

To investigate the differences in fish abundance, species richness and community structure between natural and two types of artificial reefs, I sampled fish communities on each habitat at each of three locations using fortnightly to monthly underwater visual surveys from late spring to the end of autumn (November to June) for two consecutive years. Fish were identified to species and their ontogenetic stage was also recorded. The fish counts were performed in two stages, first an observer recorded all mobile species associating with the habitat in the sampled area from a distance of ~ 2 m for a maximum of 5 min, then the sampled area was carefully checked for approximately another 3 min for any small individuals and cryptic species. A high power LED torch was used to examine cracks and crevices.

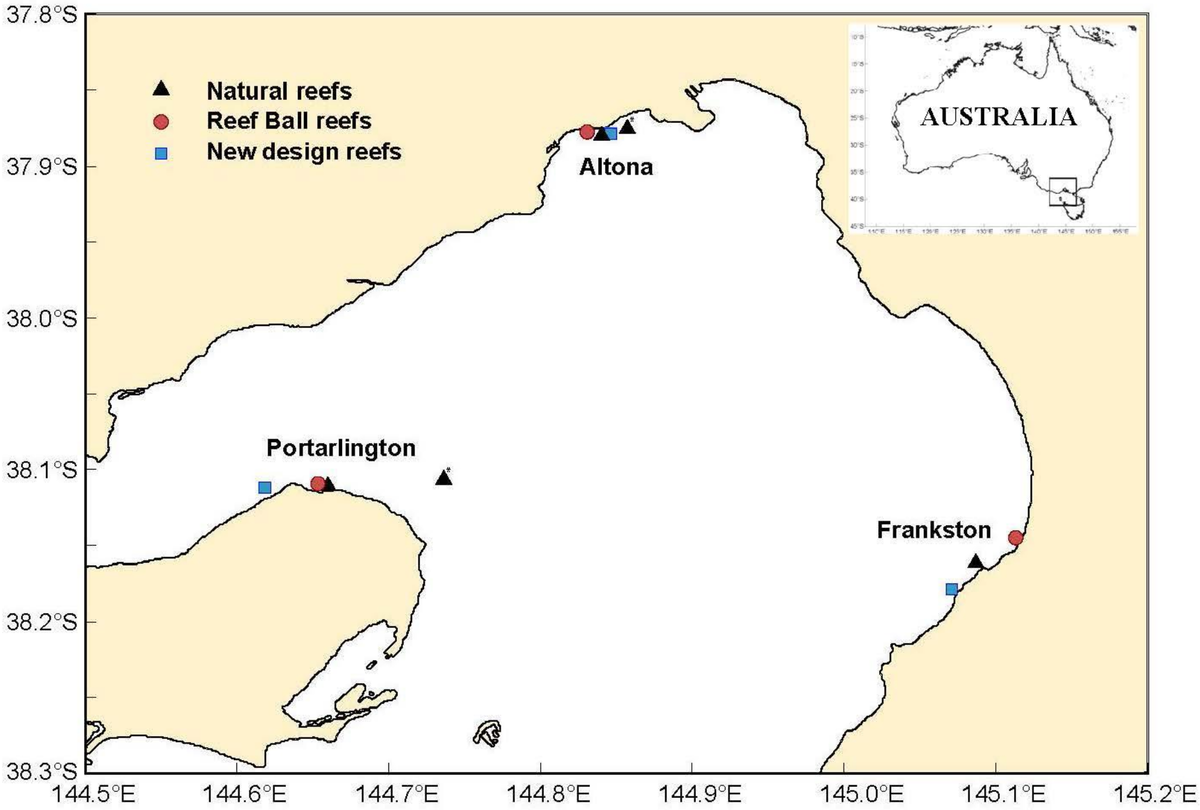


Fig. 3.1 Study area of Port Phillip Bay, Victoria, Australia. Black triangles identify location of natural reefs at each location. For Portarlington asterisk indicates Prince George Bank natural reef (Natural reef), while black triangle without asterisk indicates Steele's Rocks natural reef (Natural 2). For Altona asterisk indicates Natural reef 1, while black triangle without asterisk indicates Natural reef 2. Red circles identify position of Reef Ball reefs at each location. Blue squares indicate position of new design artificial reefs at each location. The coastline was derived from the full resolution version of the Global Self-consistent, Hierarchical, High-resolution Geography (GSHHS) database (Wessel and Smith, 1996).

On the Reef Ball reefs each of the 5-Reef-Ball unit arrangements was treated as a replicate (Figure 2.3). To match with the area taken up by a 5-Reef-Ball unit arrangement, an area of 2.5 meter in diameter was sampled on natural reef. When possible all 18 5-Reef-Ball unit arrangements were sampled on Reef Ball reefs and 18 point counts were conducted on natural reefs. Due to weather constraints it was not possible to sample all arrangements at some locations each sampling round; and therefore, a minimum of 5 5-Reef-Ball unit arrangements on Reef Ball reefs and 12 point counts on natural reef were sampled. On a natural reef, point counts were selected randomly for each sampling round and a minimum of

5 m distance was maintained between each sampling point. All new design artificial reefs were surveyed each sampling round. Fish abundance was converted to density for all three habitats (details for natural reefs and Reef Balls in Chapter 2). The exact dimensions of new design artificial reefs were known, which facilitated surface area calculations. Surfaces that were not available for fish (for e.g. bottoms of lids) were excluded from calculations.

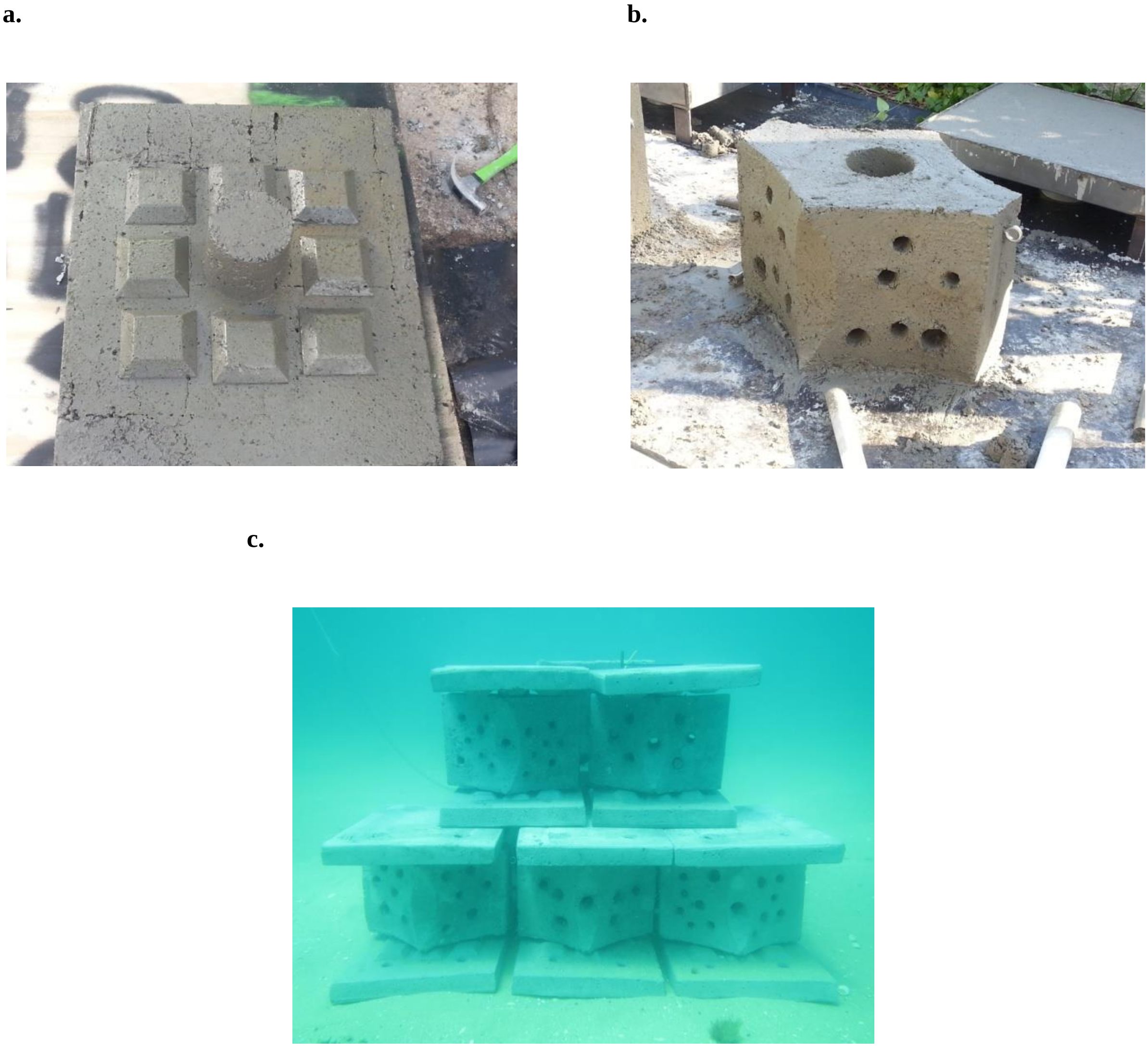


Fig. 3.2 New design artificial reef. a. Lid b. Central piece c. One assembled reef.

Statistical analysis

Univariate and multivariate analyses were performed using PRIMER-E v6 with the PERMANOVA (Permutational Multivariate Analysis of Variance) add-on (McArdle and

Anderson, 2001). Clarke and Gorley (2006) and Anderson *et al.* (2008) state that the use of PERMANOVA is appropriate for univariate analyses. Univariate Permanova is an approach similar to parametric ANOVA; however, it is not restricted by as many assumptions and is better suited for unbalanced data.

Fish density

To determine the effects of the year, location, habitat and survey on fish density, I used univariate PERMANOVA. Fish density was log+1 transformed. While PERMANOVA is more robust to the violations of the assumptions of parametric tests, the overall model fit the log+1 transformed data better than the raw data. A univariate PERMANOVA test, with fish density as the dependent variable, was run on Euclidean distance matrices with 9999 permutations. For this analysis the data from the two natural reefs at Altona were pooled, as well as the data from the two natural reefs at Portarlington. Year (2 levels), Location (3 levels) and Habitat (3 levels) were identified as fixed factors and Survey as a random factor nested within Year and Location (as not all surveys were conducted at each location in each year). My primary interest was the effects of Year, Location and Habitat on fish density, rather than Survey. I expected to have a large amount of variability between Surveys due to temporal variability in fish density. Due to the complexity of the design I used permutation of residuals under a reduced model permutation method with Type III sum of squares.

Due to significant two-way interactions between fixed factors (Year x Habitat & Location x Habitat), I conducted a separate PERMANOVA test for each Location within each Year using the same methodology as above. For this analysis the data from all natural reefs was treated separately. A Bonferroni-adjusted alpha level was used to correct for multiple non-independent tests (Table 3.1). Pair-wise PERMANOVA tests were conducted as a post hoc test to identify which habitats were significantly different from each other in fish densities within each year and location (Table 3.2).

Fish species richness

To determine the effects of year, location, habitat and survey on fish species richness, I also used PERMANOVA. A univariate PERMANOVA test, with fish species richness as the dependent variable, was run on Euclidean distance matrices with 9999 permutations The model design and methodology were identical to that described above for fish density. As previously, the data from the two natural reefs at Altona and Portarlington were pooled. Due to a significant Year x Habitat interaction, separate analyses for each Year were performed using the same methods as described above (Table 3.1). As there was a significant habitat effect for the second year of sampling, pair-wise PERMANOVA tests were conducted as a post hoc test to identify which habitats were significantly different from each other in fish species richness for each location during that year (Table 3.3).

Fish community structure

To determine the effects of year, location, habitat and survey on the fish community structure, a multivariate PERMANOVA analysis using a Bray-Curtis similarity matrix of fourth root transformed density data with 9999 permutations was conducted. Fourth root transformation was applied to reduce the influence of species that occurred in extremely high densities. Due to the complexity of the design I used permutation of residuals under a reduced model permutation method with Type III sum of squares. The community data included individual species and, when recorded, life stage (recruits, juveniles, and adults). Only the species with raw abundances over 10 individuals across all samples were included in the analysis. Several of the species were pooled together to create generic taxonomic groups with sufficient numbers for inclusion: other Monacanthid recruits; other leatherjacket juveniles; other leather jacket adults; sand blennies and other blennies, *Scorpis aequipinnis/lineolata* and *Parma victoriae/microlepis*. A total of 69 dependent variables was used in the analysis. Because Bray-Curtis coefficients cannot deal with multiple blank samples (samples containing no species), for the resemblance matrix the zero value samples were removed as recommended by Clarke & Gorley (2006). The model structure and methodology were as described for the two univariate PERMANOVA tests.

Due to a significant Year x Location x Habitat interaction, I conducted separate PERMANOVA tests for each Location within each Year and again used a Bonferroni-adjusted alpha to account for multiple non-independent tests. For this analysis the data from all natural reefs was treated separately. Community composition for each Location and Year was visualised using a principal coordinates analysis (PCO) plot, which is a recommended approach for data where "within-group" dissimilarities are smaller than "between-group" dissimilarities (Anderson *et al.*, 2008). The vectors overlying the plot represent the correlations (Spearman correlation coefficients) between taxa and PCO axes. Spearman correlations were chosen as they are better suited to deal with non-linear relationships that are common in ecological data sets. The 'similarity percentage' routine (SIMPER) was used to identify the contribution of each taxa to a significant community change between habitats within each Location and Year. The consistency of the contribution of each taxon to the community variance is represented by the ratio of each taxon's average dissimilarity to the standard deviation of dissimilarities (Diss/SD), with values greater than 1 representing taxa which consistently contribute to community change among habitats.

3.4 Results

Fish density

Overall, fish densities increased from late spring to mid-summer and declined from mid-summer to autumn in both years, at all locations, and on most habitats (Figure 3.3), but given the significant Year x Habitat and Location x Habitat interactions, these effects were not consistent (Table 3.1).

When analysed separately by location within each year, as expected, in most cases there were significant interactions with Survey and a significant effect of Survey at Altona and Frankston, due to seasonal variability in fish densities. At Portarlington, however, there was no significant Survey effect and no significant interactions. For all three locations there was a significant effect of Habitat (Table 3.1).

At Frankston, natural reef supported between two to four times higher densities (survey dependent) than the Reef Ball reef and the new design artificial reef during the first year of sampling. During the second year of sampling all three habitats were significantly different from each other (Table 3.2, Figure 3.3 a), with natural reef again supporting two to five times as high fish densities than the other two habitats. New design artificial reefs supported fish densities approximately twice as high as Reef Ball reef during this sampling season at this location (Table 3.2, Figure 3.3 a).

At Altona, Natural reef 1, in general, had lower densities than most other habitats (Table 3.2, Figure 3.3 b). For both sampling years natural reef 1 supported at least three times lower fish densities the natural reef 2 and new design artificial reef. New design artificial reef supported, on average, twice as high fish densities as Reef Ball reef at this location (Table 3.2, Figure 3.3 b).

At Portarlington, the new design artificial reef, in general, had lower densities than other habitats (Figure 3.3 c). During the 2014/2015 sampling season, all of the habitats were, on average, significantly different from each other with the exception of Reef Ball reef and Natural reef 2 (Steele's rock reef) (Table 3.2, Figure 3.3 c). During the 2015/2016 sampling season, both natural reefs, new design artificial reef and Reef Ball reef and new design artificial reef and Natural reef 1 (Prince George Bank reef) were all significantly different from each other. Prince George Bank natural reef had slightly higher average fish densities than Steele's Rock reef, Reef Ball reef and Prince George Bank reef had higher average fish densities than new design artificial reef (Table 3.2, Figure 3.3 c).

Fish species richness

Over the two years of the study, species richness on the new design artificial reefs increased to almost twice that for Reef Ball reefs and natural reefs (Figure 3.4). There was a significant interaction between Year and Habitat (Table 3.1), largely as a result of a significant increase in average species richness for all locations for the new design artificial reefs between years (Figure 3.4). In 2014/2015 there was only a significant effect of survey, but in 2015/2016 there was a significant affect of Habitat, predominantly drive by new design artificial reefs on average supporting twice as rich fish communities as most other habitats across all three locations (Table 3.3, Figure 3.4).

While new design artificial reefs on average supported much higher fish species richness than other habitats across all locations and years, the natural reefs supported greater total fish species richness. Overall, the highest number of fish species was seen on Pelican reef during the 2015/2016 sampling season (35 species). The lowest total species richness was observed on new design artificial reef at Altona during the same sampling season (10 species).

Table 3.1 Results from univariate PERMANOVA on Euclidean distances to test for Year (2014/2015 and 2015/2016 sampling season), Location (Frankston, Altona, Portarlington), and Habitat (Natural reef, New Design Artificial reef, Reef Ball reef) differences on fish density and species richness. The test statistic (F*) is a pseudo-F value and the probability value (P†) are computed by the PERMANOVA routine with max 9,999 permutations under a reduced model. Sum of squares is Type III (partial). Fish density data was log+1 transformed. Bonferroni correction is applied to fish density ** for each location with each year and significance is set at 0.008 level. A 0.05 level of significance was applied to all other tests. Year, Location and Habitat were treated as fixed factors where applicable, while Survey was treated as a random factor nested within Year and Location, where applicable. For the univariate PERMANOVA tests for each Location, the data on fish density from all natural reefs was treated separately.

Variable type	**Source**	**df**	**SS**	**MS**	**F***	**P†**	**Unique permutations**
Fish density	Year	1	19.045	19.045	10.171	**0.0029**	9843
Overall	Location	2	42.627	21.314	11.231	**0.0001**	9945
	Habitat	2	108.09	54.043	34.268	**0.0001**	9956
	Survey(Year&Location)	37	70.713	1.9112	2.4995	**0.0001**	9891
	Year x Location	2	4.11	2.0548	1.0915	0.3501	9953
	Year x Habitat	2	31.4	15.698	9.9541	**0.001**	9951
	Location x Habitat	4	192.57	48.142	29.997	**0.0001**	9949
	Habitat x Survey(Year&Location)	74	123.01	1.6622	2.1739	**0.0001**	9823
	Year x Location x Habitat	4	5.4	1.3502	0.8413	0.4727	9951
	Error	1551	1185.9	0.7645			
	Total	1679	2062.5				
Fish density**	Habitat	2	250.85	125.42	82.513	**0.0001**	9952

2014/2015	Survey(Location)	6	3.313	0.5522	0.96822	0.4245	9948
Frankston	Habitat x Survey(Location)	12	18.377	1.5314	2.6851	**0.0046**	9917
	Error	232	132.32	0.5703			
	Total	252	421.37				
Fish density**	Habitat	2	108.96	54.482	23.506	**0.0002**	9960
2015/2016	Survey(Location)	10	42.564	4.256	4.6284	**0.0001**	9944
Frankston	Habitat x Survey(Location)	20	46.692	2.335	2.5386	**0.0006**	9890
	Error	337	309.91	0.92			
	Total	369	528.14				
Fish density**	Habitat	3	46.031	15.344	8.3224	**0.0017**	9939
2014/2015	Survey(Location)	7	12.062	1.723	5.4483	**0.0001**	9940
Altona	Habitat x Survey(Location)	19	35.53	1.87	5.9126	**0.0001**	9917
	Error	283	89.506	0.313			
	Total	312	202.07				
Fish density**	Habitat	3	58.138	19.379	13.636	**0.0037**	9960
2015/2016	Survey(Location)	3	6.959	2.32	5.345	**0.0015**	9953
Altona	Habitat x Survey(Location)	9	12.93	1.437	3.311	**0.0017**	9936
	Error	152	65.962	0.434			
	Total	167	138.89				

Fish density** 2014/2015 Portarlington	Habitat	3	60.173	20.058	13.326	**0.0009**	9961
	Survey(Location)	5	6.5649	1.313	1.2501	0.2815	9952
	Habitat x Survey(Location)	15	22.801	1.52	1.4472	0.1313	9929
	Error	254	266.78	1.0503			
	Total	277	360.48				
Fish density** 2015/2016 Portarlington	Habitat	3	21.186	7.062	7.045	**0.0056**	9952
	Survey(Location)	6	8.221	1.3701	2.1201	0.0522	9955
	Habitat x Survey(Location)	18	18.234	1.013	1.568	0.0717	9906
	Error	270	174.49	0.6463			
	Total	297	225.63				
Fish species richness Overall	Year	1	148.72	148.72	10.877	**0.0029**	9817
	Location	2	112.82	56.409	4.0936	**0.0254**	9949
	Habitat	2	204.07	102.04	14.771	**0.0002**	9950
	Survey(Year&Location)	37	521.02	14.082	7.2088	**0.0001**	9887
	Year x Location	2	14.976	7.4881	0.54341	0.5855	9953
	Year x Habitat	2	70.943	35.472	5.1348	**0.015**	9952
	Location x Habitat	4	31.332	7.8329	1.1067	0.3457	9955
	Habitat x Survey(Year&Location)	74	549.65	7.4277	3.8024	**0.0001**	9862
	Year x Location x Habitat	4	14.06	3.5151	0.49662	0.7025	9944

	Error	1551	3029.7	1.9534			
	Total	1679	5409.3				
Fish species richness 2014/2015	Location	2	30.186	15.093	1.245	0.3163	9960
	Habitat	2	30.166	15.083	2.3661	0.1191	9949
	Survey(Location)	18	219.03	12.168	6.7521	**0.0001**	9922
	Location x Habitat	4	42.797	10.699	1.6516	0.1963	9956
	Habitat x Survey(Location)	36	238.97	6.6381	3.6834	0.0001	9866
	Error	781	1407.5	1.8022			
	Total	843	2178				
Fish species richness 2015/2016	Location	2	85.822	42.911	2.8229	0.0876	9949
	Habitat	2	236.86	118.43	15.949	**0.0003**	9935
	Survey(Location)	19	301.99	15.894	7.5443	**0.0001**	9913
	Location x Habitat	4	8.3252	2.0813	0.27451	0.87	9949
	Habitat x Survey(Location)	38	310.68	8.1757	3.8806	**0.0001**	9888
	Error	770	1622.2	2.1068			
	Total	835	3002				

Table 3.2 Results from pair-wise tests of univariate PERMANOVA on Euclidean distances to test for Habitat (Natural reef, new design artificial reef, Reef Ball reef) differences at each Location with each Year on fish density. The test statistic (F*) is a pseudo-F value and the probability value ($P^{\dagger}$) are computed by the PERMANOVA routine with max 9,999 permutations under a reduced model. Sum of squares is Type III (partial). Fish density data were log+1 transformed. The level of significance is set at 0.05. Habitat was treated as a fixed factor. Only differences between Habitats within each year and location are considered. The data on fish density from all natural reefs was treated separately for this analysis. Note: at Portaringtom natural reef 1 is also known as Prince George Bank reef and natural reef 2 as Steele's Rock reef.

Groups	**t**	**P**	**Unique permutations**	**Groups**	**t**	**P**	**Unique permutations**
Frankston 2014/2015				**Frankston 2015/2016**			
New Artificial reef vs Natural	8.9643	**0.0003**	9880	New Artificial reef vs Natural	3.1848	**0.0026**	9857
New Artificial reef vs Reef Balls	0.26727	0.7996	9819	New Artificial reef vs Reef Balls	2.943	**0.011**	9844
Natural vs Reef Balls	9.2924	**0.0004**	9919	Natural vs Reef Balls	5.258	**0.0006**	9837
Altona 2014/2015				**Altona 2015/2016**			
Natural 1 vs Natural 2	3.4345	**0.021**	9846	Natural 1 vs Natural 2	4.0329	**0.0439**	7720
Natural 1 vs Reef Balls	0.18161	0.8606	9838	Natural 1 vs Reef Balls	2.197	0.1251	7825
Natural 1 vs New Artificial reef	4.7492	**0.0011**	9856	Natural 1 vs New Artificial reef	9.4216	**0.0284**	7239
Natural 2 vs Reef Balls	1.8054	0.1382	9860	Natural 2 vs Reef Balls	1.6622	0.2135	7698
Natural 2 vs New Artificial reef	0.081828	0.9488	9867	Natural 2 vs New Artificial reef	2.6455	0.0786	6245
Reef Balls vs New Artificial reef	3.5336	**0.0117**	9881	Reef Balls vs New Artificial reef	4.1068	**0.0347**	3154
Portarlington 2014/2015				**Portarlington 2015/2016**			
Natural 1 vs Natural 2	3.4054	**0.0235**	9848	Natural 1 vs Natural 2	4.7181	**0.0041**	9802
Natural 1 vs Reef Balls	3.9718	**0.0146**	9856	Natural 1 vs Reef Balls	1.2619	0.2564	9797
Natural 1 vs New Artificial reef	13.859	**0.0028**	9688	Natural 1 vs New Artificial reef	6.5646	**0.0004**	9868
Natural 2 vs Reef Balls	0.61628	0.5584	9833	Natural 2 vs Reef Balls	0.98932	0.4142	9899

Natural 2 vs New Artificial reef	3.6459	**0.0119**	9723	Natural 2 vs New Artificial reef	1.8905	0.1137	9840
Reef Balls vs New Artificial reef	2.8898	**0.0278**	9825	Reef Balls vs New Artificial reef	2.9311	**0.0238**	9822

Table 3.3 Results from pair-wise tests of univariate PERMANOVA on Euclidean distances to test for Habitat (Natural reef, new design artificial reef, Reef Ball reef) differences at each Location during the second year of sampling on fish species richness. The test statistic (F*) is a pseudo-F value and the probability value ($P^{\dagger}$) are computed by the PERMANOVA routine with max 9,999 permutations under a reduced model. Sum of squares is Type III (partial). The level of significance is set at 0.05. Habitat was treated as fixed factors. Only differences between Habitats within location are considered. The data on fish species richness from all natural reefs was treated separately for this analysis. Note: at Portarington natural reef 1 is also known as Prince George bank reef and natural reef 2 as Steele's Rock reef.

Groups	**t**	**P**	**Unique permutations**
Frankston 2015/2016			
New Artificial reef x Natural	7.728	**0.0001**	9846
New Artificial reef x Reef Balls	3.106	**0.01**	9820
Natural x Reef Balls	1.035	0.3301	9812
Altona 2015/2016			
Natural 1 x Natural 2	9.49	**0.023**	7459
Natural x Reef Balls	0.6758	0.6417	7852
Natural x New Artificial reef	11.071	**0.0283**	6875
Natural 2 x Reef Balls	0.953	0.4092	7753
Natural 2 x New Artificial reef	6.207	**0.0254**	6262
Reef Balls x New Artificial reef	2.9144	0.087	3110
Portarlington 2015/2016			
Natural 1 x Natural 2	4.052	**0.0075**	9834
Natural 1 x Reef Balls	0.824	0.4656	9845

Natural 1 x New Artificial reef	2.234	**0.0698**	9886
Natural 2 x Reef Balls	2.613	**0.042**	9864
Natural 2 x New Artificial reef	3.9171	**0.0053**	9844
Reef Balls x New Artificial reef	3.348	**0.0159**	9822

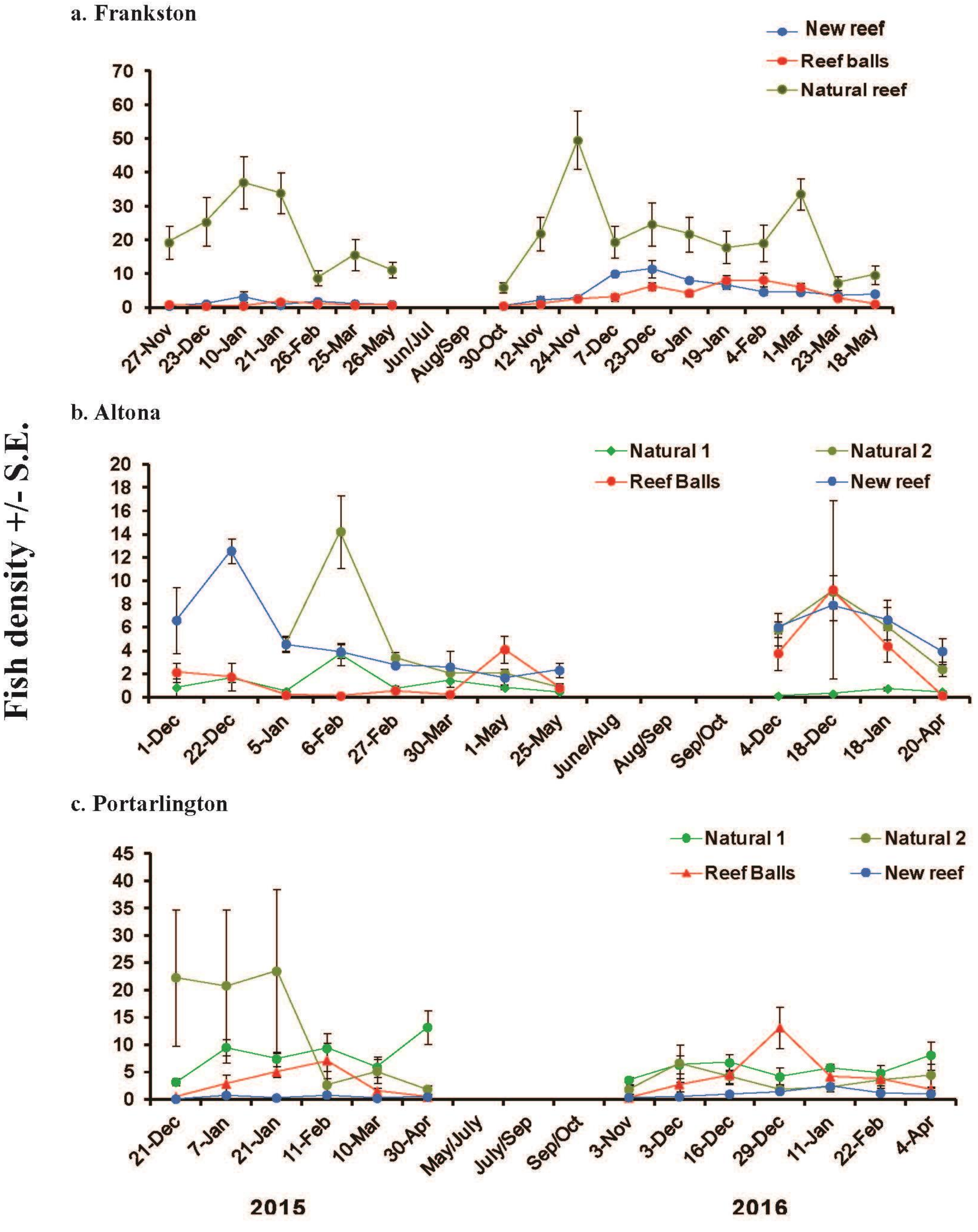


Fig. 3.3 Fish density (fish /m^2) observed over two sampling seasons on three habitats (Reef Ball reefs, natural reefs and new design artificial reefs) at three locations (a. Frankston; b. Altona; c. Portarlington) in Port Phillip Bay, Victoria, Australia.

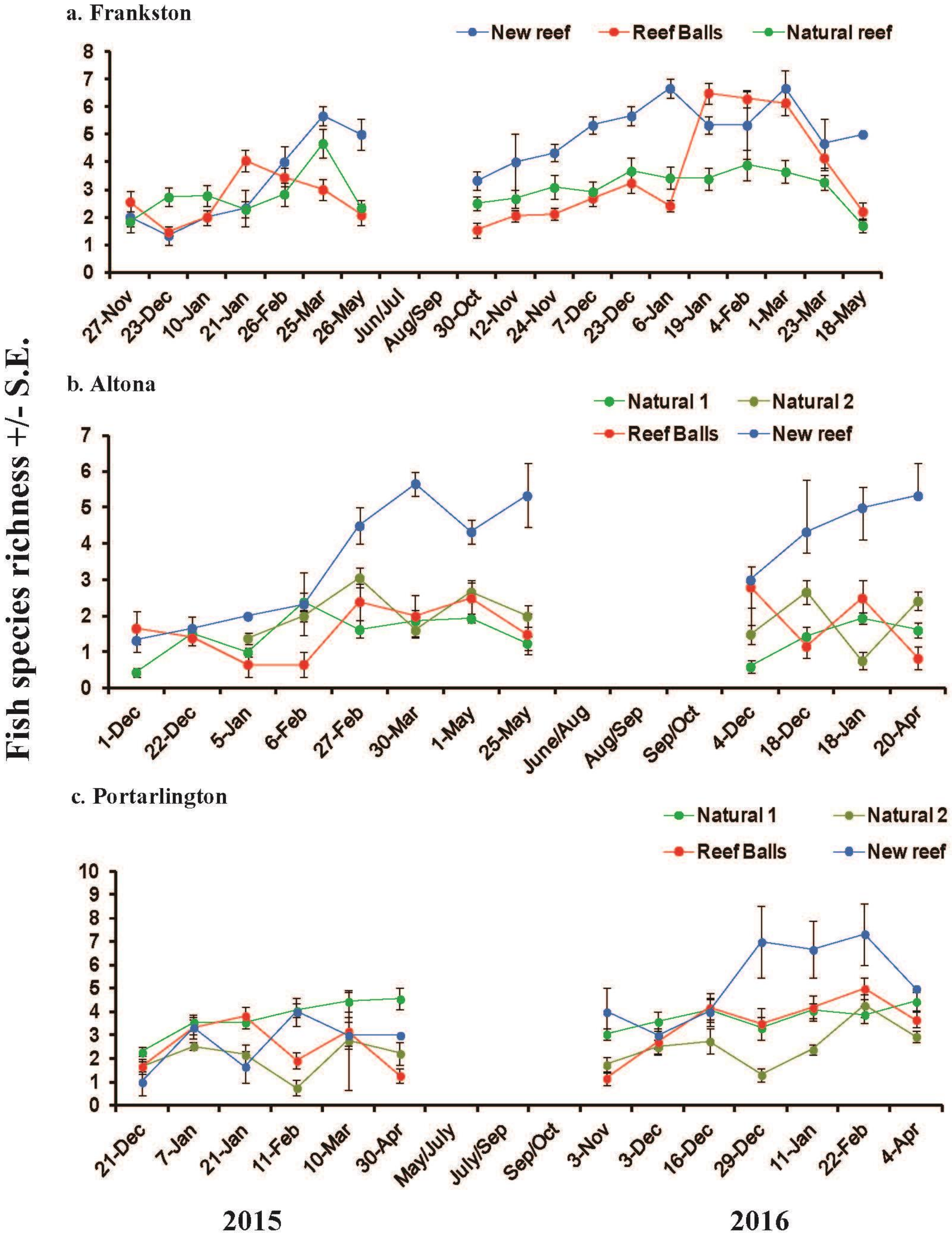


Fig. 3.4 Fish species richness observed over two sampling seasons on three habitats (Reef Ball reefs, natural reefs and new design artificial reefs) at three locations (a. Frankston; b. Altona; c. Portarlington) in Port Phillip Bay, Victoria, Australia.

Fish community structure

There was no general effect of reef type on fish assemblage structure, with differences among reef types dependent on the location and time of sampling (Figure 3.5). Fish community structure varied by year, location and habitat (Table 3.4, Figure 3.5). There was a significant effect of habitat on fish community structure for each year and each location (Table 3.4, Figure 3.5). The dissimilarities between habitats within each year and location were quite large, over 70% in most cases. The smallest dissimilarities calculated by SIMPER were between new design artificial reef and natural reef 2 at Altona (67.28% for 2014/2015 and 49.44% for 2015/2016) and new design artificial reef and natural reef (Pelican reef) at Frankston (78.51% in 2014/2015 and 62.92% in 2015/2016). Reef ball reefs had some of the largest dissimilarities with natural reefs at most location and years (mostly over 90%) (Table 3.5).

PCO plots of fish communities at different locations during the two sampling years identified two main clusters for each year and location (Figure 3.5).

At Altona and Frankston, fish communities associated with new design artificial reef and natural reef were more different from Reef Ball reefs in their structure and more similar to each other. Moreover, fish community structure at these two locations between natural reefs and new design artificial reef became more similar over time (Figure 3.5 a-d, Table 3.5). *Trachinops caudimaculatus* (all life stages) was one of the main species driving the differences between habitats, in many cases contributing over 10% to the dissimilarities. This species was predominantly associated with natural reefs and new design artificial reef (Figure 3.5, Table 3.6). At Altona *Parablennius tasmanianus* and *Trinorfolkia clarkei* were also typical of a natural reef community (Figure 3.5 c-d, Table 3.6). At Frankston, leatherjacket juveniles and *Diodon nichthemerus* were major contributors to the dissimilarities between habitats in both years, being strongly associated with Reef Ball reefs (Figure 3.5 a-b, Table 3.6).

At Portarlington, the similarities in fish communities were greater between Reef Ball reef and new design artificial reef and more different from natural reefs during both sampling years (Figure 3.5 e-f). *Notolabrus tetricus* and *Upeneichthys vlamingii* were typical species on natural reefs (Figure 3.5 e-f, Table 3.6). *Neoodax balteatus* was often associated with natural reefs and Reef Balls and was driving community differences at most locations and sampling years (Figure 3.5 e-f, Table 3.6). *Vincentia conspersa* occurred on most habitats, but was particularly common on Reef Ball reefs and new design artificial reefs at Portarlington. *Parma victoriae*, *Tilodon sexfasciatum* and to a lesser extent *Scorpis aequipinnis* largely typified a natural reef community at most locations and years (Figure 3.5 e-f, Table 3.6).

Table 3.4 Results from multivariate PERMANOVA using Bray-Curtis similarity values to test for Year (2014/2015 and 2015/2016 sampling season), Location (Frankston, Altona, Portarlington), and Habitat (Natural reef, New Design Artificial reef, Reef Ball reef) differences on fish community structure. The test statistic (F*) is a pseudo-F value and the probability values (P†) are computed by the PERMANOVA routine with max of 9,999 permutations under a reduced model. Sum of squares is Type III (partial). The data was fourth root transformed. Bonferroni correction is applied to the fish community** analysis split by Location and Year and significance is set at 0.008. Year, Location and Habitat were treated as fixed factors where applicable, while Survey was treated as a random factor nested within Year and Location, where applicable. For the multivariate PERMANOVA tests for each Year and Location the data on fish density from all natural reefs was treated separately.

Variable type	Source	df	SS	MS	F*	P†	Unique permutations
Fish community **Overall**	Year	1	37499	37499	3.3763	**0.0067**	9954
	Location	2	147770	73885	6.5799	**0.0001**	9915
	Habitat	2	409510	204750	37.497	**0.0001**	9917
	Survey(Year&Location)	37	427890	11565	4.6942	**0.0001**	9643
	Year x Location	2	26370	13185	1.1742	0.2988	9937
	Year x Habitat	2	51603	25801	4.725	**0.0001**	9920
	Location x Habitat	4	216070	54017	9.5982	**0.0001**	9891
	Habitat x Survey(Year&Location)	74	438420	5924.5	2.4048	**0.0001**	9505
		4	55955	13989	2.4856	**0.0001**	9893
	Year x Location x Habitat	1469	3619000	2463.6			
	Error	1597	6248700				
	Total						
Fish community** **Frankston 2014/2015**	Habitat	2	308940	154470	86.701	**0.0001**	9925
	Survey	6	84068	14011	7.8643	**0.0001**	9868
	Habitat x Survey	12	87412	7284.4	4.0886	**0.0001**	9825
	Error	228	406210	1781.6			
	Total	248	895830				
Fish community** **Frankston 2015/2016**	Habitat	2	236460	118230	63.701	**0.0001**	9923
	Survey	10	159690	15969	8.6041	**0.0001**	9857
	Habitat x Survey	20	78783	3939.2	2.1224	**0.0001**	9783
	Error	335	621760	1856			
	Total	367	1202500				

Fish community Altona 2014/2015**	Habitat	3	158200	52733	6.6537	**0.0001**	9926
	Survey	7	87167	12452	5.8538	**0.0001**	9853
	Habitat x Survey	19	152880	8046.5	3.7826	**0.0001**	9796
	Error	249	529680	2127.2			
	Total	278	1058300				
Fish community Altona 2015/2016**	Habitat	3	127800	42600	7.9732	**0.0002**	9929
	Survey	3	25280	8426.8	3.813	**0.0001**	9909
	Habitat x Survey	9	49350	5483.4	2.4811	**0.0001**	9849
	Error	133	293940	2210			
	Total	148	506780				
Fish community Portarlington 2014/2015**	Habitat	3	187910	62637	10.608	**0.0001**	9918
	Survey	5	39579	7915.8	2.822	**0.0002**	9836
	Habitat x Survey	15	93901	6260.1	2.2318	**0.0001**	9740
	Error	237	664790	2805			
	Total	260	1026500				
Fish community Portarlington 2015/2016**	Habitat	3	141260	47086	9.3242	**0.0001**	9919
	Survey	6	81448	13575	5.0723	**0.0001**	9862
	Habitat x Survey	18	92383	5132.4	1.9178	**0.0001**	9748
	Error	264	706520	2676.2			
	Total	291	1055500				

Table 3.5 Results of SIMPER for the effects of Habitat within each Location and Year that caused a significant change in fish community. Average dissimilarity of each pair of Habitats within each Location and Year is presented. The data was fourth root transformed. The analysis was conducted on Bray-Curtis similarity matrices. The data on each species density from all natural reefs was treated separately for this analysis. Note: at Portarington Natural reef 1 is also known as Prince George Bank reef and Natural reef 2 as Steele's Rock reef.

Frankston 2014/2015

Habitat	**Natural**	**Reef Balls**
New Design Artificial reef	78.51	90.33
Reef Balls	96.79	

Frankston 2015/2016

Habitat	**Natural**	**Reef Balls**
New Design Artificial reef	62.92	68.90
Reef Balls	81.52	

Altona 2014/2015

Habitat	**Natural 1**	**Natural 2**	**Reef Balls**
New Design Artificial reef	84.62	67.28	89.04
Reef Balls	95.99	98.88	
Natural 2	72.55		

Altona 2015/2016

Habitat	**Natural 1**	**Natural 2**	**Reef Balls**
New Design Artificial reef	77.93	49.44	98.57
Reef Balls	97.55	97.69	
Natural 2	78.18		

Portarlington 2014/2015

Habitat	**Natural 1**	**Natural 2**	**Reef Balls**
New Design Artificial reef	93.94	95.26	80.89
Reef Balls	92.62	94.44	

Natural 2	88.12		

Portarlington 2015/2016			
Habitat	**Natural 1**	**Natural 2**	**Reef Balls**
New Design Artificial reef	87.09	81.47	74.59
Reef Balls	83.06	84.42	
Natural 2	80.72		

Table 3.6 Results of SIMPER analysis showing the Diss/SD and the percent contribution to the dissimilarity of each species at each location and year with Spearman correlation of 0.5 from PCO analysis (Figure 3.5) in order of: Natural reef 1 (NR) vs Reef Balls (RB); Natural reef 2 (NR2) vs Reef Balls (RB) (exp. Frankston); Natural reef 1 (NR) vs new design artificial reef (NDAR); Natural reef 2 (NR2) vs new design artificial reef (NDAR) (exp. Frankston); Reef Balls (RB) vs new design artificial reef (NDAR); Natural reef 1 (NR) vs Natural reef 2 (NR2) (exp Frankston).

FRANKSTON 2014/2015			
Species	**Habitats**	**Diss/SD**	**% Contribution**
T. caudimaculatus (Adult)	NR vs RB	2.09	29.2
	NR vs NDAR	2.04	34.4
	RB vs NDAR	n/a	n/a
T. caudimaculatus (Juv)	NR vs RB	1.01	12.53
	NR vs NDAR	1.15	12.41
	RB vs NDAR	1.11	15.07
Other Monacanthidae (Juv)	NR vs RB	0.78	5.73
	NR vs NDAR	n/a	n/a
	RB vs NDAR	0.85	7.78
D. nichthemerus	NR vs RB	1.15	9.29
	NR vs NDAR	0.54	2.64
	RB vs NDAR	1.11	15.07
FRANKSTON 2015/2016			
Species	**Habitats**	**Diss/SD**	**% Contribution**
T. caudimaculatus (Adult)	NR vs RB	1.43	19.31
	NR vs NDAR	1.78	15.83
	RB vs NDAR	1.88	15.33
T. caudimaculatus (Juv)	NR vs RB	0.75	8.81
	NR vs NDAR	0.88	9.43
	RB vs NDAR	0.67	6.32
T. caudimaculatus (Rec)	NR vs RB	0.76	10.16
	NR vs NDAR	0.76	9.23
	RB vs NDAR	0.67	8.45
D. nichthemerus	NR vs RB	1	9.97

	NR vs NDAR	0.73	4.34
	RB vs NDAR	1.2	8.87
N. balteatus	NR vs RB	0.61	3.75
	NR vs NDAR	n/a	n/a
	RB vs NDAR	0.61	2.84

ALTONA 2014/2015

Species	**Habitats**	**Diss/SD**	**% Contribution**
T. caudimaculatus (Adult)	NR vs RB	0.5	8.79
	NR2 vs RB	1.52	22.97
	NR vs NDAR	0.98	11.23
	NR2 vs NDAR	1.51	25.39
	RB vs NDAR	0.68	5.06
	NR vs NR2	1.49	31.38
T. caudimaculatus (Juv)	NR vs RB	n/a	n/a
	NR2 vs RB	0.66	8.14
	NR vs NDAR	1.75	28.75
	NR2 vs NDAR	1.24	20.17
	RB vs NDAR	1.84	26.66
	NR vs NR2	0.8	13.88
P. tasmanianus	NR vs RB	0.64	9.95
	NR2 vs RB	0.47	3.11
	NR vs NDAR	0.97	7.08
	NR2 vs NDAR	1.16	8.45
	RB vs NDAR	1.05	6.66
	NR vs NR2	0.69	10.01
T. clarkei	NR vs RB	0.65	8.32
	NR2 vs RB	0.84	11.06
	NR vs NDAR	0.64	3.82
	NR2 vs NDAR	0.84	4.81
	RB vs NDAR	0.82	5.67
	NR vs NR2	0.59	7.27

ALTONA2015/2016

Species	**Habitats**	**Diss/SD**	**% Contribution**
T. caudimaculatus (Adult)	NR vs RB	n/a	n/a
	NR2 vs RB	1.41	16.29
	NR vs NDAR	3.25	22.95
	NR2 vs NDAR	1.22	16.08
	RB vs NDAR	3.8	17.18
	NR vs NR2	1.3	21.19
T. caudimaculatus (Juv)	NR vs RB	n/a	n/a
	NR2 vs RB	1.1	12.68
	NR vs NDAR	2.65	22.98
	NR2 vs NDAR	1.05	16.88
	RB vs NDAR	1.97	15.83
	NR vs NR2	1.1	17.03
T. caudimaculatus (Rec)	NR vs RB	n/a	n/a
	NR2 vs RB	0.62	5.78
	NR vs NDAR	0.71	10.35
	NR2 vs NDAR	0.47	5.51
	RB vs NDAR	0.95	9.93

	NR vs NR2	0.5	6.02
T. clarkei	NR vs RB	1.24	18.13
	NR2 vs RB	0.96	9.55
	NR vs NDAR	0.84	5.94
	NR2 vs NDAR	1.02	8.54
	RB vs NDAR	1.47	8.43
	NR vs NR2	0.82	10.27

PORTARLINGTON 2014/2015

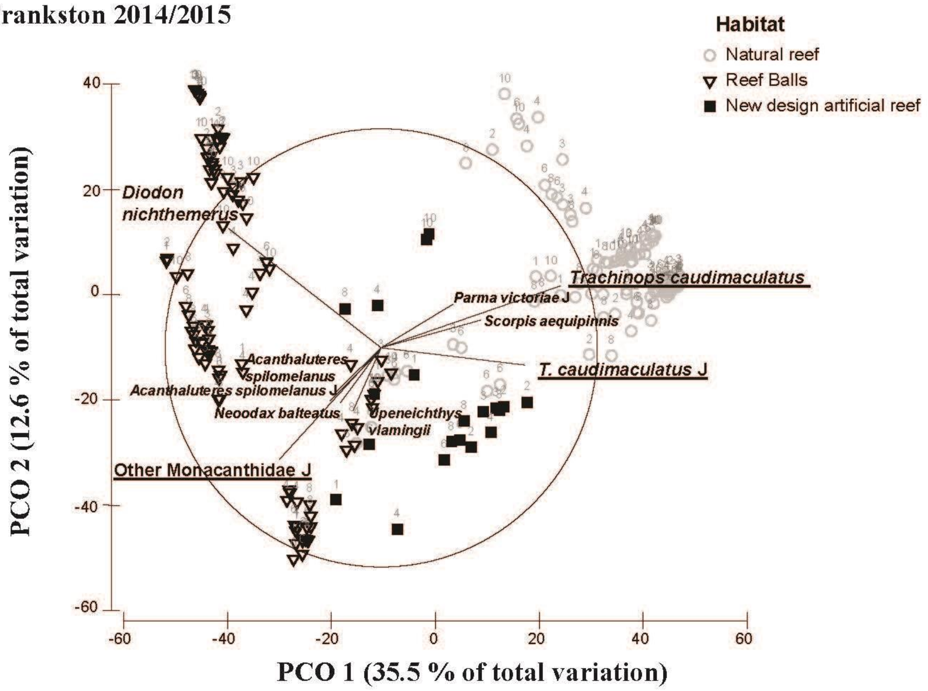
Species	**Habitats**	**Diss/SD**	**% Contribution**
T. caudimaculatus (Adult)	NR vs RB	1.36	19.46
	NR2 vs RB	n/a	n/a
	NR vs NDAR	1.42	21.16
	NR2 vs NDAR	0.62	6.71
	RB vs NDAR	n/a	n/a
	NR vs NR2	1.16	18.27
N. balteatus	NR vs RB	1.21	11.44
	NR2 vs RB	0.4	3.6
	NR vs NDAR	1.33	12.03
	NR2 vs NDAR	0.29	2.19
	RB vs NDAR	n/a	n/a
	NR vs NR2	1.17	11.48
N. tetricus	NR vs RB	0.79	5.34
	NR2 vs RB	n/a	n/a
	NR vs NDAR	0.87	5.77
	NR2 vs NDAR	n/a	n/a
	RB vs NDAR	n/a	n/a
	NR vs NR2	0.73	5.18
U. vlamingii	NR vs RB	0.81	9.4
	NR2 vs RB	0.46	5.03
	NR vs NDAR	0.81	6.87
	NR2 vs NDAR	0.49	5.61
	RB vs NDAR	0.72	9.77
	NR vs NR2	0.75	10.21
T. sexfasciatum	NR vs RB	n/a	n/a
	NR2 vs RB	0.58	6.14
	NR vs NDAR	n/a	n/a
	NR2 vs NDAR	0.6	7.28
	RB vs NDAR	n/a	n/a
	NR vs NR2	0.61	4.75
Other Monacanthidae (Juv)	NR vs RB	0.85	8
	NR2 vs RB	0.77	10.23
	NR vs NDAR	0.97	9.86
	NR2 vs NDAR	0.82	12.36
	RB vs NDAR	0.94	14.59
	NR vs NR2	0.52	5.62

PORTARLINGTON 2015/2016

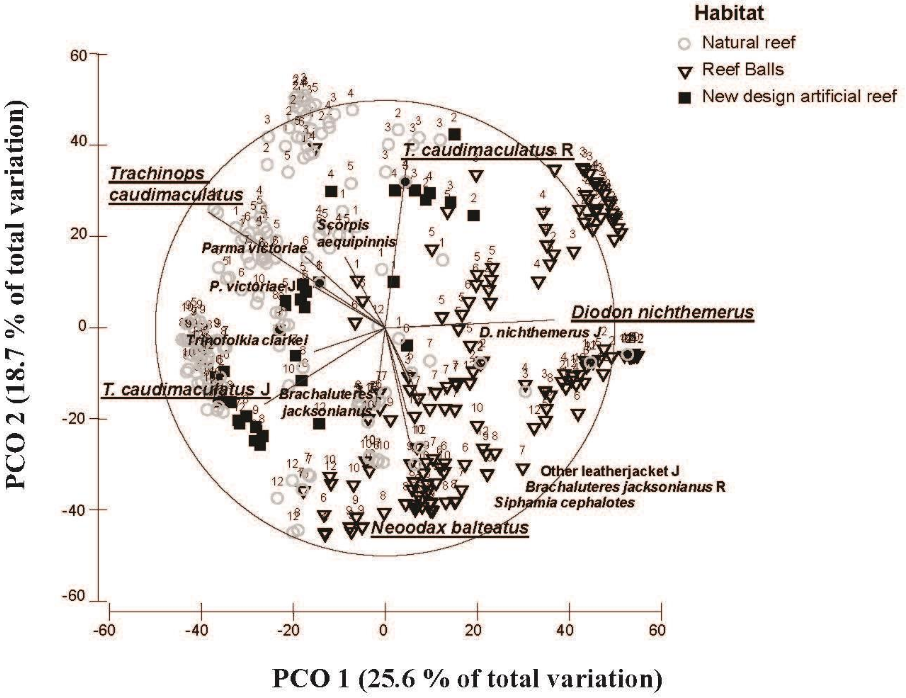
Species	**Habitats**	**Diss/SD**	**% Contribution**
T. caudimaculatus (Adult)	NR vs RB	1.1	14.61
	NR2 vs RB	0.62	7.85

	NR vs NDAR	1.09	12.7
	NR2 vs NDAR	0.63	6.84
	RB vs NDAR	0.9	6.4
	NR vs NR2	1.02	15.58
N. balteatus	NR vs RB	0.78	6.31
	NR2 vs RB	0.93	8.72
	NR vs NDAR	0.93	6.95
	NR2 vs NDAR	0.73	4.12
	RB vs NDAR	0.6	6.36
	NR vs NR2	0.86	9.7
V. conspersa	NR vs RB	0.8	6.49
	NR2 vs RB	0.81	8.55
	NR vs NDAR	1.96	11.62
	NR2 vs NDAR	1.27	10.99
	RB vs NDAR	1.13	9.34
	NR vs NR2	0.65	5.09

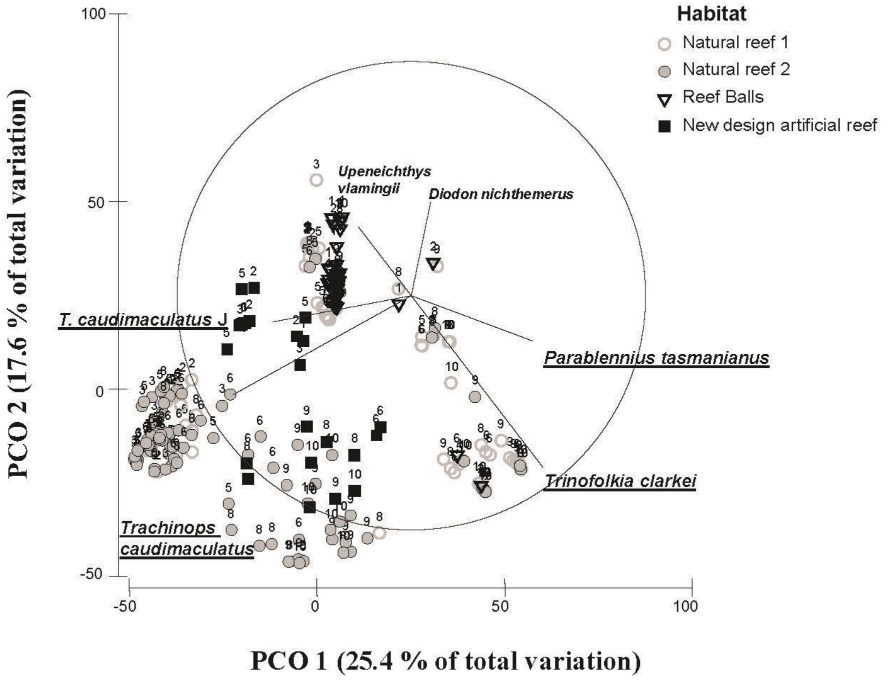
a. Frankston 2014/2015



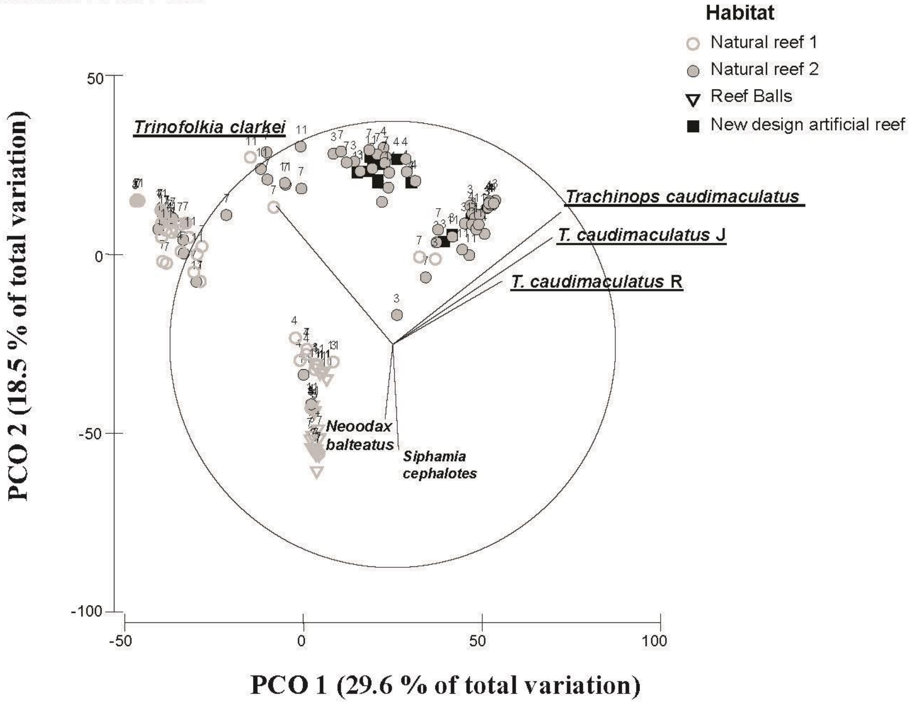
b. Frankston 2015/2016



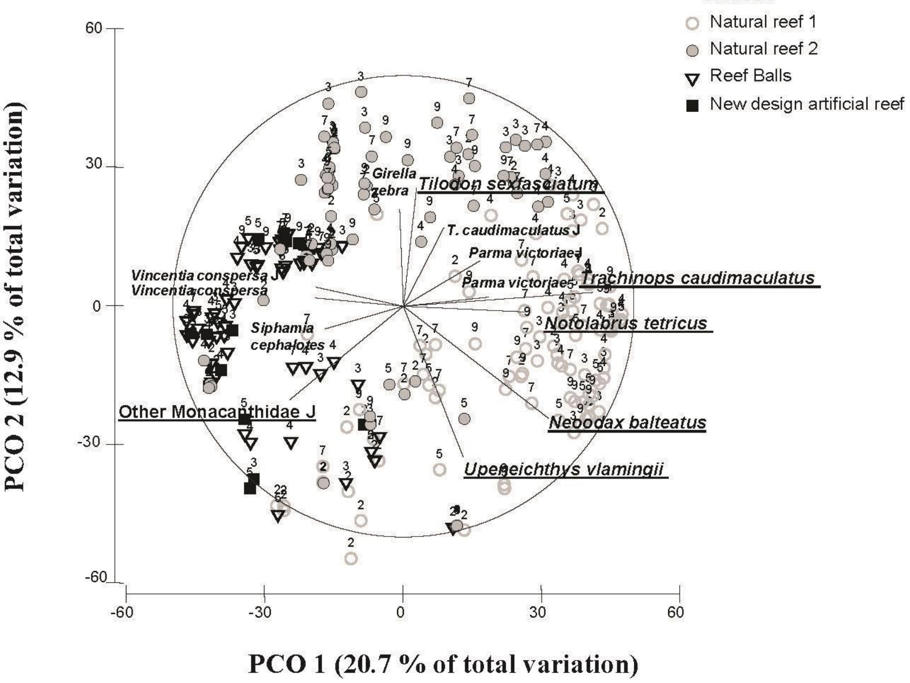
c. Altona 2014/2015



d. Altona 2015/2016



e. Portarlington 2014/2015



f. Portarlington 2015/2016

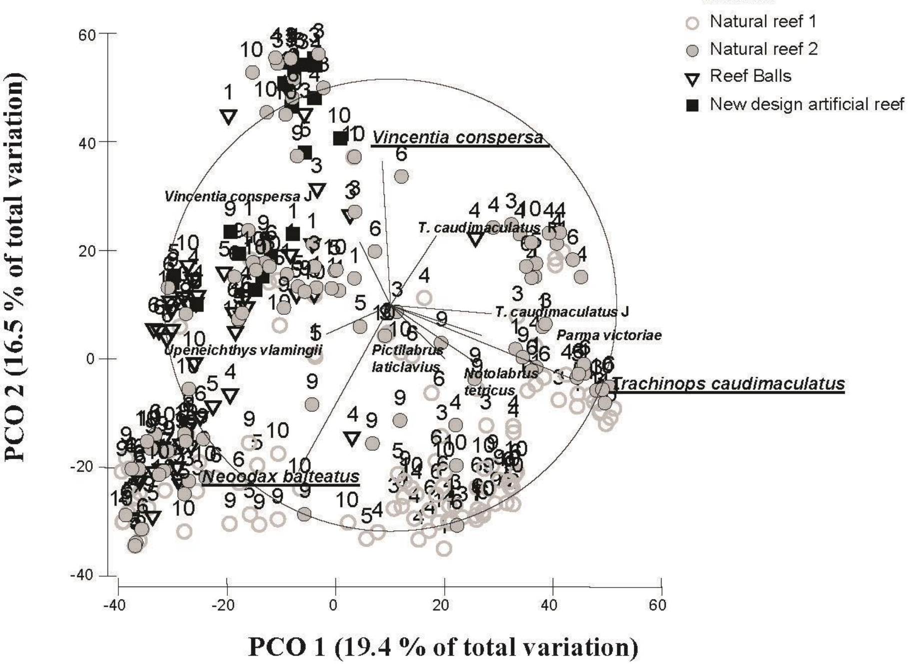


Fig. 3.5 PCO ordination based on Bray-Curtis similarity index for each fish community associated with different habitats (natural reefs, new design artificial reef and Reef Ball reefs) in Port Phillip Bay across three locations (Frankston, Altona and Portarlington) and two sampling years (2014/2015 and 2015/2016). The sampling was conducted fortnightly to monthly, when possible, from November to May each year. The numbers above data points indicate the sampling round. Projected vectors show changes in the abundance of species with Spearman correlations of > 0.3 with either of the first two ordination axes. Projected vectors with species names in bold and underlined show change in abundances of species with Spearman correlations of > 0.5 with either of the first two ordination axes.

3.5 Discussion

The main purpose of this study was to investigate whether reef design influences the reef fish assemblage that forms on artificial reefs over time and whether enhancing the structural complexity of artificial reefs can bring the composition of the fish community closer to that found on local natural reefs. The expectation was that species richness would vary between reef types due to differences in habitat structure. Generally, structurally more complex habitats present a greater diversity of refuge sites and, thus, support more species and at higher abundances (Kellison and Sedberry, 1998; Gratwicke and Speight, 2005; Komyakova *et al.*, 2013). Complexity was not directly measured in this study and hence is unknown, in particular for natural reef. However, based on their construction, the new design artificial reefs have larger numbers and diversity of refuge sites in comparison to Reef Ball reefs.

Location and habitat

Previous studies have suggested that it is the location of artificial reef deployments more so than their design that influences overall fish densities and species richness (Bohnsack and Sutherland, 1985; Workman *et al.*, 1985; Kellison and Sedberry, 1998). Some studies propose that higher densities and diversity should be expected on artificial reefs that are located in close proximity to natural reefs, through potentially an attraction effect, when some species extend their travel distances from the natural reef to visit the artificial reef, and through increased local detectability (Shulman, 1985; Workman *et al.*, 1985; dos Santos *et al.*, 2010). The results of this study only partially support this hypothesis.

Location had a great influence on the overall fish density detected on each habitat within each location. Pelican reef (Frankston natural reef) supported the highest fish densities over the two years across all location and habitats, which may be due to high *Trachinops caudimaculatus* populations in this general location (Hunt *et al.*, 2011). As large reefs are likely to attract higher numbers of recruits due to their higher detectability and attractability (MacArthur and Wilson, 1967; Brown and Kodric-Brown, 1977), it is not surprising that one of the larger continuous natural reefs (Pelican reef, Frankston) monitored here supported one of the highest fish densities. At Altona and Portarlington, there was little difference in overall fish densities supported by the different habitats. Overall, most habitats in these two locations exhibited much lower densities than Pelican reef. However, fish densities on both types of artificial reefs were similar between Altona and Frankston and the Reef Ball reef at Portarlington. The relatively high fish densities on Frankston artificial reefs may have been influenced by their proximity to good quality natural reef. At Altona, location also appeared to influence fish densities. Comparatively high fish densities of natural reef 2, which was located in close proximity to the new design artificial reef, might have influenced the elevated fish densities on the new design artificial reef at that location by increasing the detectability of the new habitat. At the Portarlington Reef Ball reef, the relatively high fish density might have been influenced by the nearby location of a highly complex breakwater wall that supports a diverse and abundant fish community. Conversely, as small isolated habitat patches receive lower recruitment and immigration due to lower encounter rates (Brown and Kodric-Brown, 1977; Turner, 1989; Serrano and Tella, 2003; Hale *et al.*, 2015), the new design artificial reef at Portarlington was potentially difficult for new individuals to detect given its isolation and placement on a barren mud bottom. Regardless, fish densities supported by the two types of artificial reefs at each location were comparable. However, new design artificial reefs supported significantly higher average species richness at all locations examined than any other habitat.

Previous studies have suggested that fish assemblages may change on artificial reefs over time through the development of the sessile benthic community (Coll *et al.*, 1998; Folpp *et al.*, 2011; Simon *et al.*, 2013). Indeed, fish species richness supported by the new design artificial reefs, the youngest reefs studied, increased over time. The fish community structure across all of the habitats and locations also changed over the two years. Simon *et al.* (2013) suggested that the successional changes on artificial reefs over time may not lead to a fish community structure comparable to that on nearby natural reefs. The results of my study only partially support these conclusions.

Although location appeared to have little influence on the number of species supported by artificial reefs in general, it did influence community structure. The fish community structure across all of the habitats and locations did change over time. However, unlike the suggestion by Simon *et al.* (2013), that time does not necessarily lead to greater convergence of fish community structure between natural and artificial reefs, the dissimilarities between the new design artificial reef and natural reefs at Altona and Frankston decreased from the 2014/2015 sampling season to the 2015/2016 sampling season, as the communities became more similar. This pattern was not observed between the Reef Ball reefs and natural reefs at any location. Furthermore, the lowest average dissimilarity in fish community structure calculated was for Natural reef 2 and the new design artificial reef at Altona for both years (67.28 and 49.44 respectively). These two habitats were located in the closest proximity to each other (a few meters) across all of the habitats studied, which again contradicts the findings of Simon *et al.* (2013).

While the average dissimilarities in fish community structure between habitats within each location where quite large (mostly over 70%), new design artificial reefs and natural reefs showed the lowest average dissimilarity in fish community structure for two of the locations (Altona and Frankston) for both sampling years, ranging from 49.42% between the new design artificial reef and Natural reef 2 at Altona during the 2015/2016 sampling season to 78.51% between the new design artificial reef and Pelican reef at Frankston during the 2014/2015 sampling season (Simper analysis). In contrast, average dissimilarity between Reef Ball reefs and natural reefs was greater than 80% for all of locations across both years, at Portarlington. The lowest dissimilarities between habitats were observed between Reef Ball reefs and new design artificial reef for both years at this location. These results might be driven by high isolation and hence low detectability of the new design artificial reef at Portarlington, which could have hindered the development of the fish community.

The differences in fish community structure across reef types were largely driven by *Trachinops caudimaculatus*, one of the most abundant fish species in Port Philip Bay. Adults, juveniles and new recruits of this species were mostly associated with natural reefs and new design artificial reefs across most locations, particularly in the 2015/2016 sampling season when greater recruitment of this species occurred. *Vincentia conspersa* was responsible for the similarity in fish community structure between Natural reef 2 (Steele's rock reef) and new design artificial reef at Portarlington, while *Trinofolkia clarkei* influenced the similarities between fish communities supported by Natural reef 2 and new design artificial reef at Altona. *Diodon nichthemerus*, Monacanthidae juveniles and, to lesser extent, *Neoodax balteatus* were important constituents of the fish community supported by Reef Ball reefs at most of the locations across the two years. *Parma victoriae* and *Tilodon sexfasciatum* were some of the species that were very specific to the natural reefs at all of the locations examined.

On the whole, these results partially support the predictions by Simon *et al.* (2013), that the distance to natural reef may not be that influential to the fish assemblage formed on artificial reefs, implying that the design of the artificial reef has the greatest influence on the fish assemblage structure that it sustains. Indeed, the results of my study indicate that one of the major factors influencing how close the structure of the fish community supported by artificial reef is to the fish community structure on nearby natural reef is the design of the artificial reef; however, they also indicate that the proximity of the natural reef may play a major part in structuring fish communities on artificial habitats, at least during the early colonization period. The new design artificial reef investigated in this study, in general, supported a reef fish community more similar to natural reefs than Reef Ball reefs, particularly in locations where new design artificial reefs were positioned in close proximity to high quality natural reefs.

Seasonality

Consistent with previous studies (Rooker *et al.*, 1997; Kellison and Sedberry, 1998), there was a high degree of seasonal variation with an increase in abundance across most locations and habitats during peak recruitment time and a decline in abundance towards the colder months. A similar, albeit less obvious pattern, was observed for most of the habitats for species richness. The declines in density and species richness towards the end of the recruitment season have been previously explained by post-recruitment mortality, as well as immigration of some species and individuals due to declines in temperature (Horn, 1980; Warlen and Burke, 1990; Tremain and Adams, 1995; Kellison and Sedberry, 1998; Garvey *et al.*, 2004). Lower temperatures may also affect activity levels, potentially making individuals of some species less detectable (Craig, 1977; Fraser *et al.*, 1993; Garvey *et al.*, 2004). Regardless of the underlying causes, most habitats across the three locations followed similar seasonal patterns, indicating consistency in general community response to bay-wide seasonal changes in environmental conditions.

Inter-annual patterns

There was a significant interaction between Year x Location and Year x Habitat for density, and Year x Habitat for species richness. In general, the sampling season of 2015/2016 displayed higher and more consistent density patterns for most of the locations and habitats in comparison to the previous sampling year. Two factors are probably playing a major role in explaining these results. The summer of 2015/2016 experienced one of the strongest El Niño events on record (Cole, 2015). In Port Philip Bay, water temperature was on average about 1°C warmer than the previous summer (Australian Bureau of Meteorology 2016), which potentially led to higher recruitment rates, causing greater overall fish densities that year. Although density patterns were similar among habitats at Portarlington, for Altona and Frankston habitats, there was an obvious change in densities supported by different habitats between the two years of sampling. In particular, new design artificial reefs supported greater densities during the second sampling year, potentially due to more established fish and epifaunal communities, making this type of habitat more detectable and attractive for new settlers (Bailey-Brock, 1989; Svane and Petersen, 2001; Perkol-Finkel and Benayahu, 2007; Langhamer *et al.*, 2009).

Summary

The results of my study suggest that the location of deployment, rather than design, has a more significant influence on fish abundances on artificial reefs, whereas the design of the artificial reef is an important determinant of the number of species supported irrespective of location. As a consequence, both location and design play an important role in determining fish community composition on artificial reefs.

Several attributes of the design of artificial reefs have previously been highlighted as promoting greater species richness (Kellison and Sedberry, 1998). In particular, the vertical relief and the presence of holes (aka. refuge sites) were positively correlated with greater fish species richness (Hixon and Beets, 1989; Kellison and Sedberry, 1998; Wilhelmsson *et al.*, 2006; Langhamer and Wilhelmsson, 2009). The assumption that more complex habitats tend to support more species (Gratwicke and Speight, 2005; Wilson *et al.*, 2007; Hackradt *et al.*, 2011; Messmer *et al.*, 2011; Komyakova *et al.*, 2013). However, may not be valid in some instances. For example, monotypic branching coral stands may score a high complexity value but provide limited diversity of shelter sites due to a single coral morphology (Talbot 1965 in Luckhurst and Luckhurst 1978).

Indeed, several studies have shown that it is the diversity of the shelter sites available, not just a general complexity of the habitat, which is beneficial to species richness (Messmer *et al.*, 2011; Komyakova *et al.*, 2013). Previous studies have demonstrated that many different fish species often use holes of approximately their own body diameter as shelter (Hixon and Beets, 1993; Holbrook *et al.*, 2002). Therefore, habitats that provide a large variety of holes with different diameters are expected to support higher fish species richness (Hixon and Beets 1989). The results of my study indicate that by increasing vertical relief and providing a large variety of refuge sites (different holes of variable diameter, cracks and crevices), the new design artificial reefs are able to support more species regardless of the location of deployment.

Conclusion and implications

Millions of dollars are spent on the construction and deployment of artificial reefs all around the world (Thierry, 1988; Branden *et al.*, 1994; Clark and Edwards, 1999; Baine, 2001; Fabi *et al.*, 2011). In recent decades, habitat restoration and fish species conservation have become two of the main purposes of artificial reef deployment. Therefore, the expectations are that artificial reefs mimic the structure of the local natural reefs and will consequently support similar fish communities to natural reefs. However, artificial reefs often support vastly different fish communities compared to the local natural reefs (Rooker *et al.*, 1997; Thanner *et al.*, 2006; Burt *et al.*, 2009; Hackradt *et al.*, 2011; Folpp *et al.*, 2013; Simon *et al.*, 2013), hence failing to achieve their goals. Baine (2001) reports that only about 50% of reviewed case studies on artificial reef performance provide evidence of the successful artificial reef deployment outcomes. In tropical environments the effects of unsuitable artificial reef design may be reduced over time, as corals would be expected to settle to hard substrates and form the diverse and complex habitat required to support local fish communities. However, in temperate environments where many habitat forming species such as kelps and seaweeds are seasonal (Steinberg, 1995; Blanchette, 1996; Sogn Andersen *et al.*, 2011), the structure of the hard substrate itself may be particularly important and should mimic the natural reef structure as closely as possible. Even in tropical environments the type of the hard substrate used and the design of the artificial reef may influence the type of coral community that will form on the artificial reef, which in turn may influence the associated fish community (Messmer *et al.*, 2011). Therefore, not only the stability and longevity of an artificial reef has to be considered in its design, but also whether its structure will provide the habitat requirements of the local animal community.

Although Reef Ball reefs have shown some promising positive results in tropical environments, the evidence is limited (Quinn, 2009; dos Santos *et al.*, 2010; Hackradt *et al.*, 2011). In more temperate environments it appears they do not provide the habitat structure that is necessary to support resident reef fish communities that are typically dominated by small-bodied species. Therefore, when deploying such reefs for the purposes of habitat restoration, mixed reef designs should be considered in order to provide greater habitat diversity to better mimic the structure of local natural reefs.

The deployment of poorly designed artificial reefs that lead to the creation of unusual fish communities may cause negative impacts on adjacent natural reefs if, for example, the artificial reef attracts higher number of predators to the area. The differences in the fish community structure between natural and artificial reefs may be driven by the initial habitat selection processes, with some of the species identifying artificial reefs as an unsuitable habitat. However, these differences may also be driven by post-settlement mortality, if artificial reefs provide appropriate habitat cues but lower survival leading to maladaptive habitat choice (Bohnsack, 1989; Battin, 2004; Robertson and Hutto, 2006; Hale and Swearer, 2016). Such effects may not result in significant negative impacts in areas where reef habitat is limiting as any additional habitat should lead to increases in overall abundance. However, with the majority of habitats around the world being overfished and many fish populations being in decline (Jackson *et al.*, 2001; Sale, 2002; Halpern *et al.*, 2008), habitat may not be limiting in many areas and hence the provision of more attractive but poorer quality habitat may lead to serious negative consequences to fish communities that we are trying to manage and protect.

3.6 References

Almany, G. R. (2004) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos*, 106(2), 275-284.

Australian Bereou of Meterology (2016) < http://www.bom.gov.au/> Accessed January 2017

Anderson, M. J., Gorley, R. N. and R, C. K. (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods. *PRIMER-E Ltd: Plymouth, UK.*

Bailey-Brock, J. H. (1989) Fouling community development on an artificial reef in Hawaiian waters. *Bulletin of Marine Science*, 44(2), 580-591.

Baine, M. (2001) Artificial reefs: a review of their design, application, management and performance. *Ocean & Coastal Management*, 44(3–4), 241-259.

Battin, J. (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, 18(6), 1482-1491.

Behrents, K. C. (1987) The influence of shelter availability on recruitment and early juvenile survivorship of *Lythrypnus dalli* Gilbert (Pisces: Gobiidae). *Journal of Experimental Marine Biology and Ecology*, 107(1), 45-59.

Blanchette, C. A. (1996) Seasonal patterns of disturbance influence recruitment of the sea palm, Postelsia palmaeformis. *Journal of Experimental Marine Biology and Ecology*, 197(1), 1-14.

Bohnsack, J. A. (1989) Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? *Bulletin of Marine Science*, 44(2), 631-645.

Bohnsack, J. A., Harper, D. E., McClellan, D. B. and Hulsbeck, M. (1994) Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off Southeastern Florida, U.S.A. *Bulletin of Marine Science*, 55(2-3), 796-823.

Bohnsack, J. A. and Sutherland, D. L. (1985) Artificial reef research: a review with recommendations for future priorities. *Bulletin of Marine Science*, 37(1), 11-39.

Branden, K. L., Pollard, D. A. and Reimers, H. A. (1994) A review of recent artificial reef developments in Australia. *Bulletin of Marine Science*, 55(2-3), 982-994.

Brown, J. H. and Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, 58(2), 445-449.

Burt, J., Bartholomew, A., Usseglio, P., Bauman, A. and Sale, P. (2009) Are artificial reefs surrogates of natural habitats for corals and fish in Dubai, United Arab Emirates? *Coral Reefs*, 28(3), 663-675.

Carr, M. H. and Hixon, M. A. (1997) Artificial reefs: the importance of comparisons with natural reefs. *Fisheries*, 22(4), 28-33.

Clark, S. and Edwards, A. J. (1999) An evaluation of artificial reef structures as tools for marine habitat rehabilitation in the Maldives. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 9(1), 5-21.

Clarke, K. R. and Gorley, R. N. (2006) *PRIMER V6: user manual-tutorial*, Plymouth Marine Laboratory.

Claudet, J. and Pelletier, D. (2004) Marine protected areas and artificial reefs: A review of the interactions between management and scientific studies. *Aquatic Living Resources*, 17(2), 129-138.

Cole, S. a. G., E. (2015) NASA examines global impacts of the 2015 El Niño. . *NASA <https://www.nasa.gov/press-release/nasa-examines-global-impacts-of-the-2015-el-ni-o> Accessed January 2017.*

Coll, J., Moranta, J., Reñones, O., García-Rubies, A. and Moreno, I. (1998) Influence of substrate and deployment time on fish assemblages on an artificial reef at Formentera Island (Balearic Islands, western Mediterranean). *Hydrobiologia*, 385(1), 139-152.

Collins, K. J. and Jensen, A. C. (1995) Stabilized coal ash artificial reef studies. *Chemistry and Ecology*, 10(3-4), 193-203.

Collins, K. J., Jensen, A. C. and Albert, S. (1995) A review of waste tyre utilisation in the marine environment. *Chemistry and Ecology*, 10(3-4), 205-216.

Collins, K. J., Jensen, A. C. and Lockwood, A. P. M. (1992) Stability of a coal waste artificial reef. *Chemistry and Ecology*, 6(1-4), 79-93.

Collins, K. J., Jensen, A. C., Lockwood, A. P. M. and Lockwood, S. J. (1994) Coastal structures, waste materials and fishery enhancement. *Bulletin of Marine Science*, 55(2-3), 1240-1250.

Collins, K. J., Jensen, A. C., Mallinson, J. J., Roenelle, V. and Smith, I. P. (2002) Environmental impact assessment of a scrap tyre artificial reef. *ICES Journal of Marine Science: Journal du Conseil*, 59(suppl), S243-S249.

Craig, J. F. (1977) Seasonal changes in the day and night activity of adult perch, Perca fluviatilis L. *Journal of Fish Biology*, 11(2), 161-166.

Dafforn, K. A., Mayer-Pinto, M., Morris, R. L. and Waltham, N. J. (2015) Application of management tools to integrate ecological principles with the design of marine infrastructure. *Journal of Environmental Management*, 158, 61-73.

Day, K. E., Holtze, K. E., Metcalfe-Smith, J. L., Bishop, C. T. and Dutka, B. J. (1993) Toxicity of leachate from automobile tires to aquatic biota. *Chemosphere*, 27(4), 665-675.

dos Santos, L. N., Brotto, D. S. and Zalmon, I. R. (2010) Fish responses to increasing distance from artificial reefs on the Southeastern Brazilian Coast. *Journal of Experimental Marine Biology and Ecology*, 386(1–2), 54-60.

Fabi, G., Spagnolo, A., Bellan-Santini, D., Charbonnel, E., Çiçek, B. A., García, J. J. G., Jensen, A. C., Kallianiotis, A. and Santos, M. N. d. (2011) Overview on artificial reefs in Europe. *Brazilian Journal of Oceanography*, 59, 155-166.

Folpp, H., Lowry, M., Gregson, M. and Suthers, I. M. (2011) Colonization and community development of fish assemblages associated with estuarine artificial reefs. *Brazilian Journal of Oceanography*, 59, 55-67.

Folpp, H., Lowry, M., Gregson, M. and Suthers, I. M. (2013) Fish assemblages on estuarine artificial reefs: natural rocky-reef mimics or discrete assemblages? *PLoS ONE*, 8(6), e63505.

Ford, J. R. and Swearer, S. E. (2013) Two's company, three's a crowd: food and shelter limitation outweigh the benefits of group living in a shoaling fish. *Ecology*, 94(5), 1069-1077.

Fraser, N. H., Metcalfe, N. B. and Thorpe, J. E. (1993) Temperature-dependent switch between diurnal and nocturnal foraging in salmon. *Proceedings of the Royal Society of London B: Biological Sciences*, 252(1334), 135-139.

Garvey, J. E., Ostrand, K. G. and Wahl, D. H. (2004) Energetics, predation, and ration affect size-dependent growth and mortality of fish during winter. *Ecology*, 85(10), 2860-2871.

Gratwicke, B. and Speight, M. R. (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology*, 66(3), 650-667.

Grove, R. S., Sonu, C. J. and Nakamura, M. (1991) Design and engineering of manufactured habitats for fisheries enhancement. In *Artificial habitats for marine and freshwater fisheries* (Eds. W. J. Seaman and L. M. Sprague), Academic Press, Inc., San Diego, California, pp. 109-152.

Hackradt, C. W., Félix-Hackradt, F. C. and García-Charton, J. A. (2011) Influence of habitat structure on fish assemblage of an artificial reef in southern Brazil. *Marine Environmental Research*, 72(5), 235-247.

Hale, R. and Swearer, S. E. (2016) Ecological traps: current evidence and future directions. *Proceedings of the Royal Society B: Biological Sciences*, 283(1824).

Hale, R., Treml, E. A. and Swearer, S. E. (2015) Evaluating the metapopulation consequences of ecological traps. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1804), 20142930.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R. and Watson, R. (2008) A global map of human impact on marine ecosystems. *Science*, 319(5865), 948-952.

Hamilton, K. L., Nelson, W. G. and Curley, J. L. (1993) Toxicological evaluation of the effects of waste-to-energy ash-concrete on two marine species. *Environmental Toxicology and Chemistry*, 12(10), 1919-1930.

Hixon, M. A. and Beets, J. P. (1989) Shelter characteristics and caribbean fish assemblages: experiments with artificial reefs. *Bulletin of Marine Science*, 44(2), 666-680.

Hixon, M. A. and Beets, J. P. (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs*, 63(1), 77-101.

Hixon, M. A. and Menge, B. A. (1991) Species diversity: prey refuges modify the interactive effects of predation and competition. *Theoretical Population Biology*, 39(2), 178-200.

Holbrook, S. J., Brooks, A. J. and Schmitt, R. J. (2002) Variation in structural attributes of patch-forming corals and in patterns of abundance of associated fishes. *Marine and Freshwater Research*, 53(7), 1045-1053.

Horn, M. H. (1980) Diel and seasonal variation in abundance and diversity of shallow-water fish populations in Morro Bay, California. *Fishery Bulletin*, 78(3), 759-769.

Hunt, T. L., Ford, J. R. and Swearer, S. E. (2011) Ecological determinants of recruitment to populations of a temperate reef fish, *Trachinops caudimaculatus* (Plesiopidae). *Marine and Freshwater Research*, 62(5), 502-509.

Jackson, J. B. C. (2008) Ecological extinction and evolution in the brave new ocean. *Proceedings of the National Academy of Sciences*, 105(Supplement 1), 11458-11465.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. and Warner, R. R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293(5530), 629-637.

Jiang, C. and Zhao, G.-F. (2015) A preliminary study of 3D printing on rock mechanics. *Rock Mechanics and Rock Engineering*, 48(3), 1041-1050.

Kellison, T. G. and Sedberry, G. R. (1998) The effects of artificial reef vertical profile and hole diameter on fishes off South Carolina. *Bulletin of Marine Science*, 62(3), 763-780.

Komyakova, V., Munday, P. L. and Jones, G. P. (2013) Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. *PLoS ONE*, 8(12), e83178.

Langhamer, O. and Wilhelmsson, D. (2009) Colonisation of fish and crabs of wave energy foundations and the effects of manufactured holes – a field experiment. *Marine Environmental Research*, 68(4), 151-157.

Langhamer, O., Wilhelmsson, D. and Engström, J. (2009) Artificial reef effect and fouling impacts on offshore wave power foundations and buoys – a pilot study. *Estuarine, Coastal and Shelf Science*, 82(3), 426-432.

Lechanteur, Y. A. R. G. and Griffiths, C. L. (2001) Fish associated with artificial reefs in False Bay, South Africa: a preliminary survey. *African Zoology*, 36(1), 87-93.

Luckhurst, B.E. and Luckhurst, K. (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology* 49, 317-323.

MacArthur, R. H. and Wilson, E. O. (1967) *The theory of island biogeography,* Princeton University Press.

Matthews, K. R. (1985) Species similarity and movement of fishes on natural and artificial reefs in Monterey Bay, California. *Bulletin of Marine Science*, 37(1), 252-270.

McArdle, B. H. and Anderson, M. J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology,* 82(1), 290-297.

Messmer, V., Jones, G. P., Munday, P. L., Holbrook, S. J., Schmitt, R. J. and Brooks, A. J. (2011) Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology*, 92(12), 2285-2298.

Pardo, N. (2013) Underwater city: 3D printed reef restores Bahrain's marine life. . *Available <http://blogs.ptc.com/2013/08/01/under water-city-3d-printed-reef-restores-bahrains-marine-life/> Accessed April 2017*

Perkol-Finkel, S. and Benayahu, Y. (2007) Differential recruitment of benthic communities on neighboring artificial and natural reefs. *Journal of Experimental Marine Biology and Ecology*, 340(1), 25-39.

Quinn, T. P. (2009) The influence of artificial reef associated fish assemblages and varying substrates on coral recruitment. Doctoral dissertation. Nova Southeastern University. Retrieved from NSUWorks, Oceanographic Center. (50) http://nsuworks.nova.edu/occ_stuetd/50.

Rilov, G. and Benayahu, Y. (1998) Vertical artificial structures as an alternative habitat for coral reef fishes in disturbed environments. *Marine Environmental Research*, 45(4–5), 431-451.

Robertson, B. A. and Hutto, R. L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, 87(5), 1075-1085.

Rooker, J., Dokken, Q., Pattengill, C. and Holt, G. (1997) Fish assemblages on artificial and natural reefs in the Flower Garden Banks National Marine Sanctuary, USA. *Coral Reefs*, 16(2), 83-92.

Sale, P. F. (2002) Chapter 16 - The science we need to develop for more effective management. In *Coral Reef Fishes*, Academic Press, San Diego, pp. 361-376.

Seaman, W. and Lindberg, W. J. (2009) Artificial Reefs A2 - Steele, John H. In *Encyclopedia of Ocean Sciences (Second Edition)*, Academic Press, Oxford, pp. 226-233.

Serrano, D. and Tella, J. L. (2003) Dispersal within a spatially structured population of lesser kestrels: the role of spatial isolation and conspecific attraction. *Journal of Animal Ecology*, 72(3), 400-410.

Shulman, M. J. (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology*, 66(3), 1056-1066.

Simon, T., Joyeux, J.-C. and Pinheiro, H. T. (2013) Fish assemblages on shipwrecks and natural rocky reefs strongly differ in trophic structure. *Marine Environmental Research*, 90, 55-65.

Sogn Andersen, G., Steen, H., Christie, H., Fredriksen, S. and Moy, F. E. (2011) Seasonal patterns of sporophyte growth, fertility, fouling, and mortality of Saccharina latissima in Skagerrak, Norway: implications for forest recovery. *Journal of Marine Biology*, 2011.

Spieler, R. E., Gilliam, D. S. and Sherman, R. L. (2001) Artificial substrate and coral reef restoration: what do we need to know to know what we need. *Bulletin of Marine Science*, 69(2), 1013-1030.

Steinberg, P. D. (1995) Seasonal variation in the relationship between growth rate and phlorotannin production in the kelp *Ecklonia radiata*. *Oecologia*, 102(2), 169-173.

Stunz, G. W. and Minello, T. J. (2001) Habitat-related predation on juvenile wild-caught and hatchery-reared red drum *Sciaenops ocellatus* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, 260(1), 13-25.

Svane, I. and Petersen, Jens K. (2001) On the problems of epibioses, fouling and artificial reefs, a review. *Marine Ecology*, 22(3), 169-188.

Thanner, S. E., McIntosh, T. L. and Blair, S. M. (2006) Development of benthic and fish assemblages on artificial reef materials compared to adjacent natural reef assemblages in Miami-Dade County, Florida. *Bulletin of Marine Science*, 78(1), 57-70.

Thierry, J.-M. (1988) Artificial reefs in Japan — a general outline. *Aquacultural Engineering*, 7(5), 321-348.

Tremain, D. M. and Adams, D. H. (1995) Seasonal variations in species diversity, abundance, and composition of fish communities in the northern Indian River Lagoon, Florida. *Bulletin of Marine Science*, 57(1), 171-192.

Turner, M. G. (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics*, 20(1), 171-197.

Vose, F. E. and Nelson, W. G. (1998) An assessment of the use of stabilized coal and oil ash for construction of artificial fishing reefs: comparison of fishes observed on small ash and concrete reefs. *Marine Pollution Bulletin*, 36(12), 980-988.

Wakeman, C., Dockweiler, E., Stover, H. and Whiteneck, L. (1958), Use of concrete in marine environments, paper presented at Journal Proceedings.

Warlen, S. M. and Burke, J. S. (1990) Immigration of larvae of fall/winter spawning marine fishes into a North Carolina estuary. *Estuaries and Coasts*, 13(4), 453-461.

Wessel, P. and Smith, W. H. F. (1996) A global self-consistent, hierarchical, high-resolution shoreline database. *Journal of Geophysical Research, 101*, 8741-8743.

Wik, A. and Dave, G. (2009) Occurrence and effects of tire wear particles in the environment – a critical review and an initial risk assessment. *Environmental Pollution*, 157(1), 1-11.

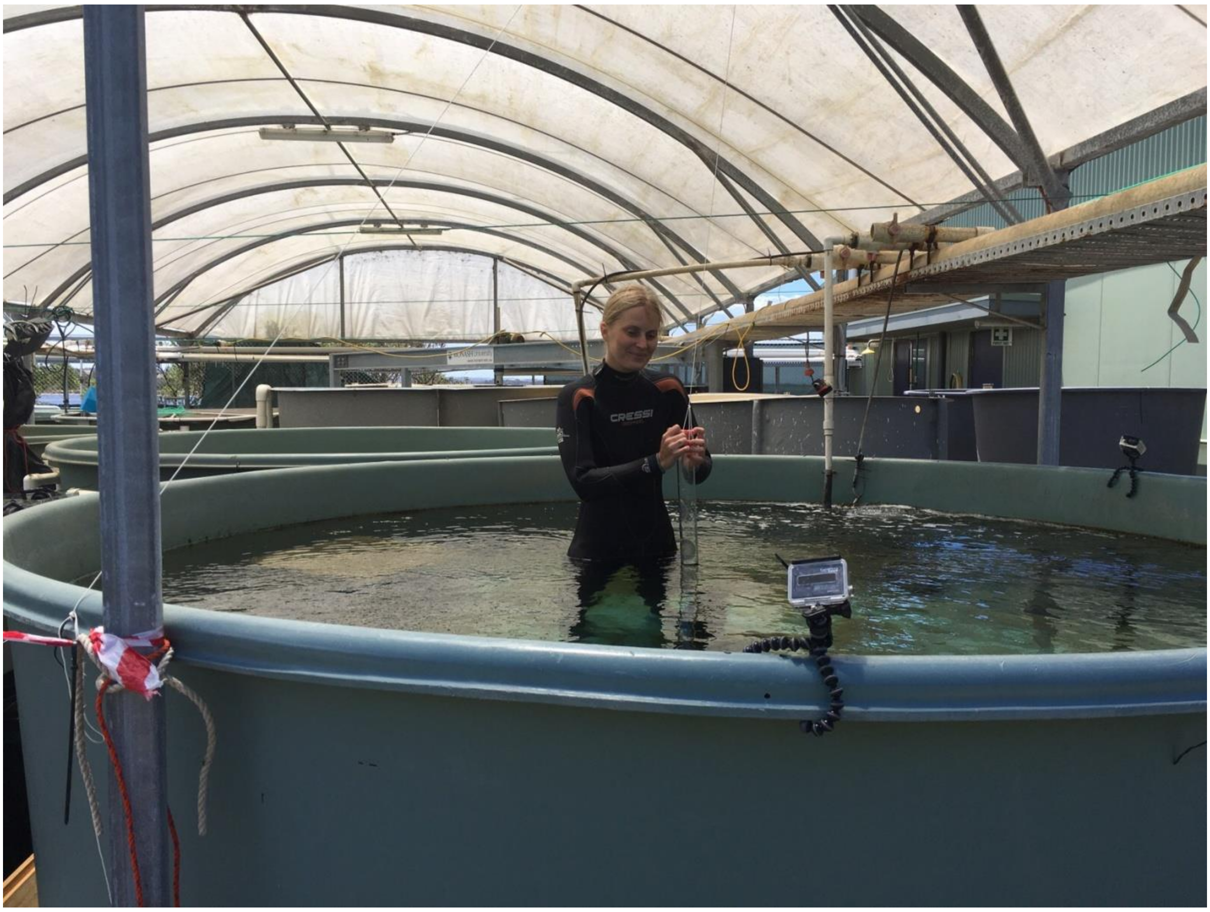
Wilhelmsson, D., Yahya, S. A. S. and Öhman, M. C. (2006) Effects of high-relief structures on cold temperate fish assemblages: A field experiment. *Marine Biology Research*, 2(2), 136-147.

Wilson, S., Graham, N. and Polunin, N. (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology*, 151(3), 1069-1076.

Workman, I. K., Landry, J. A. M., Watson, J. J. W. and Blackwell, J. W. (1985) A Midwater fish attraction device study conducted from hydrolab. *Bulletin of Marine Science*, 37(1), 377-386.

CHAPTER FOUR:

Contrasting patterns in habitat selection and recruitment of temperate reef fishes among natural and artificial reefs



Setting up habitat choice experiment at VMSC, Queenscliff, Victoria, Australia

4.1 Abstract

Artificial reefs, a common management tool for stock enhancement of recreational fisheries, species conservation and marine habitat restoration, have been deployed all over the world. However, little is known about the attractiveness of artificial reefs to reef fishes. Here I investigated the habitat preferences of three reef fish species: *Trachinops caudimaculatus*, *Vincentia conspersa* and *Trinorfoklia clarkei* through the observation of recruitment patterns to three study habitats: new design artificial reef, Reef Ball reef and natural reefs at three locations over two recruitment seasons in Port Phillip Bay, Victoria , Australia. Additionally, I examined habitat preferences of new recruits of *T. caudimaculatus* and *V. conspersa* using laboratory-based habitat choice experiments. In general, *T. caudimaculatus* recruitment was at least twice as high on natural reefs compared to both artificial reefs whereas *V. conspersa* recruitment was almost three times greater on the Reef Ball reef compared to the other two habitats, at least in Portarlington and *T. clarkei* recruited in equal numbers across all habitats.

A contradictory result was observed in the laboratory experiments for *T. caudimaculatus*, where recruits selected the Reef Ball reef almost three times as often as the other two habitats, while *V. conspersa* exhibited no habitat preference.

The higher preference or equal attractiveness of some artificial habitats (e.g. Reef Ball reef) may not have a large influence on fish populations when reef habitat is limiting. However, with the majority of fish populations being overfished or in decline due to other factors, such as pollution or introduction of invasive species, habitat is potentially not a limiting resource in many locations. Little is known about the performance of individuals that occupy artificial reefs. If artificial reefs are more attractive than natural reefs, yet cause lower fitness advantages such as reduced survival, they may act as ecological traps, leading to negative outcomes for fish populations.

4.2 Introduction

Habitat selection is one of the most important behavioural decisions affecting the distribution and abundance of species and the structure of animal communities (Bell *et al.*, 1991; Morris, 1992; 2003). Natural selection favours individuals that choose habitats that maximise their chances for future survival and reproduction (Morris, 1992; 2003; 2011). However, occasionally animals can preferentially select lower quality habitat over higher quality alternatives, leading to poorer fitness outcomes - what is referred to as an "ecological trap" (Schlaepfer *et al.*, 2002; Kristan, 2003; Battin, 2004; Robertson and Hutto, 2006). Robertson and Hutto (2006) have identified the three conditions necessary to demonstrate an ecological trap: (a) evidence for habitat preference; established through a variety of methods that may include, for example, settlement patterns, site fidelity or habitat choice experiments; (b) there must be differences in fitness of individuals occupying different habitats; and (c) individuals must prefer (or equally prefer) the poorer-quality habitat. To date, most ecological traps have been identified in terrestrial systems, with only a handful of studies investigating the phenomenon in aquatic environments (Hale and Swearer, 2016).

Many marine animals have planktonic larval stages in early development, prior to taking up residence in the adult habitat (Ehrlich, 1975; Richards and Lindeman, 1987; Mapstone and Fowler, 1988; Kingsford *et al.*, 2002). For reef fishes, most species spend anywhere between 10 to 120 days in the water column before settling to coral or rocky reef habitat (Brothers *et al.*, 1983; Sale, 2002). The brief transition from the pelagic to benthic environment is arguably the most critical stage in the life history of reef fishes (Kingsford *et al.*, 2002; Doherty *et al.*, 2004; Hoey and McCormick, 2004; Shima and Swearer, 2010; Baguette *et al.*, 2013; Aschenbrenner *et al.*, 2016). Patterns of recruitment to reef environments are known to be highly variable in space and time (Jones, 1984; Sale *et al.*, 1984; Doherty and Williams, 1988; Carr, 1989; Levin, 1993). Spatial patterns in recruitment can be driven by patterns in habitat selection, with larvae preferring reef structures that maximise future growth, survival and reproduction. The quality of available habitat can vary in terms of the provision of shelter, living space, food and suitable sites for reproduction (Behrents, 1987; Hixon and Beets, 1989; Hixon and Menge, 1991; Hixon and Beets, 1993; Almany, 2004). For example, loss rates can be as high as 90% within the first few days post-settlement (Doherty, 2002; Doherty *et al.*, 2004; Lecchini *et al.*, 2007), so choosing a poor quality habitat at settlement is likely to result in death. As these losses are often attributed to predation, habitat structure can often play a vital role in the survival of new recruits (Lecchini *et al.*, 2007).

In recent decades, artificial reefs have become a common management tool for stock enhancement of recreational reef fisheries, species conservation and marine habitat restoration (Seaman Jr and Sprague, 1991; Baine, 2001; Seaman and Lindberg, 2009). Many reef deployments, however, have failed to achieve these goals, largely as a result of inappropriate size and design (Pickering and Whitmarsh, 1997; Jan *et al.*, 2003; Campbell *et al.*, 2011; Hackradt *et al.*, 2011). Artificial reefs are often not successful in mimicking the habitat structure of natural reefs, particularly in the provision of small refuges for newly settled fish. However, little is known about the attractiveness of artificial reefs to settlement-stage larval reef fish in comparison to natural habitats. If artificial reefs are much less attractive than natural reefs, then they make a minimal contribution to enhancing the abundance of target species. On the other hand, if artificial reefs are much more attractive than natural reefs, but provide poorer quality habitat leading to reduced fitness, such as lower reproductive success and/or higher mortality, then they may act as ecological traps (Schlaepfer *et al.*, 2002; Battin, 2004). Increased attractiveness of poor quality artificial reefs could have serious consequences to local populations, if recruits are redirected away from more suitable natural habitats (Pickering and Whitmarsh, 1997).

The aim of this study was to examine the potential for artificial reefs to function as ecological traps for temperate reef fishes by comparing patterns of recruitment to and habitat selection among natural and artificial reefs. I focused on three temperate reef fish species that are particularly abundant in Port Phillip Bay, Victoria, Australia: *Trachinops caudimaculatus* (Plesiopidae), *Vincentia conspersa* (Apogonidae) and *Trinorfolkia clarkei* (Tripterygiidae). Firstly, I first investigated whether there are differences in recruitment patterns between natural and artificial habitats at three different sites over 2 years for all three study species. Although larger, continuous reefs are likely to support larger populations of reef fishes, recruit densities should be comparable among reef types in the same area if settling reef fishes show no habitat preference. As variation in early post-settlement mortality among reef types could obscure settlement patterns, I tested whether recently settled recruits of two of the study species demonstrated habitat preference between a constructed natural reef and two artificial reef designs in laboratory choice experiments. I postulated that if artificial reefs do function as ecological traps, then artificial reefs should exhibit much higher recruitment than natural reefs, and that individuals should exhibit a strong preference for artificial reefs when given a choice of equal availability. Although testing pre-settlement but competent larvae would have been preferable, this was not possible as previous deployments of light traps in Port Phillip Bay failed to capture these species (Jung and Swearer, 2011). However, it has previously been shown that, at least for olfactory cues in some coral reef fish, there is no difference in habitat preference displayed by naïve larvae and newly settled recruits (Dixson *et al.*, 2008). Moreover, all newly settled recruits were collected from natural reefs; and therefore, would be expected to prefer natural reef habitat if familiarity influences habitat choice, resulting in a conservative test of preference for artificial habitats.

4.3 Materials and Methods

Study species

Recruitment and habitat choice were investigated for three study species: *Vincentia conspersa* (Apogonidae), *Trinorfolkia clarkei* (Tripterygiidae) and *Trachinops caudimaculatus* (Plesiopidae). *V. conspersa* is a relatively common cryptic reef fish in Port Philip Bay that is often found on natural reefs, in nearshore seagrass beds and in estuaries, usually occupying cracks and crevices during the day (Baker *et al.*, 2008; Gomon *et al.*, 2008; Jenkins *et al.*, 2015). *T. clarkei* is another common cryptic fish species in Port Phillip Bay. It is mostly found on shallow rocky reefs and in the estuaries. *T. clarkei* is an egg-brooder, highly site attached and exhibits nest guarding behaviour (Baker *et al.*, 2008; Gomon *et al.*, 2008). *T. caudimaculatus* is a small (<100 mm), short-lived (up to 5 years), and highly abundant reef fish species in Victoria. It is usually found in large dense shoals (>1000 fish) on natural rocky reefs near caves and overhangs (Hunt *et al.*, 2011; Jung and Swearer, 2011). The individuals are highly site attached and maximum movement distances reported to date have not exceeded 20 m (Ford and Swearer, 2013a).

Natural patterns of recruitment

Study area

The study was conducted in Port Phillip Bay, Victoria, Australia, which is one of the largest natural embayments in Australia, covering an area of ~1,930 km^2 (Figure 3.1). Three locations within the bay, Frankston, Altona and Portarlington, already had Reef Ball reefs that were constructed in 2012, two years prior to the beginning of the experiment. In 2014, new design artificial reefs were deployed at each location on sandy bottoms away from natural reefs, with the exception of Altona, where the new design artificial reef lay in close proximity (a few meters) to one of the sampled natural reefs. For full site description and the design of Reef Ball reefs and new design artificial reefs see Chapter 3.

Sampling design

The sampling design to examine differences in recruitment among sites, times and reef types differed for the three species:

Trachinops caudimaculatus: I compared recruitment rates between natural and two types of artificial reefs at three study locations using fortnightly to monthly visual surveys over Australian spring/summer (November to February) in 2014/2015 and 2015/2016. New recruits of *T. caudimaculatus* were sampled at each natural and artificial reef by underwater visual census. On the Reef Ball reefs each of 5-Reef-Ball unit arrangements was treated as a replicate. To match the Reef Ball area sampled, an area of 2.5 m in diameter was sampled on natural reef. When possible all 18 5-Reef-Ball unit arrangements were sampled on Reef Ball reefs and 18 point counts were conducted on natural reefs. Due to weather constraints it was not possible to sample all arrangements at some sites each survey, leading to a variable number of surveys on Reef Ball reefs ($\bar{x}$ = 10 (5 – 18)) and natural reefs ($\bar{x}$ = 15 (12 – 18)). On natural reefs, point count locations were chosen randomly each survey. All new design artificial reefs were sampled each survey. Abundances of new recruits were converted to densities (#/m^2) for all three reef types. To minimize the potential effect of variable post-settlement survival on estimates of recruitment, only the peak recruit densities for each reef type in each year were analysed.

Trinorfolkia clarkei & *Vincentia conspersa:* Due to their cryptic nature, it was not possible to conduct fortnightly monitoring of *T. clarkei* & *V. conspersa* recruitment. A "snap shot" of recruitment for these two species was taken between early January to late February of 2016, when peak recruitment was expected for both species. Ten individual Reef Ball units, ~ 1 m diameter, on Reef Ball reefs and ten 1 m diameter point counts were conducted on natural reef at Portarlington and Frankston. All three New Design Artificial reefs were sampled at Frankston and two at Portarlington. All replicate reef types were surveyed using clove oil. The sampled area was sprayed with a clove oil solution (a 1:1:8 mixture of clove oil, ethanol, and seawater) and carefully examined for a minimum of 5 min. Anaesthetized individuals were collected, counted and transferred into mesh fish cages, where they were left to fully recovery and then released back to the reef. Recruit abundances for each species were converted to densities for all three habitats.

Habitat selection experiments

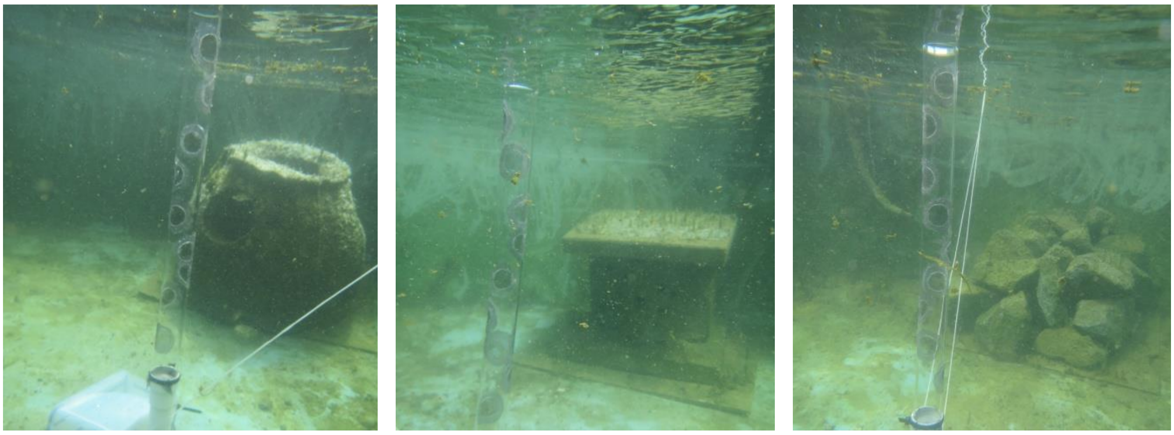
The study was conducted at the Victorian Marine Science Consortium, Queenscliff, Victoria during Austral summer, 2016.

New recruit collections

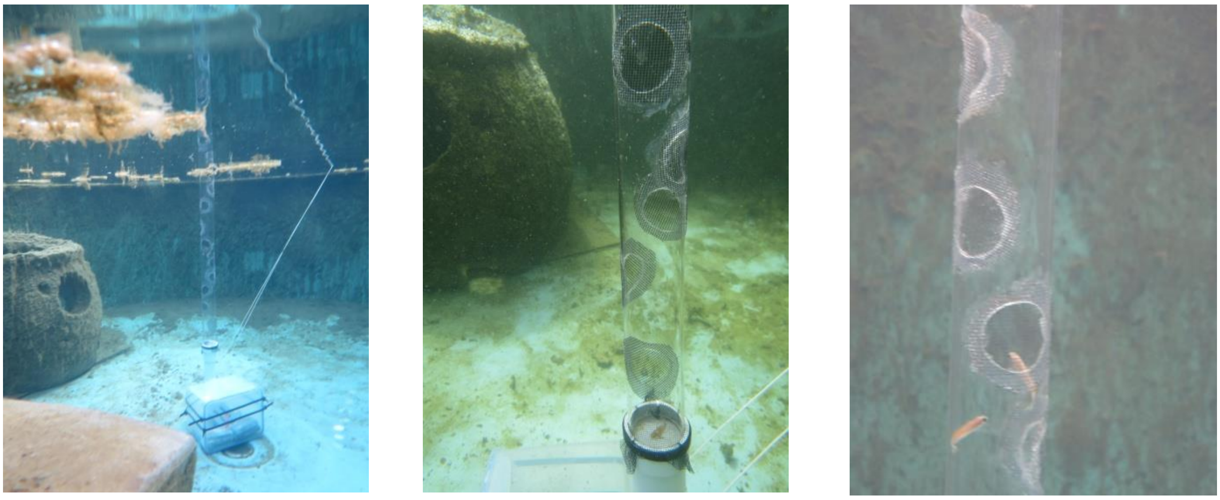
Newly recruited juveniles of two fish species, *Vincentia conspersa* and *Trachinops caudimaculatus*, were collected from different sites in Port Phillip Bay. New recruits of both species were captured from two natural reefs at Portarlington (Prince George Bank and Steele’s Rocks) and one natural reef at Frankston (Pelican reef) (Figure 3.1). *V. conspersa* new recruits were captured using a clove oil solution and small hand nets, placed in a plastic bag filled with clean seawater and then allowed to fully recover from the clove oil before being placed in an insulated container for transport. *T. caudimaculatus* were captured using a large mouthed (1,200 mm square) fine-mesh barrier nets with a 2-m tapered end. The individuals were herded into a net by a SCUBA diver, while a second diver held the net up straight and prevented escape of the individuals. *T. caudimaculatus* were captured in late December to late January, *V.conspersa* in mid January to mid February. Fish were kept in small groups of conspecifics (5-30 individuals) in aquaria supplied with constant flowing seawater from Port Phillip Bay. Fish were fed twice a day with a combination of frozen brine and mysid shrimp, as well as freshly caught mysid shrimp and other zooplankton when available (~ twice a week). Each individual was allowed a minimum of 24 hours to acclimate and recover from potential shock from capture before being used in the habitat selection experiments.

Experimental design

Habitat choice experiments were conducted during daylight hours in an outdoor 20,000 L round tank. Three different habitats were used: a single Reef Ball module (Mini-Bay ball), a new design artificial reef module and a simulated natural reef constructed from various sized granite rocks (Figure 4.1 a-c). Each reef type was positioned on the edges of the experimental tank at equal distances from each other and from the centre of the tank. Habitats were sitting on plywood used to protect the tank from potential damage. A release pipe was made out of clear acrylic with an internal diameter of 45 mm. It had several 35 mm diameter holes cut into it, which were covered with 1 mm mesh to allow recruits to see and smell the offered habitats. The release pipe was positioned in the centre of the experimental tank, with its bottom end sitting inside a PVC standpipe. The standpipe was attached to a plastic container filled with dive weights to keep it in place. The lowest release point (bottom of the release pipe) sat at 290 mm from the bottom of the tank, which approximately coincided with the centre of each of the offered habitats (Figure 4.1 d-f). Each individual was placed inside the release pipe and left to acclimatize for a minimum of 30 min. After acclimation, the release pipe was pulled up by a rope and removed. The standpipe was also pulled up and removed once individuals moved away from the release area. Three Go-Pro cameras were placed inside the tank, one next to each of the habitats in order to record habitat choice. The initial choice and the consequent habitat use were also observed from the tank surface every 30 min for 2 hours when possible and recorded. During each 2.5 hr trial, water flow remained constant but the air was turned off in the tank to allow for better visibility and to prevent the aerator affecting an individual's choice. *V. conspersa* ($\bar{x}$ size = 31.7 mm +/- 1.5 SE) recruits were tested individually. Some studies have shown that, for gregarious species, habitat selection behaviour can be affected when tested individually, with single individuals displaying less active selection behaviour (Irisson *et al.*, 2015). As *T. caudimaculatus* is a highly social species that lives in large shoals, recruits were tested in groups of five ($\bar{x}$ size = 29.7 +/- 0.7 SE) (Ford and Swearer, 2013a). A total of 20 trials were completed for each species. The position of the habitats within the tank were rotated randomly after every 3 trials. All individuals were only used once. At the end of each trial fish were re-captured using hand nets and, when required, clove oil. When small amounts of diluted clove oil were used (< 105 ml of 10% clove oil) the tank was left to flush for a minimum of 2 hours before the next trial. If larger amounts of clove oil were used the tank was left to flush overnight (at least 14 hours) before the next trial. Before the start of each trial the tank was carefully examined for any signs of clove oil.



a. Reef Ball **b. New design artificial reef** **c. Natural reef**



d. Acclimation and release set up **e. *V. conspersa* juvenile during acclimation time** **f. *T. caudimaculatus* juveniles during acclimation time**

Fig. 4.1 Habitat types and fish release mechanism used in laboratory based habitat choice experiments.

Statistical analyses

Natural patterns of recruitment

As recruit densities for all three species were overdispersed, with a large number of zero values, data were log-transformed and univariate analyses were performed using PRIMER-E v6 with the PERMANOVA (Permutational Multivariate Analysis of Variance) add-on (McArdle and Anderson, 2001). Clarke and Gorley (2006) and Anderson *et al.* (2008) both state that PERMANOVA is appropriate for univariate analysis.

All factors used were treated as fixed and for *Trachinops caudimaculatus* included: year, location and habitat; for *V. conspersa*: location and habitat and for *Trinorfolkia clarkei*: habitat only. For this analysis, the data for *T. caudimaculatus* from the two natural reefs at Altona were pooled together, as well as the data from the two natural reefs at Portarlington. Similarly, for *V. conspersa* the data from the two natural reefs at Portarlington were also pooled. All univariate PERMANOVA tests were run using Euclidean distance matrices based on recruit densities with a maximum of 9999 permutations.

As there were two significant two-way interactions for *T. caudimaculatus*: location x habitat and year x location (Table 4.1), tests for the effect of year and reef habitat were performed separately for each location (n = 3 models). For this analysis all natural reefs were treated separately and a sequential Bonferroni correction was applied to account for multiple testing. Due to the complexity of the design, I used permutation of residuals under a reduced model permutation method with Type III sum of squares for all of the above tests with the exception of recruit densities of *T. clarkei* when unrestricted permutations of raw data were used as there was only one fixed factor (habitat) in the model (Clarke and Gorley, 2006; Anderson *et al.*, 2008). For Altona, there was a significant two-way interaction for recruit densities of *T. caudimaculatus*: year x habitat (Table 4.1), therefore, I tested for the effect of habitat separately for each year. As there was only one fixed factor (habitat) in the later model, I also used unrestricted permutation of raw data for this analysis.

Pair-wise PERMANOVA tests were conducted as a post-hoc test to identify which habitats were significantly different from each other in fish recruit densities for all three study species. A Monte Carlo random sample from the asymptotic permutation distribution was used to obtain p values, because for most terms in the analysis, there were insufficient permutable units to get reasonable test by permutation (Clarke and Gorley, 2006; Anderson *et al.*, 2008).

Habitat selection experiments

Vincentia conspersa

Out of the 20 individuals tested, only 5 changed their initial choice. These changes occurred within 5 minutes of the experiment and no further changes were observed. Consequently, I used the habitat selected at the end of the trial and tested for habitat preferences using a chi-square test in SPSS.

Trachinops caudimaculatus

T. caudimaculatus individuals were significantly more mobile than *V. conspersa*, moving freely between offered habitats, and it was difficult to detect all five individuals at all observation periods. Therefore, for consistency with the analysis of *V. conspersa* habitat preference and because the initial choice could have been biased by startle responses during release from the pipe, only the final choice was analysed. As *T. caudimaculatus* were tested in groups of five and because I was particularly interested in whether individuals preferred Reef Balls, one-sample, two-tailed t-tests were calculated by comparing the mean proportion of individuals occupying the Reef Ball reef against a null expectation of 0.33 in SPSS. A similar data analysis approach was used in previous choice experiments involving groups of fish (Hale *et al.*, 2009).

4.4 Results

Natural patterns of recruitment

There were substantial interspecific and spatiotemporal differences in recruitment rates among natural and artificial reefs.

Trachinops caudimaculatus

In general, the 2015/2016 season received on average five times higher recruitment at all locations than in 2014/2015 (Figure 4.2). Most Frankston habitats in both years received higher recruitment than habitats at the other two locations, except for the Altona new design reef in 2014/2015, which received one of the highest recruit densities during this study. The highest recruitment was recorded in 2015/2016 at Pelican reef (Frankston), while some of the lowest recruit densities were recorded at most of the Portarlington locations during both sampling years (Figure 4.2 a-b).

There were significant year and habitat effects at Frankston (Table 4.1). The natural reef received the highest recruit densities of *T. caudimaculatus* in comparison to the other two habitats at this site during both sampling years. There was a significant difference in recruit densities between Pelican reef and Reef Ball reef and between Reef Ball reef and new design reef in the 2014/2015 sampling season (Table 4.2), with Pelican reef supporting 15 times higher recruit densities than the Reef Ball reef and the new design reef supporting more than double the recruit densities than the Reef Ball reef (Figure 4.2 a). In 2015/2016 there was a significant difference in *T. caudimaculatus* recruit densities between Pelican reef and Reef Ball reef only (Table 4.2), with Pelican reef supporting approximately 4 times more *T. caudimaculatus* recruits than Reef Ball reef (Figure 4.2 b).

There was only a significant year effect at Portarlington (Table 4.1). In 2014/2015 Portarlington habitats received some of the lowest recruit densities of *T. caudimaculatus* across all other locations and habitats. There was no recruitment to new design artificial reefs by *T. caudimaculatus* in that year, while the Reef Ball reef and both natural reefs received very low recruitment. In 2015/2016 all habitats received low recruitment of *T. caudimaculatus*, with natural reefs and the Reef Ball reef receiving more than triple the amount of recruitment of *T. caudimaculatus* compared to the new design artificial reef; however, no significant habitat effect was detected (Figure 4.2 c-d).

In 2014/2015 the new design reefs at Altona received the highest recruitment compared to all other habitats and locations. There was a significant habitat effect at Altona in 2014/2015 (Table 4.1). No recruitment was detected on both natural reefs. The new design reef supported 10 times higher *T. caudimaculatus* recruit densities than the Reef Ball reef (Table 4.2, Figure 4.2 e). However, in 2015/2016 there was a significant habitat effect (Table 4.1) with Natural reef 2 and new design artificial reef supporting 3 times higher recruit densities than Natural reef 1 and Reef Ball reef (Table 4.2, Figure 4.2 f). Overall, Frankston received lower recruitment than the other two locations that sampling season (Figure 4.2).

Table 4. 1 Results from univariate PERMANOVA on Euclidean distances to test for the fixed effects of Year (2014/2015 and 2015/2016 sampling season), Location (Frankston, Altona, Portarlington) and Habitat (Natural reef, new design artificial reef, Reef Ball reef) on *T. caudimaculatus* recruitment. The test statistic (F*), a pseudo-F value, and the probability value ($P^{\dagger}$) were computed by the PERMANOVA routine with a maximum of 9,999 permutations under a reduced model for all tests except for the separate tests of the 2014 and 2015 data from Altona when unrestricted permutations of raw data were used. Sum of squares is Type III (partial) for all tests. Recruit densities were log+1 transformed. A Bonferroni correction was applied to *T. caudimaculatus* recruit density ** for each location test. For the univariate PERMANOVA tests for each Location the data on recruit density from all natural reefs was treated separately.

Variable type	**Source**	**df**	**SS**	**MS**	**F***	**$P^{\dagger}$**	**Unique permutations**
Overall	Year	1	11.333	11.333	20.06	**0.0001**	9839
	Location	2	23.701	11.85	20.975	**0.0001**	9953
	Habitat	2	10.965	5.4827	9.7043	**0.0003**	9949
	Year x Location	2	21.212	10.606	18.772	**0.0001**	9933
	Year x Habitat	2	2.5189	1.2595	2.2292	0.1105	9957
	Location x Habitat	4	33.651	8.4128	14.89	**0.0001**	9956
	Year x Location x Habitat	4	3.4883	0.87208	1.5436	0.197	9953
	Error	222	125.43	0.56498			
	Total	239	279.78				
Frankston	Year	1	31.157	31.157	29.309	**0.0001**	9852
	Habitat	2	33.311	16.655	15.668	**0.0001**	9964
	Year x Habitat	2	1.4132	0.70659	0.66469	0.5154	9940
	Error	66	70.16	1.063			

	Total	71	150.26				
Portarlington	Year	1	2.758	2.758	5.7407	**0.0208**	9809
	Habitat	3	0.54772	0.18257	0.38002	0.7864	9945
	Year x Habitat	3	0.70906	0.23635	0.49195	0.6867	9957
	Error	74	35.553	0.48044			
	Total	81	41.296				
Altona	Year	1	0.12265	0.12265	0.76372	0.3765	9842
	Habitat	3	18.557	6.1858	38.519	**0.0001**	9948
	Year x Habitat	3	8.5142	2.8381	17.673	**0.0001**	9948
	Error	78	12.526	0.16059			
	Total	85	39.735				
Altona (2014)	Habitat	3	15.89	5.2968	62.056	**0.0001**	6427
	Error	47	4.0117	0.085356			
	Total	50	19.902				
Altona (2015)	Habitat	3	10.217	3.4056	12.4	**0.0001**	9874
	Error	31	8.5143	0.27465			
	Total	34	18.731				

Table 4. 2 Results from pair-wise tests of univariate PERMANOVA on Euclidean distances to test for the fixed effect of Habitat (Natural reef, new design artificial reef, Reef Ball reef) at Frankston and Altona on *T. caudimaculatus* recruitment between two sampling years. The test statistic (F*), a pseudo-F value, and the probability value ($P^{\dagger}$) were computed by the PERMANOVA routine with a maximum of 9,999 permutations under a reduced model for Frankston and using unrestricted permutations of raw data for Altona where tests for the 2014 and 2015 were performed separately. Sum of squares is Type III (partial) for all tests. Recruit densities were log+1 transformed. The level of significance was set at 0.05. A Monte Carlo random sample from the asymptotic permutation distribution was use to obtain p values, because for most terms in the analysis, there were not enough permutable units to get a reasonable test by permutation. The data on recruit density from the two natural reefs at Altona was treated separately for this analysis.

Groups	**t**	**P (MC)**	**Unique permutations**	**Groups**	**t**	**P (MC)**	**Unique permutations**
Frankston 2014/2015				**Frankston 2015/2016**			
New Artificial reef vs Natural	0.99818	0.3298	322	New Artificial reef vs Natural	0.93732	0.37	311
New Artificial reef vs Reef Balls	7.0628	**0.001**	11	New Artificial reef vs Reef Balls	1.7253	0.1028	606
Natural vs Reef Balls	3.596	**0.0008**	1512	Natural vs Reef Balls	3.9613	**0.0007**	9814
Altona 2014/2015				**Altona 2015/2016**			
Natural 1 vs Natural 2	Denominator is 0			Natural 1 vs Natural 2	4.4596	**0.0002**	382
Natural vs Reef Balls	3.054	**0.0032**	48	Natural vs Reef Balls	0.56695	0.5658	2
Natural vs New Artificial reef	77.76	**0.0001**	6	Natural vs New Artificial reef	21.215	**0.0001**	15
Natural 2 vs Reef Balls	3.054	**0.0068**	48	Natural 2 vs Reef Balls	2.5477	**0.023**	157
Natural 2 vs New Artificial reef	77.76	**0.0001**	6	Natural 2 vs New Artificial reef	0.6909	0.5013	186
Reef Balls vs New Artificial reef	5.3665	**0.0001**	78	Reef Balls vs New Artificial reef	12.528	**0.0001**	8

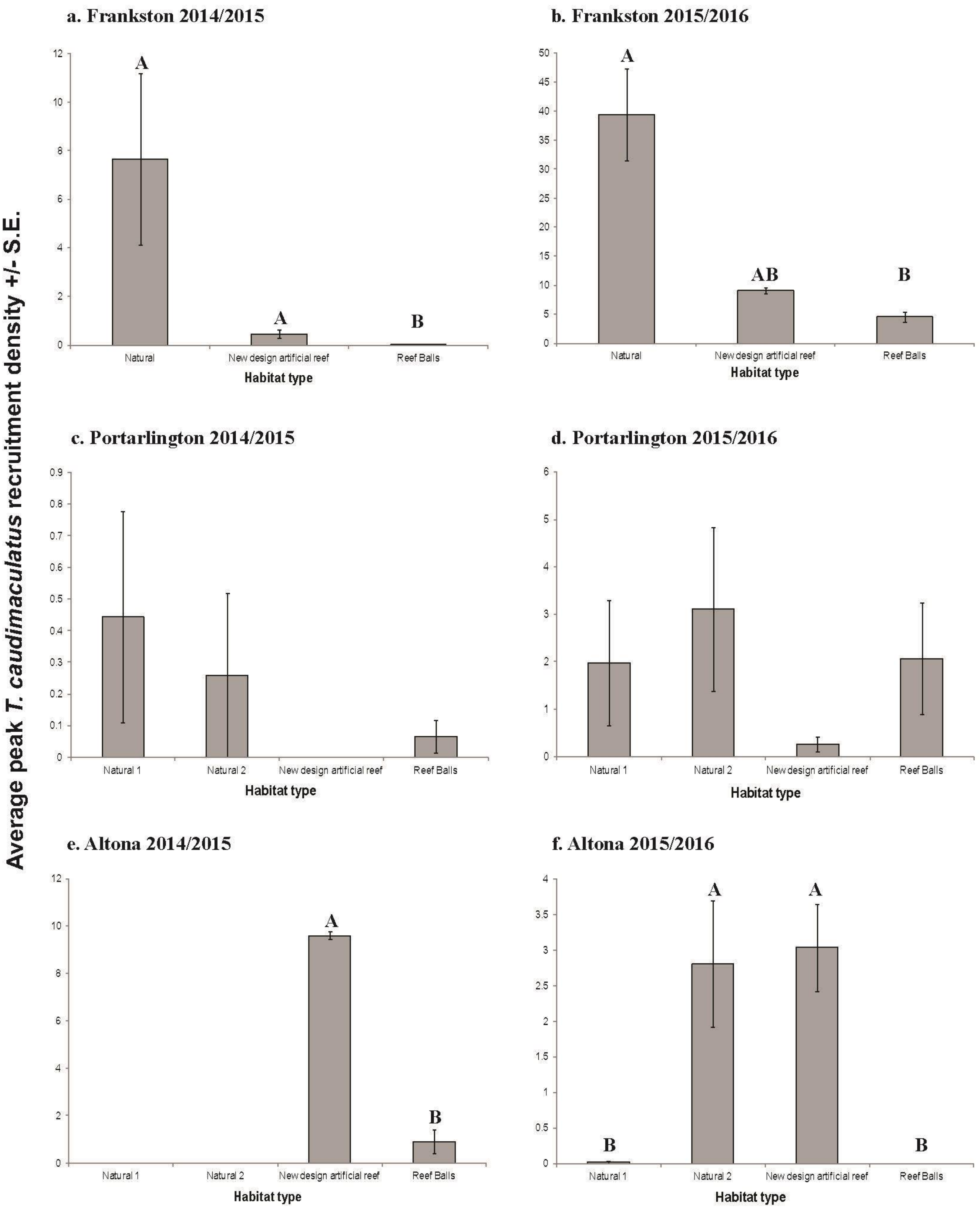


Fig. 4.2 Average peak recruitment densities of T. caudimaculatus to three habitats (natural reefs, Reef Ball reefs and new design artificial reefs) at three locations (Frankston, Portarlington, ltona) during two sampling seasons (2014/2015 and 2015/2016). At Portarlington and Altona two different natural reefs were sampled.

Vincentia conspersa

There was a significant effect of habitat on *V. conspersa* recruitment, but not location, and this effect was consistent among locations (Table 4.3). Reef Ball reefs received the highest *V. conspersa* recruit densities at both locations; however, a significant difference between natural reef and Reef Ball reef was detected only at Portarlington. On average, the Reef Ball reef at Portarlington received 2.5 times higher recruitment than natural reef. The new design artificial reefs at both locations received comparable numbers of recruits of *V. conspersa* (Table 4.4, Figure 4.3 a-b).

Trinorfolkia clarkei

T. clarkei recruit densities were similar among habitats at Frankston (Table 4.3), though the Reef Ball reef had the highest recorded *T. clarkei* recruit density (Figure 4.3 c).

Table 4. 3 Results from univariate PERMANOVA on Euclidean distances to test for the fixed effects of Location (Frankston, Portarlington) and Habitat (Natural reef, new design artificial reef, Reef Ball reef) on *V. conspersa* recruitment and Habitat (Natural reef, new design artificial reef, Reef Ball reef) on *T. clarkei* recruitment at Frankston. The test statistic (F*) is a pseudo-F value, and the probability values ($P^{\dagger}$) were computed by the PERMANOVA routine with a maximum of 9,999 permutations under a reduced model for *V. conspersa* and using unrestricted permutations of raw data.

Variable type	**Source**	**df**	**SS**	**MS**	**F***	**$P^{\dagger}$**	**Unique permutations**
V. conspersa	Location	1	0.30839	0.30839	1.7347	0.1923	9838
Overall	Habitat	2	1.6489	0.82446	4.6376	**0.0151**	9948
	Year x Location	2	0.24036	0.12018	0.676	0.5145	9955
	Error	49	8.7111	0.17778			
	Total	54	11.265				
T. clarkei	Habitat	2	1.1557	0.57786	1.3373	0.2996	2649
Frankston	Error	20	8.6422	0.43211			
	Total	22	9.7979				

Table 4. 4 Results from pair-wise tests of univariate PERMANOVA on Euclidean distances to test for the fixed effects of Habitat (Natural reef, new design artificial reef, Reef Ball reef) on *V. conspersa* recruitment between two locations (Frankston and Portarlington). The test statistic (F*), is a pseudo-F value, and the probability value ($P^{\dagger}$) were computed by the PERMANOVA routine with a maximum of 9,999 permutations under a reduced model. Sum of squares is Type III (partial) for all tests. Recruit densities were log+1 transformed. The level of significance was set at 0.05. Habitat was treated as a fixed factor. A Monte Carlo random sample from the asymptotic permutation distribution was use to obtain p values, because for most terms in the analysis, there were not enough permutable units to get a reasonable test by permutation.

Groups	**t**	**P (MC)**	**Unique permutations**	**Groups**	**t**	**P**	**Unique permutations**
Frankston				**Portarlington**			
New Artificial reef vs Natural	1.3534	0.2108	15	New Artificial reef vs Natural	0.094684	0.9267	13
New Artificial reef vs Reef Balls	0.19264	0.8508	20	New Artificial reef vs Reef Balls	1.2034	0.2485	17
Natural vs Reef Balls	1.4335	0.1723	4	Natural vs Reef Balls	2.877	**0.007**	43

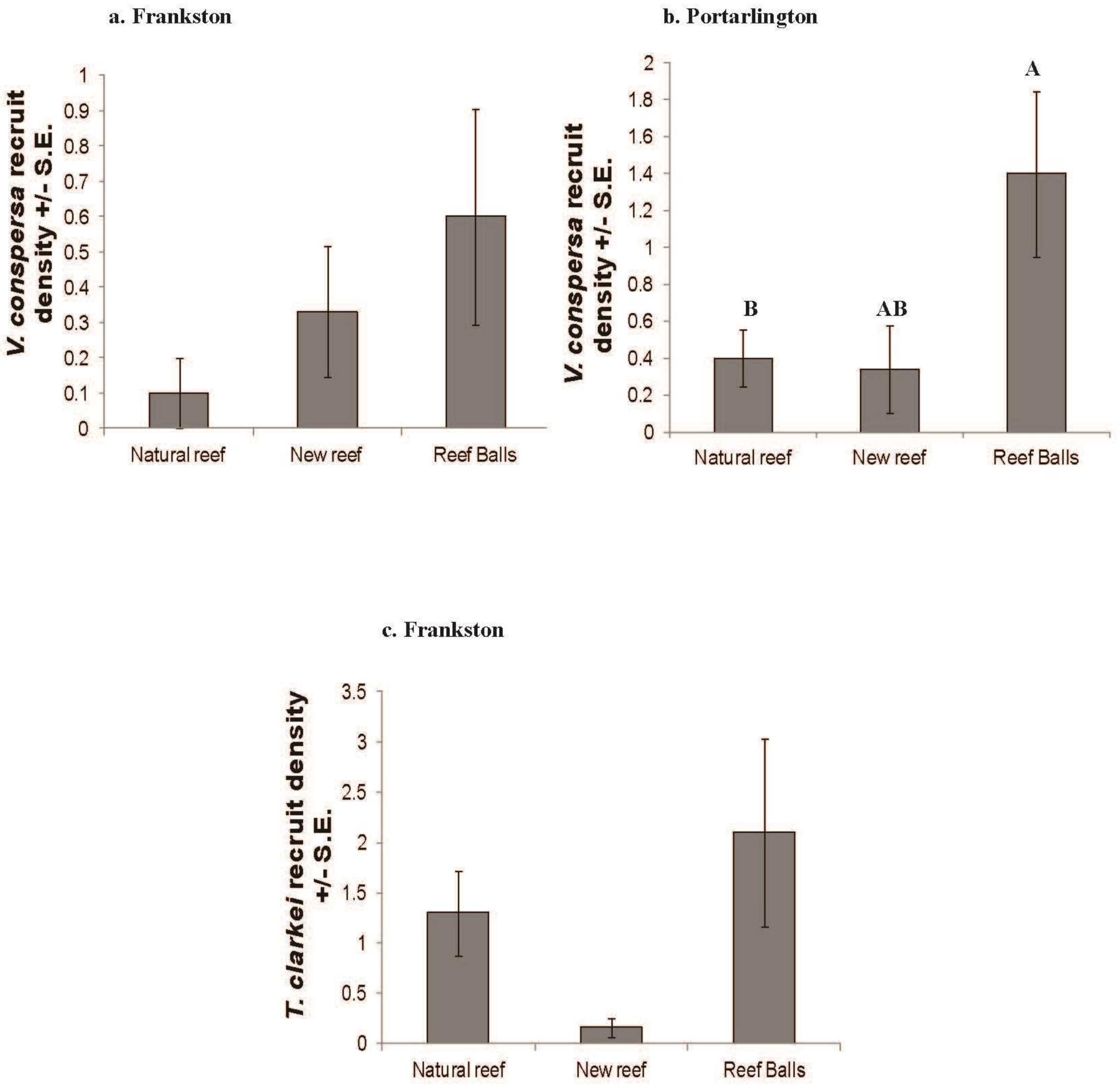


Fig. 4.3 Recruitment patterns of V. conspersa and T. clarkei in 2015/2016 in Port Phillip Bay, Victoria, Australia. **a-b** *V. conspersa* recruitment at Frankston and Portarlington, respectively. **c.** *T. clarkei* recruitment at Frankston.

Habitat selection experiments

Trachinops caudimaculatus

The proportion of *Trachinops caudimaculatus* recruits that selected the Reef Ball reef was significantly higher than expected if all three habitats were selected equally ($t = 4.3$, $p < 0.001$). The Reef Ball reef was selected six times as often as the natural reef and 3 times as often as the new design artificial reef (Figure 4.4 a).

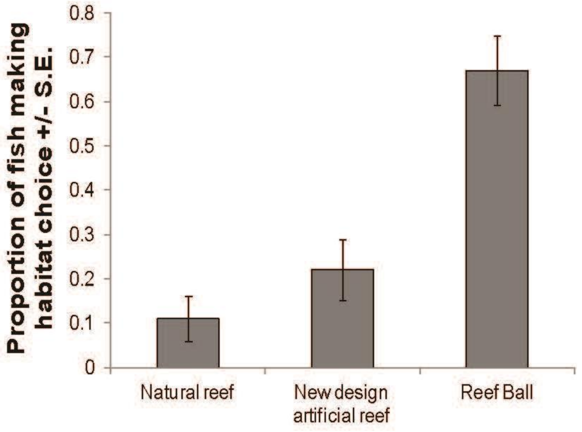
Vincentia conspersa

There was no difference in habitat preference by *V. conspersa* recruits ($\chi^2 = 2.8$, $p = 0.2466$), though 40% of individuals selected Reef Ball and natural reef each, versus 20% that selected the new design artificial reef (Figure 4.4 b). This test, however, had low power (0.302) due to the small effect size ($w = 0.37$).

4.5 Discussion

The three fish species differed in the extent to which recruitment differed among natural and artificial reefs, and their relative preferences for these habitats at settlement. Patterns in recruitment varied in timing and intensity between years, locations and habitats for all three fish species. For *T. caudimaculatus,* the new design artificial reefs received more recruitment than Reef Ball reefs; however, overall natural reef still received the highest recruitment. In contrast, laboratory choice experiments showed *T. caudimaculatus* preferred Reef Ball reefs, compared to natural reefs and new design artificial reefs. There were few differences in recruitment of *Trinorfolkia clarkei* and *Vincentia conspersa* to the different reef types, with the exception of *V. conspersa* where the Reef Ball reef received significantly higher recruitment than natural reef at one location. These results are largely consistent with the results of the laboratory habitat choice experiments for *V. conspersa*, which showed no habitat preference for this species.

a. *Trachinops caudimaculatus*



b. *Vincentia conspersa*

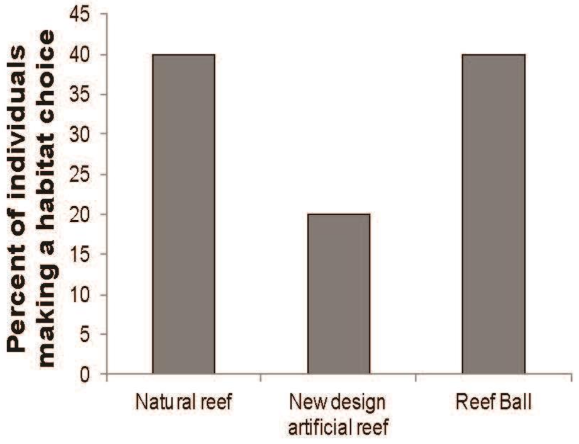


Fig. 4.4 Laboratory based habitat choice experiments for a. *T. caudimaculatus* and b. *V. conspersa* (n = 20). *T. caudimaculatus* was tested in groups of five; and therefore, the proportion of individuals making a habitat choice is displayed with standard errors. *V. conspersa* was tested individually; and therefore, the percentage of individuals making a habitat choice is displayed.

The highly variable spatial and temporal patterns in reef fish recruitment are consistent with previous findings for Port Philip Bay (Jenkins *et al.*, 1997; Jung *et al.*, 2010) and for temperate reef fishes in general (Carr, 1991; Holbrook *et al.*, 1994; Nakamura and Tsuchiya, 2008). For *Trachinops caudimaculatus*, recruitment patterns were highly inconsistent among locations, which may be driven by the composition of fish communities and the structure of natural reefs themselves at each locations. Generally speaking, natural reefs would be expected to receive higher rates of recruitment, due to their larger size and established epifaunal and fish communities. Previous studies have suggested that habitat size may greatly affect its detectability. More continuous, larger habitats provide large targets, may present stronger, more intense chemical and visual cues; and therefore, are easier to detect (Stier and Osenberg, 2010; Morton and Shima, 2013; Hale *et al.*, 2015). Moreover, larger, good quality reefs tend to support higher fish populations; and therefore, tend to be louder, adding to their detectability and attractiveness overall (Piercy *et al.*, 2014). Some of the highest recruitment rates of *T. caudimaculatus* observed during this study were on Frankston and Portarlington natural reefs which supported abundant and diverse fish populations (Chapter 2 and 3) in general, and well-established populations of *T. caudimaculatus* specifically (Hunt *et al.*, 2011; Chapter 2 and 3). These two natural reefs also appeared to be of higher quality with well-established invertebrate communities and visually higher structural complexity, than low laying Altona boulder reefs, that received some of the lowest recruitment. At Altona, natural reef 2 had higher fish abundance and diversity than natural reef 1 and was the only reef with a small *T. caudimaculatus* population (Chapter 2 and 3). At this location the new design artificial reef was located in close proximity to natural reef 2, which could have made it easier for new recruits to detect the new design artificial reef. These results suggest that in areas where good quality natural reefs support diverse and abundant fish populations they may divert recruitment from artificial reefs; however, in areas where natural reefs are of lower quality, more complex artificial reefs may become preferred habitat.

Trachinops caudimaculatus is a gregarious fish species, that lives in large dense shoals (Jung and Swearer, 2011). Hunt *et al.* (2011) and Fobert and Swearer (2017) have both shown that *T. caudimaculatus* has strong affinity for the presence of conspecifics. Generally, high abundances of conspecifics are thought to be indicative to the new recruits of the habitat quality and resource availability on the reef (Lecchini *et al.*, 2007; Lecchini *et al.*, 2014). These earlier established relationships may explain *T. caudimaculatus* recruitment patterns observed in this study, where reefs that already support established *T. caudimaculatus* populations received the highest recruitment rates. This effect is not only consistent with the high recruitment rates of *T. caudimaculatus* at Frankston and Portarlington reefs, but also from general the increase in recruitment during the second year of sampling (2015/2016 summer season) to the new design artificial reefs at Frankston which had established a small population of *T. caudimculatus* (Chapter 3 and 5) during the first year of sampling.

Although the presence of conspecifics was identified as one of the primary factors affecting *T. caudimaculatus* recruitment in previous studies, habitat structure (e.g. general complexity, vertical relief and presence of overhangs), was also highlighted as one of the major drivers of recruitment for this species (Hunt *et al.*, 2011). Hunt *et al.* (2011) suggest that the presence of small holes may be of particular importance for *T. caudimaculatus* recruits. Indeed, previous studies have demonstrated that many different fish species often use holes of approximately their own body diameter as shelter (Hixon and Beets, 1993; Holbrook *et al.*, 2002). Habitat complexity is often positively correlated with the abundance and diversity of many fish species (Wilson *et al.*, 2007; Hackradt *et al.*, 2011; Komyakova *et al.*, 2013), as it drives the outcomes of predation and competition (Behrents, 1987; Hixon and

Menge, 1991; Hixon and Beets, 1993; Stunz and Minello, 2001; Almany, 2004; Ford and Swearer, 2013b). These factors may explain the general attractiveness of the new design artificial reefs to *T. caudimaculatus* recruits *in situ*, especially in locations where good quality natural reef with large *T. caudimaculatus* population is not available (e.g. Altona), as they provide a high number of small holes and cracks, as well as good vertical relief, which may be comparable to that of natural reefs.

Reef Ball reefs did not support adult populations of *Trachinops caudimaculatus* and also were of smaller size and hence potentially lower general detectability in comparison with natural reefs. However, in the laboratory experiments, *T. caudimaculatus* recruits exhibited significantly stronger preference for the Reef Ball habitat in comparison to the natural reef and the new design reef when the size of the patch was controlled for and the influence of other variables was removed (e.g. con- and hetero- specifics). This preference is even more surprising, as the experiments were performed not on naïve larvae, but on individuals recently recruited to a natural reef and a stronger affinity for the natural reef was, therefore, expected. These results suggest that the physical structure of the Reef Ball reefs is more attractive to *T. caudimaculatus* recruits, when the primary habitat preference cues are removed. Therefore, larger, more continuous Reef Ball reefs, that have had time to form an associated fish community and a good fouling community, may potentially attract higher recruit densities than natural reefs. Furthermore, there might be a bias in the *in situ* results of this study. As recruit abundance was surveyed ~fortnightly, little is known about the immediate mortality of individuals at settlement and early post-settlement. The highest mortality often occurs directly post settlement (Caselle, 1999; Doherty *et al.*, 2004; Hoey and McCormick, 2004; Ford and Swearer, 2013b). Typically small fragmented habitats with larger edges may lead to higher mortality rates, as many predators tend to associate with the edges of the habitat (Fagan *et al.*, 1999; Laurel *et al.*, 2003; Ries *et al.*, 2004; Smith *et al.*, 2011; Macreadie *et al.*, 2012). Reef Ball reefs are small and highly fragmented reefs. It is, therefore, possible that higher, than recorded, recruitment rates were exhibited by this habitat, but were not detected in this study due to high mortality of new settlers.

Little is known about the habitat preferences of *Trinorfolkia clarkei* and *V. conspersa;* however, due to the cryptic nature of both of these species they are expected to have a preference for dark objects and spaces (Baker *et al.*, 2008; Barrett *et al.*, 2012). Indeed, *V.* conspersa has been found to associate with boulder crevices in previous studies (Baker *et al.*, 2008) and hence is expected to have an affinity for more complex habitats as well. Moreover, previous studies have also indicated strong conspecific preference for a range of species of apogonids (Gardiner and Jones, 2010) and while these relationships were not examined for *V. conspersa* specifically, it is a gregarious fish species and is likely to have certain affinity for conspecifics as well. All three habitats examined visually exhibited dark cave-like openings, though the complexity of the internal spaces differed, but this may have not been obvious to the recruits prior to settlement. All three habitats also supported populations of *V. conspersa* (Chapter 2 and 3). Morton and Shima (2013) have investigated the effects of habitat configuration and isolation on the recruitment of triplefins in New Zealand. They found that triplefin recruits tend to more abundant in clumped patches and also in isolated patches. The Reef Ball and new design artificial reefs are relatively isolated at Frankston, while Pelican reef is a large, continuous habitat equivalent to the clumped treatment in Morton and Shima (2013), making the present results similar to their general findings in terms of these habitats attracting *T. clarkei*. While previous studies from New Zealand have demonstrated that different triplefin species exhibit high levels of habitat specialisation and habitat partitioning (Feary and Clements, 2006; Wellenreuther *et al.*, 2007), Barrett et al. (2010) has found no clear pattern in the distribution of *T. clarkei* and reported that individuals are associated with general reef or reef/sand habitats. Overall, the results of my study indicate a low level of specific habitat preference for both *V. conspersa* and *T. clarkei* apart from a general association with hard substratum.

Generally speaking, the results indicate that *Trachinops caudimaculatus* exhibits complex habitat preference patterns most likely driven by a hierarchy of habitat cues, that include: the presence of conspecifics, habitat complexity, vertical relief, and habitat size, making habitat choice largely context dependent. In contrast, *V. conspersa* and *Trinorfolkia clarkei* appear to be habitat generalists, with little evidence towards any specific habitat preference. Therefore, none of the species examined showed strong differences in habitat choice and none of the offered habitats was actively avoided by any of the species.

The higher preference or equal attractiveness of some artificial habitats (e.g. Reef Ball reef) may not have large influences on fish populations in situations where habitat is limiting and any additional habitat should lead to increases in population size. However, with the majority of fish populations being overfished or in decline due to other factors, such as pollution or the introduction of invasive species (Hughes, 1994; Jackson *et al.*, 2001; Halpern *et al.*, 2008; Jackson, 2008) habitat is potentially not limited in many locations. In such situations, it is possible that new recruits that could have reached and successfully survived on a natural reef, are subsequently attracted to artificial structures causing recruitment redirection (Osenberg *et al.*, 2002; Stier and Osenberg, 2010; Morton and Shima, 2013). Artificial reefs are common targets for recreational fishermen and hence may lead to negative outcomes for fish populations in situations where they predominantly attract rather than produce new biomass (Solonsky, 1985; Pickering and Whitmarsh, 1997; Baine, 2001). Similarly, artificial reefs may also be more attractive to predatory fish, leading to high predator abundances in the vicinity of artificial reefs, which in turn may lead to higher mortality rates of prey species (Rooker *et al.*, 1997; Overholtzer-McLeod, 2004; Simon *et al.*, 2011). Little is known about the condition and consequent fitness of individuals that occupy artificial reefs. If artificial reefs are more attractive than natural reefs, yet cause lower fitness advantages, such as increased mortality rates, they may act as ecological traps, leading to further negative outcomes for fish populations (Battin, 2004; Robertson and Hutto, 2006; Hale and Swearer, 2016).

With the recent rapid expansion of marine infrastructure, often described as “ocean sprawl” (Duarte *et al.*, 2013; Heery *et al.*, 2016), it is important to better understand habitat preference patterns of new recruits between natural and artificial habitats. Additionally, the degree of attractiveness of artificial reefs for fish recruits, the potential for recruitment redirection and the formation of ecological traps is crucial if we are to estimate the effects of artificial reefs on fish populations and develop successful management and conservation strategies. This study indicates that some artificial reefs may be preferred habitat for some fish species. The next step is to determine whether there are in fitness of individuals occupying artificial structures and natural reefs.

4.6 References

Almany, G. R. (2004) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos*, 106(2), 275-284.

Anderson, M. J., Gorley, R. N. and R, C. K. (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods. *PRIMER-E Ltd: Plymouth, UK.*

Aschenbrenner, A., Hackradt, C. W. and Ferreira, B. P. (2016) Spatial variation in density and size structure indicate habitat selection throughout life stages of two Southwestern Atlantic snappers. *Marine Environmental Research*, 113, 49-55.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M. and Turlure, C. (2013) Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, 88(2), 310-326.

Baine, M. (2001) Artificial reefs: a review of their design, application, management and performance. *Ocean & Coastal Management*, 44(3–4), 241-259.

Baker, J., Shepherd, S., Brown, A., Crawford, H. and Muirhead, D. (2008) Uncommon and cryptic reef fishes: results of pilot surveys along Fleurieu Peninsula, Report for Adelaide and Mt Lofty Ranges Natural Resources Management Board.

Barrett, N., Edgar, G., Zagal, C. J., Oh, E. and Jones, D. (2012) Surveys of intertidal and subtidal biota of the Derwent Estuary-2010. *Technical Report. University of Tasmania, Hobart, Tasmania. < http://www.imas.utas.edu.au>*.

Battin, J. (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, 18(6), 1482-1491.

Behrents, K. C. (1987) The influence of shelter availability on recruitment and early juvenile survivorship of Lythrypnus dalli Gilbert (Pisces: Gobiidae). *Journal of Experimental Marine Biology and Ecology*, 107(1), 45-59.

Bell, S. S., McCoy, D. and Mushinsky, H. R. (1991) *Habitat structure: the physical arrangement of objects in space*, Chapman and Hall.

Brothers, E. B., Williams, D. M. and Sale, P. F. (1983) Length of larval life in twelve families of fishes at “One Tree Lagoon”, Great Barrier Reef, Australia. *Marine Biology*, 76(3), 319-324.

Campbell, M. D., Rose, K., Boswell, K. and Cowan, J. (2011) Individual-based modeling of an artificial reef fish community: effects of habitat quantity and degree of refuge. *Ecological Modelling*, 222(23–24), 3895-3909.

Carr, M. H. (1989) Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology*, 126(1), 59-76.

Carr, M. H. (1991) Habitat selection and recruitment of an assemblage of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology*, 146(1), 113-137.

Caselle, J. E. (1999) Early post-settlement mortality in a coral reef fish and its effects on local population size. *Ecological Monographs*, 69(2), 177-194.

Clarke, K. and Gorley, R. (2006) Primer v6: User Manual/Tutorial. *PRIMER-E: Plymouth, UK.*

Dixson, D. L., Jones, G. P., Munday, P. L., Planes, S., Pratchett, M. S., Srinivasan, M., Syms, C. and Thorrold, S. R. (2008) Coral reef fish smell leaves to find island homes. *Proceedings of the Royal Society B: Biological Sciences*, 275(1653), 2831-2839.

Doherty, P. J. (2002) Chapter 15 - Variable replenishment and the dynamics of reef fish populations A2 - Sale, Peter F. In *Coral Reef Fishes*, Academic Press, San Diego, pp. 327-355.

Doherty, P. J., Dufour, V., Galzin, R., Hixon, M. A., Meekan, M. G. and Planes, S. (2004) High mortality during settlement is a population bottleneck for a tropical surgeonfish. *Ecology*, 85(9), 2422-2428.

Doherty, P. J. and Williams, D. M. (1988) The replenishment of coral reef fish populations. *Oceanogr Mar Biol Annu Rev*, 26(48), 551.

Duarte, C. M., Pitt, K. A., Lucas, C. H., Purcell, J. E., Uye, S.-i., Robinson, K., Brotz, L., Decker, M. B., Sutherland, K. R. and Malej, A. (2013) Is global ocean sprawl a cause of jellyfish blooms? *Frontiers in Ecology and the Environment,* 11(2), 91-97.

Ehrlich, P. R. (1975) The population biology of coral reef fishes. *Annual Review of Ecology and Systematics*, 6, 211-247.

Fagan, W. F., Cantrell, R. S. and Cosner, C. (1999) How habitat edges change species interactions. *The American Naturalist*, 153(2), 165-182.

Feary, D. and Clements, K. (2006) Habitat use by triplefin species (Tripterygiidae) on rocky reefs in New Zealand. *Journal of Fish Biology,* 69(4), 1031-1046.

Fobert, E. K. and Swearer, S. E. (2017) The nose knows: linking sensory cue use, settlement decisions, and post-settlement survival in a temperate reef fish. *Oecologia*, 1-11.

Ford, J. R. and Swearer, S. E. (2013a) Shoaling behaviour enhances risk of predation from multiple predator guilds in a marine fish. *Oecologia*, 172(2), 387-397.

Ford, J. R. and Swearer, S. E. (2013b) Two's company, three's a crowd: food and shelter limitation outweigh the benefits of group living in a shoaling fish. *Ecology*, 94(5), 1069-1077.

Gardiner, N. and Jones, G. (2010) Synergistic effects of habitat preference and gregarious behaviour on habitat use in coral reef cardinalfish. *Coral Reefs*, 29(4), 845-856.

Gomon, M. F., Bray, D. J. and Kuiter, R. H. (2008) *Fishes of Australia's southern coasts / edited by Martin Gomon, Diane Bray, Rudie Kuiter*, Reed New Holland, Musuem Victoria, Chatswood, N.S.W.

Hackradt, C. W., Félix-Hackradt, F. C. and García-Charton, J. A. (2011) Influence of habitat structure on fish assemblage of an artificial reef in southern Brazil. *Marine Environmental Research*, 72(5), 235-247.

Hale, R. and Swearer, S. E. (2016) Ecological traps: current evidence and future directions. *Proceedings of the Royal Society B: Biological Sciences*, 283(1824).

Hale, R., Swearer, S. E. and Downes, B. J. (2009) Separating natural responses from experimental artefacts: habitat selection by a diadromous fish species using odours from conspecifics and natural stream water. *Oecologia*, 159(3), 679-687.

Hale, R., Treml, E. A. and Swearer, S. E. (2015) Evaluating the metapopulation consequences of ecological traps. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1804), 20142930.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R. and Watson, R. (2008) A global map of human impact on marine ecosystems. *Science*, 319(5865), 948-952.

Heery, E., Bishop, M., Critchley, L., Bugnot, A., Airoldi, L., Mayer-Pinto, M., Sheehan, E., Coleman, R., Loke, L. and Johnston, E. (2016) Identifying the consequences of ocean sprawl for sedimentary habitats. *Journal of Experimental Marine Biology and Ecology*.

Hixon, M. A. and Beets, J. P. (1989) Shelter characteristics and caribbean fish assemblages: experiments with artificial reefs. *Bulletin of Marine Science*, 44(2), 666-680.

Hixon, M. A. and Beets, J. P. (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs*, 63(1), 77-101.

Hixon, M. A. and Menge, B. A. (1991) Species diversity: prey refuges modify the interactive effects of predation and competition. *Theoretical Population Biology,* 39(2), 178-200.

Hoey, A. S. and McCormick, M. I. (2004) Selective predation for low body condition at the larval-juvenile transition of a coral reef fish. *Oecologia*, 139(1), 23-29.

Holbrook, S. J., Brooks, A. J. and Schmitt, R. J. (2002) Variation in structural attributes of patch-forming corals and in patterns of abundance of associated fishes. *Marine and Freshwater Research*, 53(7), 1045-1053.

Holbrook, S. J., Kingsford, M. J., Schmitt, R. J. and Stephens, J. S. (1994) Spatial and temporal patterns in assemblages of temperate reef fish. *American Zoologist*, 34(3), 463-475.

Hughes, T. P. (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 265(5178), 1547-1551.

Hunt, T. L., Ford, J. R. and Swearer, S. E. (2011) Ecological determinants of recruitment to populations of a temperate reef fish, *Trachinops caudimaculatus* (Plesiopidae). *Marine and Freshwater Research*, 62(5), 502-509.

Irisson, J.-O., Paris, C. B., Leis, J. M. and Yerman, M. N. (2015) With a little help from my friends: group orientation by larvae of a coral reef fish. *PLoS ONE*, 10(12), e0144060.

Jackson, J. B. C. (2008) Ecological extinction and evolution in the brave new ocean. *Proceedings of the National Academy of Sciences*, 105(Supplement 1), 11458-11465.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. and Warner, R. R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293(5530), 629-637.

Jan, R.-Q., Liu, Y.-H., Chen, C.-Y., Wang, M.-C., Song, G.-S., Lin, H.-C. and Shao, K.-T. (2003) Effects of pile size of artificial reefs on the standing stocks of fishes. *Fisheries Research*, 63(3), 327-337.

Jenkins, G. P., Black, K. P., Wheatley, M. J. and Hatton, D. N. (1997) Temporal and spatial variability in recruitment of a temperate, seagrass-associated fish is largely determined by physical processes in the pre-and post-settlement phases. *Marine Ecology Progress Series*, 23-35.

Jenkins, G. P., Kenner, T., Brown, A. and Coleman, R. (2015) Fish assemblages in locations with alternative structured habitats in an eelgrass, *Zostera*, dominated bay: biodiversity value and potential for refuge. *Estuarine, Coastal and Shelf Science*, 161, 25-37.

Jones, G. P. (1984) Population ecology of the temperate reef fish *Pseudolabrus celidotus* Bloch & Schneider (Pisces: Labridae). I. Factors influencing recruitment. *Journal of Experimental Marine Biology and Ecology*, 75(3), 257-276.

Jung, C. A. and Swearer, S. E. (2011) Reactions of temperate reef fish larvae to boat sound. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 21(4), 389-396.

Jung, C. A., Swearer, S. E. and Jenkins, G. P. (2010) Changes in diversity in the fish assemblage of a southern Australian embayment: consistent spatial structuring at decadal scales. *Marine and Freshwater Research*, 61(12), 1425-1434.

Kingsford, M. J., Leis, J. M., Shanks, A., Lindeman, K. C., Morgan, S. G. and Pineda, J. (2002) Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science*, 70(1), 309-340.

Komyakova, V., Munday, P. L. and Jones, G. P. (2013) Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. *PLoS ONE*, 8(12), e83178.

Kristan, I. I. I. W. B. (2003) The role of habitat selection behavior in population dynamics: source–sink systems and ecological traps. *Oikos*, 103(3), 457-468.

Laurel, B. J., Gregory, R. and Brown, J. (2003) Predator distribution and habitat patch area determine predation rates on age-0 juvenile cod Gadus spp. *Marine Ecology Progress Series*, 251, 245-254.

Lecchini, D., Peyrusse, K., Lanyon, R. G. and Lecellier, G. (2014) Importance of visual cues of conspecifics and predators during the habitat selection of coral reef fish larvae. *Comptes Rendus Biologies*, 337(5), 345-351.

Lecchini, D., Planes, S. and Galzin, R. (2007) The influence of habitat characteristics and conspecifics on attraction and survival of coral reef fish juveniles. *Journal of Experimental Marine Biology and Ecology*, 341(1), 85-90.

Levin, P. S. (1993) Habitat structure, conspecific presence and spatial variation in the recruitment of a temperate reef fish. *Oecologia*, 94(2), 176-185.

Macreadie, P. I., Geraldi, N. R. and Peterson, C. H. (2012) Preference for feeding at habitat edges declines among juvenile blue crabs as oyster reef patchiness increases and predation risk grows. *Marine Ecology Progress Series*, 466, 145-153.

Mapstone, B. D. and Fowler, A. J. (1988) Recruitment and the structure of assemblages of fish on coral reefs. *Trends in Ecology & Evolution*, 3(3), 72-77.

McArdle, B. H. and Anderson, M. J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, 82(1), 290-297.

Morris, D. W. (1992) Scales and costs of habitat selection in heterogeneous landscapes. *Evolutionary Ecology*, 6(5), 412-432.

Morris, D. W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, 136(1), 1-13.

Morris, D. W. (2011) Adaptation and habitat selection in the eco-evolutionary process. *Proceedings of the Royal Society B: Biological Sciences*, 278(1717), 2401-2411.

Morton, D. N. and Shima, J. S. (2013) Habitat configuration and availability influences the settlement of temperate reef fishes (Tripterygiidae). *Journal of Experimental Marine Biology and Ecology*, 449, 215-220.

Nakamura, Y. and Tsuchiya, M. (2008) Spatial and temporal patterns of seagrass habitat use by fishes at the Ryukyu Islands, Japan. *Estuarine, Coastal and Shelf Science,* 76(2), 345-356.

Osenberg, C. W., St. Mary, C. M., Wilson, J. A. and Lindberg, W. J. (2002) A quantitative framework to evaluate the attraction–production controversy. *ICES Journal of Marine Science: Journal du Conseil*, 59(suppl), S214-S221.

Overholtzer-McLeod, K. L. (2004) Variance in reef spatial structure masks density dependence in coral-reef fish populations on natural versus artificial reefs. *Marine Ecology Progress Series*, 276, 269-280.

Pickering, H. and Whitmarsh, D. (1997) Artificial reefs and fisheries exploitation: a review of the ‘attraction versus production’ debate, the influence of design and its significance for policy. *Fisheries Research*, 31(1), 39-59.

Piercy, J. J. B., Codling, E. A., Hill, A. J., Smith, D. J. and Simpson, S. D. (2014) Habitat quality affects sound production and likely distance of detection on coral reefs. *Marine Ecology Progress Series*, 516, 35-47.

Richards, W. J. and Lindeman, K. C. (1987) Recruitment dynamics of reef fishes: planktonic processes, settlement and demersal ecologies, and fishery analysis. *Bulletin of Marine Science*, 41(2), 392-410.

Ries, L., Fletcher Jr, R. J., Battin, J. and Sisk, T. D. (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annu. Rev. Ecol. Evol. Syst.*, 35, 491-522.

Robertson, B. A. and Hutto, R. L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, 87(5), 1075-1085.

Rooker, J., Dokken, Q., Pattengill, C. and Holt, G. (1997) Fish assemblages on artificial and natural reefs in the Flower Garden Banks National Marine Sanctuary, USA. *Coral Reefs*, 16(2), 83-92.

Sale, P. F. (2002) Chapter 16 - The science we need to develop for more effective management. In *Coral Reef Fishes*, Academic Press, San Diego, pp. 361-376.

Sale, P. F., Doherty, P. J., Eckert, G. J., Douglas, W. A. and Ferrell, D. J. (1984) Large scale spatial and temporal variation in recruitment to fish populations on coral reefs. *Oecologia*, 64(2), 191-198.

Schlaepfer, M. A., Runge, M. C. and Sherman, P. W. (2002) Ecological and evolutionary traps. *Trends in Ecology & Evolution*, 17(10), 474-480.

Seaman Jr, W. and Sprague, L. M. (1991) 1 - Artificial habitat practices in aquatic systems. In *Artificial habitats for marine and freshwater fisheries*, Academic Press, San Diego, pp. 1-29.

Seaman, W. and Lindberg, W. J. (2009) Artificial reefs A2 - Steele, John H. In *Encyclopedia of Ocean Sciences (Second Edition)*, Academic Press, Oxford, pp. 226-233.

Shima, J. S. and Swearer, S. E. (2010) The legacy of dispersal: larval experience shapes persistence later in the life of a reef fish. *Journal of Animal Ecology*, 79(6), 1308-1314.

Simon, T., Pinheiro, H. T. and Joyeux, J.-C. (2011) Target fishes on artificial reefs: evidences of impacts over nearby natural environments. *Science of The Total Environment*, 409(21), 4579-4584.

Smith, T. M., Hindell, J. S., Jenkins, G. P., Connolly, R. M. and Keough, M. J. (2011) Edge effects in patchy seagrass landscapes: the role of predation in determining fish distribution. *Journal of Experimental Marine Biology and Ecology*, 399(1), 8-16.

Solonsky, A. C. (1985) Fish colonization and the effect of fishing activities on two artificial reefs in Monterey Bay, California. *Bulletin of Marine Science*, 37(1), 336-347.

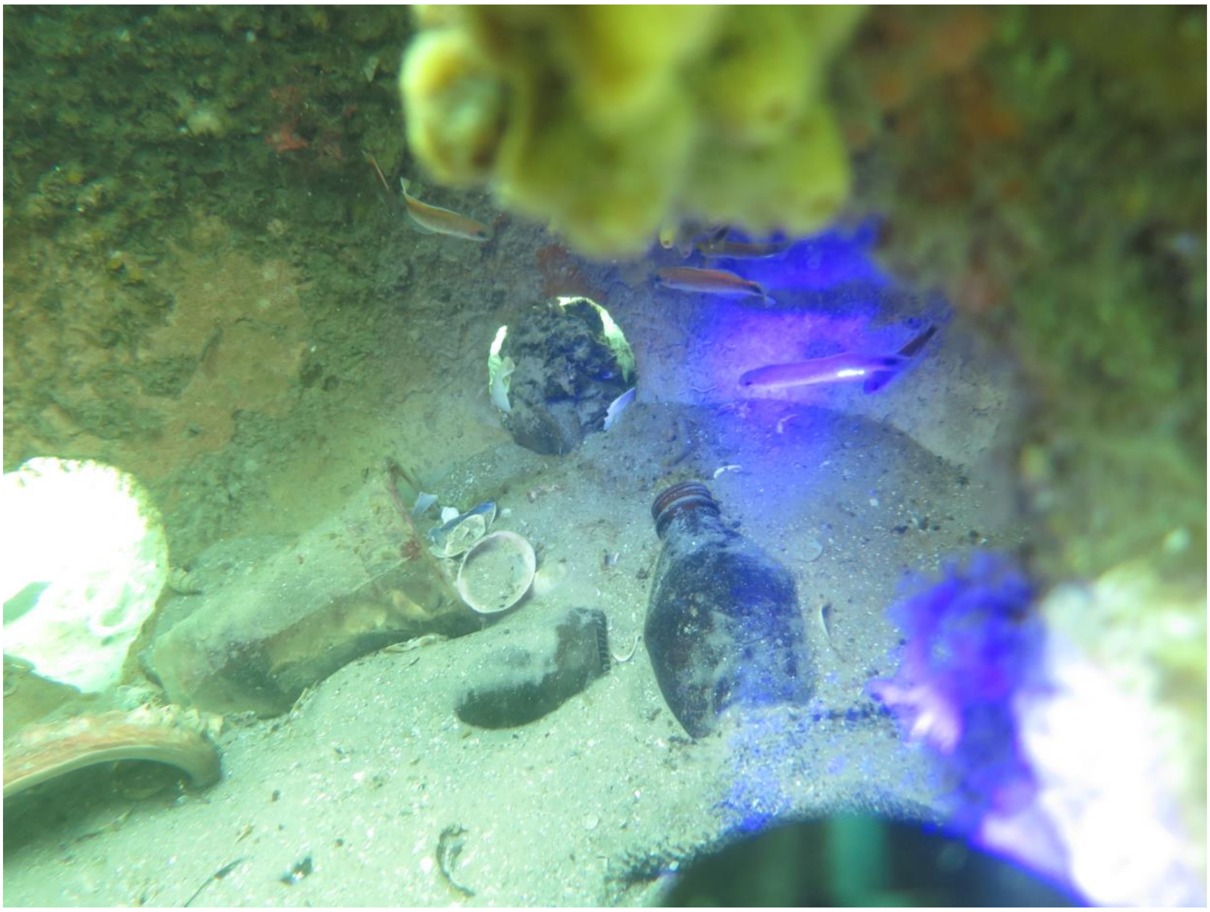
Stier, A. C. and Osenberg, C. W. (2010) Propagule redirection: habitat availability reduces colonization and increases recruitment in reef fishes. *Ecology*, 91(10), 2826-2832.

Stunz, G. W. and Minello, T. J. (2001) Habitat-related predation on juvenile wild-caught and hatchery-reared red drum *Sciaenops ocellatus* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, 260(1), 13-25.

Wellenreuther, M., Barrett, P. T. and Clements, K. D. (2007) Ecological diversification in habitat use by subtidal triplefin fishes (Tripterygiidae). *Marine Ecology Progress Series*, 330, 235-246.

Wilson, S., Graham, N. and Polunin, N. (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology*, 151(3), 1069-1076.

CHAPTER FIVE:
Artificial reefs as ecological traps: a multi-species comparison of fitness outcomes for temperate reef fishes on artificial and natural reefs



T. caudimaculatus young juveniles tagged with VIE tag inside Reef Ball reef at Frankston, Port Phillip Bay, Victoria, Australia

5.1 Abstract

The proliferation of artificial reefs (ARs), which has become a common management tool for stock enhancement of recreational fisheries and habitat restoration, has occurred all over the world with increasing intensity in recent decades. The benefits of artificial reefs, however, depend on their suitability as habitat for marine species. Artificial reefs could result in the provision of seemingly suitable habitat that provides lower fitness advantages. If animals preferentially colonize such structures, this could result in an ecological trap. I examined general condition of individuals of three study species (*Trachinops caudimaculatus*, *Vincentia conspersa* and *Trinorfolkia clarkei*) occupying three different habitats types: natural reefs, Reef Ball reefs and new design artificial reefs in Port Phillip Bay, Victoria, Australia, through comparing a range of condition indexes (HSI, GSI and Wrm). Additionally, I compared instantaneous mortality rates of *T. caudimaculatus* new recruits and juveniles between study habitats at three locations over two recruitment seasons. Finally, I examined *T. caudimaculatus* new recruits survival between three study habitats through a mark-resighting study using VIE tags at one of the locations in Port Philip Bay. The fitness data for each species was then examined in combination with previously established habitat preferences for each species. There was a large variability in individual condition among species and habitats. Generally, *V. conspersa* were in significantly better condition on Reef Ball reefs than the other two habitats. *T. clarkei* performed the best on new design artificial reefs; however, the responses were time and location driven. There was little difference in the condition of *T. caudimaculatus* occupying different habitats; however *T. caudimaculatus*, exhibited nine times higher instantaneous mortality rates on Reef Ball reefs than the other two habitats. These results were also largely supported by mark-resighting experiment. Combined with the habitat preference of *T. caudimaculatus* for Reef Ball reefs, the fitness results suggest that Reef Ball reefs may act as an ecological trap for this species.

V. conspersa results provide evidence for adaptive habitat selection, while the findings for *T. clarkei* are consistent with the likelihood for the creation of a perceptual trap. Although my results indicate that responses by fishes to different types of artificial habitats are greatly species-, location- and habitat-specific, this is one of the first studies to demonstrate the formation of ecological traps in the marine environment.

Artificial reefs are excellent management tools of degraded habitats, recreational fisheries and for fish species conservation. However, poorly designed or poorly placed artificial reefs may lead to insufficient positive outcomes or even significant negative impacts on marine communities. Combined with their high costs, these effects may in turn lead to wasted resources and negative attitude of local communities to the new artificial reef placements, which in turn could impede further management and conservation efforts.

5.2 Introduction

In the last decade the world's human population grew by over 12%, with the number of people living in urban areas projected to reach 5 billion by 2030 (Seto *et al.*, 2012). Today, ~ 3 billion people live within 200 km of a coastline, placing enormous pressure on coastal marine ecosystems from the impacts of invasive species, pollution, climate change, overfishing, and habitat fragmentation, degradation and loss. (Jackson *et al.*, 2001; Halpern *et al.*, 2008; Jackson, 2008). These impacts are global, with all marine ecosystems being affected by at least one of these impacts and almost half with multiple factors Halpern *et al.* (2008). In coastal areas, extensive infrastructure projects, for example the construction of underwater pipelines, marinas, shore extensions and even artificial islands, have resulted in widespread habitat modification and loss (Halpern *et al.*, 2008; Sih *et al.*, 2011; Sih, 2013;

Dafforn *et al.*, 2015; Firth *et al.*, 2016). Similarly, extensive fishing practices have lead to multiple fishery collapses and declines in abundances of many taxa (Jackson *et al.*, 2001; Jackson, 2008). While artificial structures have been used for centuries to attract fish for harvest (i.e., Fish Attraction Devices – FADs (Thierry, 1988; Seaman Jr and Sprague, 1991; Baine, 2001; Fabi *et al.*, 2011)) and thus have contributed to fishery exploitation, more recently artificial reefs (ARs) have also become a popular management tool for habitat restoration and marine species conservation (Thierry, 1988; Baine, 2001; Fabi *et al.*, 2011; Kheawwongjan and Kim, 2012).

The design and application of ARs differ greatly and range from accidental or intentional deployments of old wreckage to specially engineered structures (Thierry, 1988; Grove *et al.*, 1991; Branden *et al.*, 1994; Baine, 2001; Sherman *et al.*, 2002; Fabi *et al.*, 2011). Millions of dollars have been spent around the world on the deployment of ARs (Thierry, 1988; Seaman Jr and Sprague, 1991; Branden *et al.*, 1994; Baine, 2001; Fabi *et al.*, 2011). However, at least half of these deployments have failed to achieve their goals largely as a result of inappropriate size and design (Pickering and Whitmarsh, 1997; Baine, 2001; Jan *et al.*, 2003; Campbell *et al.*, 2011; Hackradt *et al.*, 2011).

Much of the ecological research has focused on monitoring animal community establishment on newly deployed ARs (Carr and Hixon, 1997; Baine, 2001; Fabi *et al.*, 2011), with considerable debate over whether they increase or simply redistribute biomass production, the “attraction – production” debate (Pickering and Whitmarsh, 1997; Brickhill *et al.*, 2005). Although several review papers have highlighted the importance of comparing ARs to nearby natural reefs in order to properly evaluate their performance, (Carr and Hixon, 1997; Pickering and Whitmarsh, 1997; Baine, 2001; Osenberg *et al.*, 2002b), few studies have been properly designed to do so, with many confounded by large distances between study sites, low replication, short monitoring times, and/or large differences in the sizes and depths of natural reefs compared to ARs (Carr and Hixon, 1997; Brickhill *et al.*, 2005; Fowler and Booth, 2012).

Evaluating whether ARs provide habitat of comparable quality to natural reefs is further constrained by the limited data on proxy and direct fitness measures (e.g., growth, condition, reproduction, survival) of individuals occupying ARs compared to natural reefs (Page *et al.*, 2007; Hallier and Gaertner, 2008; Dempster *et al.*, 2011; Reubens *et al.*, 2013). Habitat structure is known to affect the outcomes of many biological interactions such as predation and competition. For example, survival rates can often differ greatly among different habitat types, especially for new recruits and juveniles (Behrents, 1987; Hixon and Beets, 1989; Hixon and Menge, 1991; Hixon and Beets, 1993; Stunz and Minello, 2001). Furthermore, as species can often differ in their habitat requirements, whether a particular AR design provides suitable habitat is likely to depend on the species in question (Brickhill *et al.*, 2005).

When ARs are deployed for habitat restoration and/or species conservation purposes, it is important that newly established populations contribute to net population growth. When local populations of reef organisms are connected via dispersal of pelagic larvae (i.e., a metapopulation), ARs will have the greatest benefit when they function as sources, where individuals that settle survive to reproductive age and contribute to the metapopulation through their reproductive output. Therefore, studies investigating the fitness outcomes of individuals of several different species occupying artificial structures in comparison to nearby natural reefs are needed to assess the suitability of ARs as habitat for reef animals.

The impact of ARs on metapopulation dynamics also depends on how they influence where larvae choose to settle, particularly when reef habitat is not limiting. ARs could have broader ecological consequences if habitat cues used by marine fish larvae to evaluate suitability of benthic habitat for settlement fail to distinguish poor quality habitats, with poor quality habitat providing cues similar to the natural habitat. Although ARs may mimic the habitat selection cues of a natural reef used by marine fish larvae to find suitable habitat and falsely appear to be more attractive to the individuals than suitable natural reefs, as the artificial reef may fail to provide required diversity and complexity of refuge sites, causing increased mortality rates. The situation when an animal preferentially selects a lower quality habitat that causes reduced fitness outcomes has been referred to in the literature as an "ecological trap" (Kingsford *et al.*, 2002; Schlaepfer *et al.*, 2002; Kristan, 2003; Battin, 2004; Robertson and Hutto, 2006). According to Robertson and Hutto (2006), two types of ecological traps may occur: a "severe trap", when an individual preferentially selects a poor quality habitat that leads to reduced fitness advantages (e.g. high mortality) or an "equal preference trap" when an individual exhibits equal preference for a good quality and a poor quality habitat. Robertson and Hutto (2006) have also identified the means by which an ecological trap can be established: (a) the habitat preference has to be established through a variety of methods that may include, for example, settlement patterns, site fidelity or habitat choice experiments; (b) there must be differences in fitness of individuals occupying modified and natural habitats; and (c) fitness of individuals occupying modified habitats must be lower than the fitness of individuals occupying natural habitats. While the ecological trap question has received a large amount of attention in terrestrial systems, only a handful of studies have investigated this question in aquatic environments and none have assessed the phenomenon in the context of artificial structures in general, or reefs in particular (Battin, 2004; Robertson and Hutto, 2006; Hale and Swearer, 2016).

In this chapter, I investigate indexes of performance (relative weight (*W*rm), hepatosomatic index and gonadosomatic index) for three species of temperate reef fish (*Trachinops caudimaculatus*, *Vincentia conspersa* and *Trinorfolkia clarkei*) and estimate mortality rates for *T. caudimaculatus* among three different habitat types (two types of artificial reefs and natural reef). Habitat preferences for each of these species have been previously established (Chapter 4). The condition and mortality rate estimates, in combination with known habitat preferences, are used to resolve whether artificial reefs can act as ecological traps for fish population.

5.3 Materials and Methods

Sample collection

Individuals of three study species (*Trinorfolkia clarkei, Vincentia conspersa* and *Trachinops caudimaculatus*) were collected in two consecutive years using a low dose clove oil mixture (one part clove oil, one part 100 % ethanol and eight parts sea water) and hand nets from two study locations, Frankston and Altona, within Port Phillip Bay, Australia (Figure 3.1). The Frankston location contained one new design artificial reef, one Reef Ball reef and one adjacent natural reef. The Altona location contained one new design artificial reef, one Reef Ball reef and two adjacent natural reefs. A full description of the study sites, the new design artificial reef and Reef Ball reefs, and deployment details can be found in Chapter 3. A brief description of the study species is given in Chapter 4. Individuals were sampled from mid May to early July in 2015 and from mid May to late June in 2016. When possible new recruits of each species were targeted. An minimum of 2 and a maximum of 26 individuals was collected for each species from each location and habitat during each sampling season (Table 5.1).

Table 5. 1 Total number of individuals collected per location, habitat and species during each sampling season for HIS and GSI analysis. Number in brackets indicates the number of individuals used for *W*r analysis, when different to HIS and GSI.

	2014/2015	**Species**		
Site	**Habitat**	***Vincentia conspersa***	***Trinorfolkia clarkei***	
Altona	Natural reef 1	5	25	
	New design artificial reef	9 (11)	21 (26)	
	Reef Balls	0	10	
	Natural reef 2	8	14	
Frankston	Natural reef (Pelican reef)	23	17 (20)	
	New design artificial reef	10 (12)	11	
	Reef Balls	3	25	
	2015/2016		**Species**	
	Habitat	***Vincentia conspersa***	***Trinorfolkia clarkei***	***Trachinops caudimaculatus***
Altona	Natural reef 1	4 (5)	20	0
	New design artificial reef	8 (9)	18 (20)	17
	Reef Balls	3 (4)	2	0
	Natural reef 2	5 (9)	11 (12)	6
Frankston	Natural reef (Pelican reef)	13	17 (21)	17 (20)
	New design artificial reef	13 (14)	18	17 (20)
	Reef Balls	20	18 (20)	0

Condition indices

Upon collection fish were humanly killed using clove oil and placed on ice. Each individual was weighed and measured to the nearest mm using callipers (standard length; SL). Each individual was dissected and intestine, liver and gonad (when locatable) were removed and weighed. Sex was determined by macroscopic examination of the gonads. Three condition indices were calculated. Relative weight (*W*rm) (Froese 2006), a measure of overall body condition, that calculates the deviation of each sample from the overall length – weight relationship for fish collected from all studied populations (*Trachinops caudimaculatus*: $R^2 = 0.96$, $p < 0.05$, $n = 66$; *V. conspersa*: $R^2 = 0.97$, $p < 0.05$, $n = 136$; *Trinorfolkia clarkei*: $R^2 = 0.96$, $p < 0.05$, $n = 244$), using equation: $W\mathrm{rm} = (\mathrm{WW}/{}_{a}\mathrm{SL}^{b)}$ x 100, where WW – gutted wet weight and SL - standard length (mm). The hepatosomatic index (HSI) was calculated with the formula: HSI = (LW/(WW-SW)) X 100, where LW - liver weight. Finally, gonadosomatic index (GSI) was calculated with the formula: GSI = (GW/(WW-SW)) X 100, where GW - gonad weight.

Mortality rates

Mortality rates were estimated for one of the study species: *Trachinops caudimaculatus*, using two different methods.

Population census

To investigate the differences in survival rates between natural and two types of artificial reefs, declines in total abundance (recruit, juvenile and adult abundances combined) of *Trachinops caudimaculatus* were monitored at three study locations using fortnightly to monthly visual surveys after the end of the recruitment season (March to June) for two consecutive years.

Trachinops caudimaculatus populations were surveyed at each natural and artificial reef by underwater visual census. On the Reef Ball reefs, most Reef Balls are arranged in groups of 5, as on a dice for five points, in close proximity to each other (between 0.5-1 m). As such, each of these 5-Reef-Ball arrangements was treated as a single sampling unit (i.e., replicate). Each 5-Reef-Ball unit covers a circular area of ~ 2.5 m in diameter so an area of 2.5 m in diameter was sampled on natural reef. Each Reef Ball reef consists of 18 5-Reef-Ball units. When possible all 18 5-Reef-Ball units were sampled on Reef Ball reefs and 18 point counts were conducted on natural reefs. Due to weather constraints it was not possible to sample all replicates at each location each sampling round, resulting in a minimum of 5 5-Reef-Ball units on Reef Ball reefs and 12 point counts on natural reefs. On a natural reef point counts were selected randomly for each sampling period. All of the fish were counted on the new design artificial reefs each sampling period. The abundances of each life stage of *T. caudimaculatus* were converted to density for all three habitats.

VIE tagging

At Frankston, newly recruited *Trachinops caudimaculatus* were captured as above, measured to the nearest mm and tagged with visible implant elastomer fluorescent tag (VIE) at the lower half of the body near the base of the tail using a 29 gauge hypodermic needle (Northwest Marine Technology). Tagged individuals were left in the large container with constant air supply for 2 hours to recover. After recovery a minimum of 14 individuals per replicate were placed back on each of the three habitats. Each habitat had a total of 3 replicate tagged fish groups. Highest mortality rates were expected to occur in the first few weeks after settlement (Caselle, 1999; Doherty *et al.*, 2004; Hoey and McCormick, 2004; Ford and Swearer, 2013b); and therefore, visual counts of tagged individuals were conducted on days 2, 4 and 13 post tagging. A blue LED light torch (FDG/Riff TL3000BE torch kit) was used to fluoresce the tags in the field (firedivegear.com). All of the artificial reefs and ~10 meters in diameter around the release point on natural reefs were examined each survey. Two observers were used on natural reefs due to the greater difficulty in detecting tags on continuous reef habitat. Re-sightings of tagged fish were used to estimate survival rates.

Statistical analysis

Condition indices

HSI, GSI and *W*rm data was log+1 transformed and univariate analyses were performed using PRIMER-E v6 with the PERMANOVA (Permutational Multivariate Analysis of Variance) add-on (McArdle and Anderson, 2001). (Clarke and Gorley, 2006) and (Anderson *et al.*, 2008) both state that PERMANOVA is appropriate for a univariate analysis.

For the analysis of HSI and GSI the fixed effects included into the model were Year (2014/2015 and 2015/2016 sampling season), Location (Frankston, Altona), Habitat (Natural reef, new design artificial reef, Reef Ball reef) and Sex (Male, Female) for all study species, with the exception of *Trachinops caudimaculatus*, where data was available from only one year of sampling (2015/2016) and only from new design artificial reef and Natural reef. For the analysis of *W*rm all of the above fixed factors were included in the models with the exception of Sex, where female and male data was pooled together. Juveniles were excluded from the analysis of HSI and GSI for all study species, but included into the analysis of *W*rm (Table 5.1). Sex was treated as a blocking factor and all interactions with Sex variable were excluded from all models. Due to missing data for *V. conspersa* Habitat x Location interaction and Year x Location x Habitat interaction were also excluded from all models. For Altona, the data from both natural reefs was pooled for all study species. All univariate PERMANOVA tests were run using Euclidean distance matrices based on HSI, GSI or *W*rm with a maximum of 9999 permutations.

As there was a significant three-way interaction for *Trinorfolkia clarkei* HSI: year x location x habitat (Table 5.2), tests for the effect of location, reef habitat and sex were performed separately for each year (n = 2 models). Due to the complexity of the design, I used permutation of residuals under a reduced model permutation method with Type III sum of squares for all of the above tests. Pair-wise PERMANOVA tests were conducted as a post-hoc test to identify which habitats were significantly different from each other in HSI, GSI and *W*rm for all three study species. The exact comparisons made were dictated by the results of the overall models (Table 5.3).

Mortality rates

Population census

The daily instantaneous mortality rate data for combined recruits and juveniles abundance was calculated by fitting a function to the Ln (fish abundance) versus day since peak abundance. The function was fit separately for all combinations of year, location, and habitat where there were sufficient fish numbers to estimate the rate (n = 16). Abundances were pooled across all replicate habitat types within a year and location to reduce variance in counts. The instantaneous mortality rate was logit transformed to fit the assumptions of a least square fit one-way ANOVA with year and location included as blocking factors. To identify which habitats were significantly different from each other one-way ANOVA was followed up with Tuckey's HD post hoc test. The analysis was conducted in JMP statistical computer package.

VIE tagging

Differences in mortality of tagged juveniles between different habitats (natural reef, new design artificial reef and Reef Balls) were compared using survival analysis in SPSS computer package. Survival trajectories were plotted using the Kaplan-Meier product-limit method, which is a non-parametric method to estimate survival that allows to compare trajectories of censored (incomplete) observations, such as typical of continuous field observations. The log rank test (Mantel-Cox) was used to test for differences in the tagged juvenile overall survival distributions between habitats. The overall test was followed by pair-wise comparison tests.

5.4 Results

Condition indices

As expected for all three study species there was a significant effect of Sex on HSI an GSI, with females having higher HSI and GSI than males (Table 5.2). However, the main aim of this study was to investigate the difference in individuals' condition occupying three different habitats (natural, new design artificial reef, Reef Ball reef); therefore, significant effects of habitat were of primary interest.

Trachinops caudimaculatus

Generally, there was little difference in HSI, GSI and *W*rm of *T. caudimaculatus* between two habitats (new design artificial reef and natural reef) (Figure 5.1 a,b,c). There was a significant effect of Location on HIS; however, no effect of habitat. The was no significant difference in HSI and GSI between new design artificial reefs and natural reefs (Table 5.3, Figure 5.1 a,b). There was a significant two-way interaction: location x habitat for *W*rm, with individuals occupying new design artificial reefs at Frankston having ~10 % higher *W*rm than individuals occupying natural reefs. No significant difference in *W*rm of individuals from two different habitats were detected at Altona (Table 5.2, Table 5.3, Figure 5.1 c).

Trinorfolkia clarkei

By and large, individuals of *T. clarkei* from new design artificial reef exhibited better condition than individuals from other two habitats, in particularly at Frankston (Figure 5.1 d,e,f). There was a significant two-way interaction for HSI in 2014/2015 sampling season: location x habitat (Table 5.2). Individuals that occupied new design artificial reef at Frankston had ~40% higher HSI than natural reef. At Altona, however, individuals occupying new design artificial reef had HSI ~50% lower than individuals occupying the other two habitats (Table 5.3, Figure 5.1 d). There was no significant interaction for HSI in 2015/2016; however, there was a significant habitat effect (Table 5.2). At Frankston, there was no significant difference in individuals HSI between habitats; however, at Altona individuals occupying new design artificial reef had ~40% higher HSI than individuals occupying natural reef (Table 5.3, Figure 5.1 d). Variability in HSI of individuals occupying Reef Ball reef at Altona in 2015/2016 was very high, due to low replication (*n* = 2) to allow for any specific conclusions.

There was a significant two-way interaction for GSI: location x habitat (Table 5.2). At Frankston there was significant difference between all habitats, with natural reef individuals having the lowest GSI and new design artificial reef having the highest GSI, ~75 % higher than that on natural reefs and ~60 % higher than Reef Ball reefs (Table 5.3, Figure 5.1 e). At Altona the pattern was reversed with individuals occupying new design artificial reefs having GSI about 50% lower than that on Reef Ball reefs and natural reefs (Table 5.3, Figure 5.1 e).

There were two significant two-way interactions for *W*rm: year x habitat and location x habitat (Table 5.2). At Frankston in 2014/2015 *W*rm of individuals occupying new design artificial reef was ~10% higher than that of individuals occupying natural reef; however, an opposite trend was observed in 2015/2016 *W*rm of individuals on new design artificial reef was ~20% lower than that of individuals occupying the other two habitats. At Altona the trend was similar between two sampling years, with *W*rm of individuals occupying new design artificial reef being ~10% than that of individuals occupying natural reef (Table 5.3, Figure 5.1 f).

V. conspersa

In general, individuals of *V. conspersa* occupying Reef Ball reefs were in better condition than individuals occupying other two habitats (Figure 5.1 g, h, j). There was a significant two-way interaction for HSI: year x habitat (Table 5.2). There was no significant difference in HSI of individuals occupying three habitats in 2014/2015; however, in 2015/2016 HSI of individuals inhabiting Reef Ball reefs was ~35% higher than that of individuals from new design artificial reefs and ~20% higher than that of individuals from natural reefs (Table 5.3, Figure 5.1 g).

There was a significant effect of habitat for GSI (Table 5.2), with individuals occupying Reef Ball reefs having ~10-30% higher GSI than the individuals from the other two habitats (Table 5.3, Figure 5.1 h).

There was a significant two-way interaction for *W*rm: year x habitat (Table 5.2). In 2014/2015 individuals inhabiting new design artificial reefs had ~10% lower *W*rm than individuals from the other 2 habitats. In 2015/2016 there was no difference in *W*rm of individuals from new design artificial reefs and natural reefs; however, individuals from Reef Ball reefs had ~10% *W*rm (Table 5.3, Figure 5.1 j).

Table 5. 2 Results from univariate PERMANOVA on Euclidean distances to test for several fixed effects on HSI, GSI and *W*rm of *T. caudimaculatus*, *V. conspersa* and *T. clarkei*. For the analysis of HSI and GSI the fixed effects included into the model were Year (2014/2015 and 2015/2016 sampling season), Location (Frankston, Altona), Habitat (Natural reef, new design artificial reef, Reef Ball reef) and Sex (Male, Female) for all study species, with the exception of *T. caudimaculatus*, where data was available from only one year of sampling (2015/2016) and only from new design artificial reef and Natural reef. For the analysis of *W*rm all of the above fixed factors were included in the models with the exception of Sex, where Female and Male data was pooled together. Juveniles were excluded from the analysis of HSI and GSI for all study species, but included into the analysis of *W*rm. Sex was treated as a blocking factor and all interactions with Sex variable were excluded from all models. Due to missing data for *V. conspersa* Habitat x Location interaction and Year x Location x Habitat interaction were also excluded from all models. The test statistic (F*), a pseudo-F value, and the probability value (P†) were computed by the PERMANOVA routine with a maximum of 9,999 permutations under a reduced model. Sum of squares was Type III (partial) for all tests. HSI, GSI and *W*rm were log+1 transformed. For the analysis of the effects of fixed factor on HSI of *T. clarkei* separate tests were performed for both sampling years due to a significant three way interaction (Year x Location x Habitat). For Altona the data from both natural reefs was pooled for all study species.

Variable type	Source	df	SS	MS	F*	P†	Unique permutations
***T. caudimaculatus* HSI**	Location	1	0.2192	0.2192	6.0633	**0.0175**	9848
	Habitat	1	0.0062	0.0062	0.17019	0.6816	9832
	Sex	1	0.8622	0.8622	23.851	**0.0001**	9835
	Location x Habitat	1	0.00002	0.00002	0.0006	0.979	9830
	Error	52	1.8798	0.0362			
	Total	56	2.9122				
***T. caudimaculatus* GSI**	Location	1	0.1636	0.1636	3.7313	0.0585	9824
	Habitat	1	0.0515	0.0515	1.1748	0.2825	9817
	Sex	1	1.4769	1.4769	33.682	**0.0001**	9824
	Location x Habitat	1	0.014	0.014	0.31941	0.5731	9842
	Error	52	2.2802	0.0439			

	Total	56	4.0055				
T. caudimaculatus Wrm	Location	1	0.0009	0.0009	0.1068	0.7396	9818
	Habitat	1	0.0264	0.0264	3.2216	0.0796	9823
	Location x Habitat	1	0.0515	0.0515	6.2771	**0.0146**	9833
	Error	59	0.4836	0.0082			
	Total	62	0.6087				
***T. clarkei* HIS**	Year	1	0.0038	0.0038	0.0356	0.8529	9827
	Location	1	0.0124	0.0124	0.1171	0.7258	9824
	Habitat	2	0.4232	0.2116	2.0058	0.1295	9951
	Sex	1	8.2915	8.2915	78.6	**0.0001**	9845
	Year x Location	1	0.1235	0.1235	1.1703	0.2799	9830
	Year x Habitat	2	0.6022	0.3011	2.8544	0.058	9958
	Location x Habitat	2	0.9132	0.4566	4.3285	**0.0157**	9956
	Year x Location x Habitat	2	1.2296	0.6148	5.8278	**0.0027**	9948
	Error	214	22.575	0.1055			
	Total	226	35.47				
T. clarkei	Location	1	0.1413	0.1413	1.4671	0.219	9835

HIS	Habitat	2	0.0801	0.0401	0.416	0.6587	9939
2015	Sex	1	5.2256	5.2256	54.258	**0.0001**	9824
	Location x Habitat	2	1.6427	0.82135	8.5281	**0.0005**	9958
	Error	116	11.172	0.09631			
	Total	122	19.445				
T. clarkei	Location	1	0.0149	0.0149	0.12743	0.7242	9852
HIS	Habitat	2	1.0071	0.50355	4.3017	**0.0164**	9939
2016	Sex	1	3.1143	3.1143	26.605	**0.0001**	9839
	Location x Habitat	2	0.2335	0.11675	0.99738	0.3669	9944
	Error	97	11.355	0.11706			
	Total	103	15.95				
T. clarkei	Year	1	0.64328	0.64328	6.0594	**0.0154**	9837
GSI	Location	1	0.0207	0.0207	0.19497	0.6265	9842
	Habitat	2	0.9178	0.45891	4.3228	**0.0166**	9951
	Sex	1	18.659	18.659	175.76	**0.0001**	9850
	Year x Location	1	0.0052	0.0052	0.049	0.8318	9844
	Year x Habitat	2	0.3106	0.15532	1.4631	0.2311	9955
	Location x Habitat	2	6.7471	3.3736	31.778	**0.0001**	9961

	Year x Location x Habitat	2	0.4076	0.20381	1.9199	0.1517	9963
	Error	214	22.718	0.10616			
	Total	226	53.268				
T. clarkei	Year	1	0.00234	0.00234	0.089	0.7594	9809
Wrm	Location	1	0.0186	0.0186	0.70848	0.3886	9816
	Habitat	2	0.30703	0.15352	5.8493	**0.0083**	9941
	Year x Location	1	0.0878	0.0878	3.3459	0.0661	9803
	Year x Habitat	2	0.2585	0.12923	4.9238	**0.0129**	9930
	Location x Habitat	2	0.3946	0.19732	7.5181	**0.0046**	9935
	Year x Location x Habitat	2	0.066	0.033	1.2578	0.2753	9953
	Error	232	6.0889	0.0262			
	Total	243	7.4156				
V. conspersa	Year	1	0.0506	0.0506	2.1692	0.1396	9846
HSI	Location	1	0.2795	0.2795	11.976	**0.0008**	9841
	Habitat	2	0.2119	0.1059	4.539	**0.0134**	9943
	Sex	1	0.2494	0.2494	10.688	**0.001**	9827
	Year x Location	1	0.0153	0.0153	0.6562	0.4202	9830
	Year x Habitat	2	0.2281	0.1141	4.8877	**0.0098**	9953

	Error	115	2.6838	0.02334			
	Total	123	4.4609				
V. conspersa	Year	1	0.1125	0.1125	6.3112	**0.0111**	9847
GSI	Location	1	0.0314	0.0314	1.7641	0.1861	9799
	Habitat	2	0.1455	0.0727	4.0818	**0.0165**	9959
	Sex	1	8.2465	8.2465	462.79	**0.0001**	9834
	Year x Location	1	0.0096	0.0096	0.53723	0.4635	9850
	Year x Habitat	2	0.0658	0.0329	1.8463	0.1595	9957
	Error	115	2.0492	0.0178			
	Total	123	11.63				
V. conspersa	Year	1	0.0172	0.0172	1.2833	0.2595	9826
Wrm	Location	1	0.0049	0.0049	0.36487	0.5458	9849
	Habitat	2	0.10482	0.0524	3.9076	**0.023**	9957
	Year x Location	1	0.0085	0.0085	0.63359	0.4291	9840
	Year x Habitat	2	0.0867	0.0434	3.2339	**0.0408**	9958
	Error	128	1.7167	0.0134			
	Total	135	2.0656				

Table 5. 3 Results from pair-wise tests of univariate PERMANOVA on Euclidean distances to test for the fixed effect of Habitat (Natural reef, new design artificial reef, Reef Ball reef) on HSI, GSI and *W*rm from two Locations (Frankston and Altona) and both sampling years (2014/2015 and 2015/2016 sampling seasons) when applicable for all study species, with the exception of *T. caudimaculatus* when only the data from one sampling year (2015/2016) and only from new design artificial reef and Natural reef was available. The exact model used depended on the results of overall analysis of dependant variables for each of the three study species (Table 5.2). Footnotes: The test statistic (F*), a pseudo-F value, and the probability value ($P^{\dagger}$) were computed by the PERMANOVA routine with a maximum of 9,999 permutations under a reduced model. Sum of squares is Type III (partial) for all tests. HIS, GSI and *W*rm were log+1 transformed. The level of significance was set at 0.05. For Altona the data from both natural reefs was pooled for all study species.

Groups	t	P	Unique permutations	Groups	t	P	Unique permutations
***T. caudimaculatus W*rm** **Frankston**				***T. caudimaculatus W*rm** **Altona**			
New artificial reef x Natural	3.5647	**0.0013**	9833	New artificial reef x Natural	0.52277	0.6136	9399
***T. clarkei* 2014/2015 HIS** **Altona**				***T. clarkei* 2015/2016 HIS** **Altona**			
Natural x Reef Balls	0.68213	0.5089	9856	Natural x Reef Balls	0.57496	0.5086	527
Natural x New artificial reef	3.7031	**0.0004**	9832	Natural x New artificial reef	2.9303	**0.0071**	9838
New artificial reef x Reef Balls	2.3682	**0.0235**	9822	New artificial reef x Reef Balls	1.2395	0.2137	190
***T. clarkei* 2014/2015 HIS** **Frankston**				***T. clarkei* 2015/2016 HIS** **Frankston**			
Natural x Reef Balls	1.4202	0.1571	9845	Natural x Reef Balls	1.1427	0.2611	9853
Natural x New artificial reef	2.8087	**0.0085**	9844	Natural x New artificial reef	1.5008	0.1409	9838
New artificial reef x Reef Balls	1.2039	0.2394	9845	New artificial reef x Reef Balls	0.69365	0.4903	9826

T. clarkei **GSI** **Altona**				***T. clarkei*** **GSI** **Frankston**			
Natural x Reef Balls	0.51269	0.6173	9817	Natural x Reef Balls	2.2979	**0.024**	9817
Natural x New artificial reef	3.5411	**0.0006**	9836	Natural x New artificial reef	5.1192	**0.0001**	9831
New artificial reef x Reef Balls	1.962	0.0519	9831	New artificial reef x Reef Balls	3.3367	**0.0012**	9829
T. clarkei **2014/2015** ***W*****rm** **Frankston**				***T. clarkei*** **2015/2016** ***W*****rm** **Frankston**			
Natural x Reef Balls	2.6079	**0.0108**	9842	Natural x Reef Balls	1.3267	0.1959	9854
Natural x New artificial reef	2.3327	**0.0258**	9835	Natural x New artificial reef	2.7084	**0.0059**	9869
New artificial reef x Reef Balls	0.41106	0.6875	9837	New artificial reef x Reef Balls	2.0473	**0.0458**	9854
T. clarkei **2014/2015** ***W*****rm** **Altona**				***T. clarkei*** **2015/2016** ***W*****rm** **Altona**			
Natural x Reef Balls	1.9485	0.0531	9830	Natural x Reef Balls	1.0346	0.2749	**561**
Natural x New artificial reef	3.6575	**0.0005**	9828	Natural x New artificial reef	1.9924	**0.0491**	9853
New artificial reef x Reef Balls	5.08	**0.0001**	9834	New artificial reef x Reef Balls	0.24813	0.8562	**231**
V. conspersa **2014/2015 HSI**				***V. conspersa*** **2015/2016 HSI**			
Natural x Reef Balls	0.57967	0.5679	9838	Natural x Reef Balls	3.6684	**0.0008**	9850
Natural x New artificial reef	0.39653	0.6856	9819	Natural x New artificial reef	2.7949	**0.0057**	9852
New artificial reef x Reef Balls	0.3484	0.7316	9850	New artificial reef x Reef Balls	8.4745	**0.0001**	9835

V. conspersa* 2014/2015 *Wrm				***V. conspersa* 2015/2016 *Wrm***			
Natural x Reef Balls	0.4076	0.689	9823	Natural x Reef Balls	2.862	**0.0069**	9829
Natural x New artificial reef	2.9929	**0.0046**	9839	Natural x New artificial reef	0.5662	0.5823	9847
New artificial reef x Reef Balls	1.869	0.0701	9831	New artificial reef x Reef Balls	3.1313	**0.0035**	9829
***V. conspersa* GSI**							
Natural x Reef Balls	1.789	0.0923	9810				
Natural x New artificial reef	1.4515	0.1491	9841				
New artificial reef x Reef Balls	2.201	**0.0336**	9837				

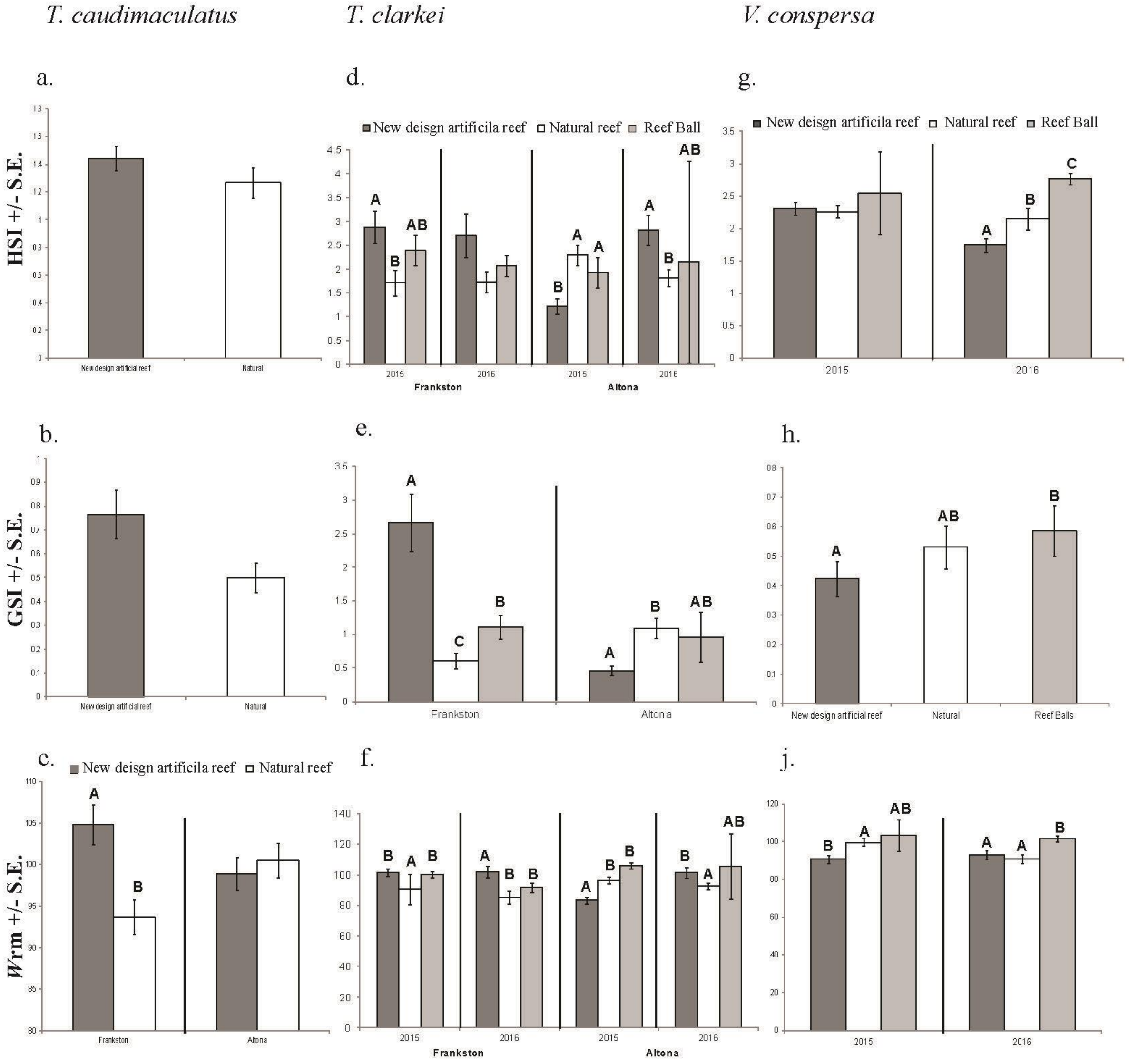


Fig. 5.1 HSI, GSI and *W*rm of three study species (*Trachinops caudimaculatus*, *Trinorfolkia clarkei*, *V. conspersa*) over 2 recruitment seasons on three habitats (Reef Ball reef, natural reef and new design artificial reef) at two locations (Frankston and Altona). **Note:** *T. caudimaculatus* individuals were only collected during 2015/2016 recruitment season.

Mortality rates

Population census

There was a significant effect of habitat only for instantaneous mortality rates of combined juveniles and recruits of *Trachinops caudimaculatus*, with Reef Ball reefs having nine times higher mortality rates than the other two habitats (Table 5.4, Figure 5.2).

Table 5. 4 Least square fit one-way ANOVA & Tuckey's HD post hoc test of the instantaneous mortality rates of combined new recruits and juveniles of *T. caudimaculatus.*

ANOVA

Source	DF	Sum of Squares	F Ratio	p
Year	1	0.5583	0.5701	0.4676
Location	2	0.8411	0.4294	0.6623
Habitat	2	11.1446	5.6899	**0.0224**

Tuckey's HD

Level		Least Sq Mean
Reef Ball reefs	A	- 2.7404
New design artificial reefs	B	- 4.651
Natural reefs	B	- 4.7681

Levels not connected by the same letter are significantly different at 0.05 level.

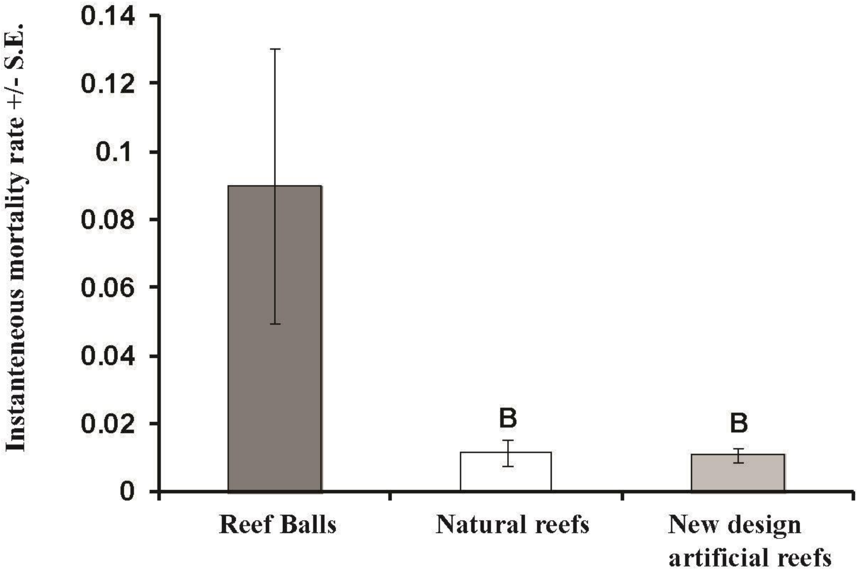


Fig. 5.2 Instantaneous mortality rates of combined juveniles and recruits of *T. caudimaculatus* from three habitats (Reef Ball reef, natural reef and new design artificial reef) at Frankston, Port Phillip Bay, Victoria, Australia.

VIE tagging

The initial trajectories of survival distributions from all 3 habitats were similar to one another with the first census losses ranging from 38 to 50%. However, by the 13th day post tagging only 6.8% of tagged juveniles were recovered from Reef Ball reef, compared to 22.2% and 34.6% recovered from natural reef and new design artificial reef respectively (Figure 5.3). There was a significant difference in the survival distributions between three habitats ($\chi^2 = 6.4$, $p = 0.041$). The survival of individuals was significantly higher on new design artificial reef in comparison to Reef Ball reef ($\chi^2 = 6.531$, $p = 0.011$); however, there was no significant difference in survival distributions of Reef Ball reef and natural reef ($\chi^2 = 0.601$, $p = 0.438$) and new design artificial reef and natural reef ($\chi^2 = 2.053$, $p = 0.152$).

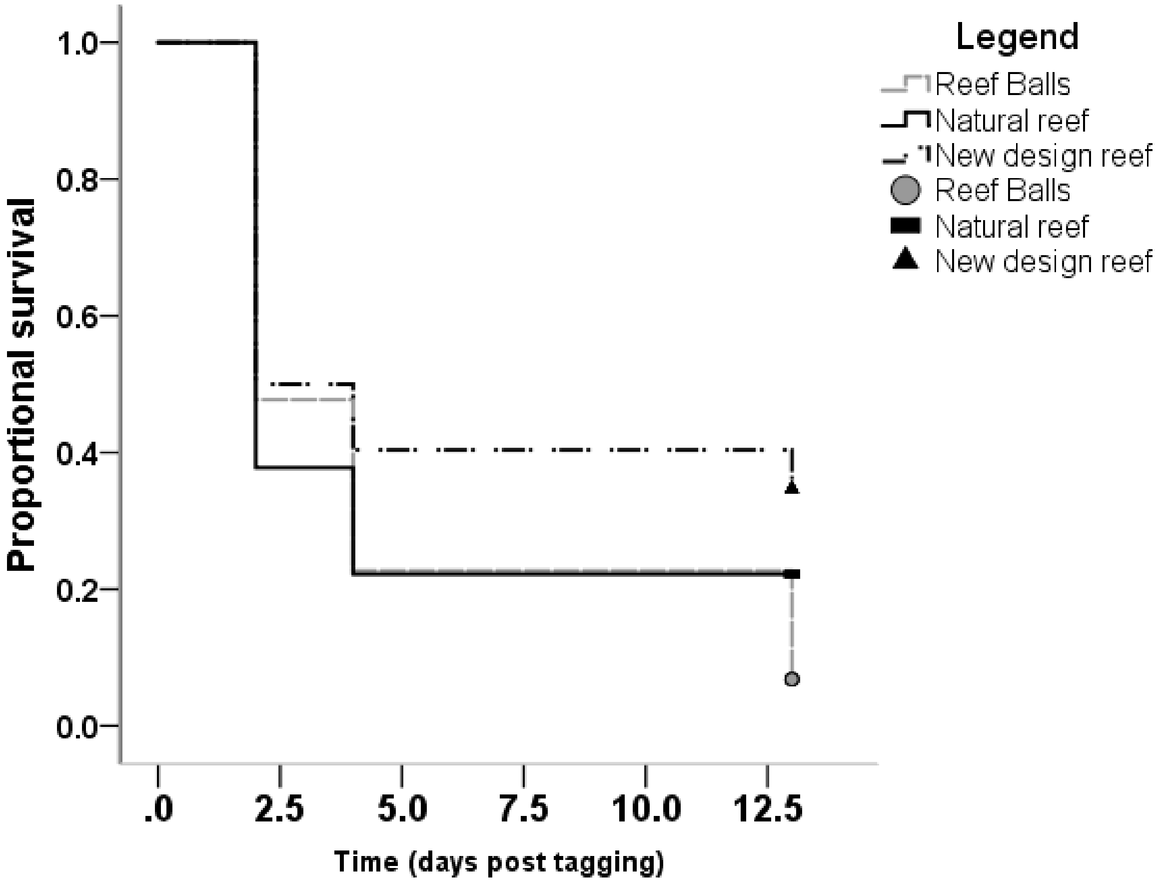


Fig. 5.3 Kaplan–Meier survival trajectories for young juveniles from Reef Ball reef (grey dashed line and grey circle, n = 44), natural reef (black solid line and black rectangular, n = 45) and new design artificial reef (black dashed line and black triangle, *n* = 52).

5.5 Discussion

The fitness responses of individuals varied according to specie and habitat type. The condition of *Trachinops caudimaculatus* differed little for the different habitats examined. However, the mortality of the new recruits was greatest on Reef Ball reefs than the other two habitats. The experiments presented in Chapter 4 (Table 5.5) demonstrated some habitat preference of *T. caudimaculatus* for Reef Ball reefs, making this the first study to demonstrate ecological trap formation in the marine environment. If indeed *T. caudimaculatus* is more attracted to large Reef Ball reefs as new recruits and they suffer high mortality rates on these reefs, then Reef Ball reefs would act as a severe ecological trap for this fish species and pose a serious threat to population maintenance (Schlaepfer *et al.*, 2002; Battin, 2004; Robertson and Hutto, 2006; Hale *et al.*, 2015; Hale and Swearer, 2016). While *T. caudimaculatus* is a small reef fish, they are an important food source for many other fish and invertebrate species and a population decline may negatively affect many animal communities in Port Phillip Bay (Ford and Swearer, 2013a).

A different response was observed for *Vincentia conspersa* where individuals were in significantly better condition when occupying Reef Ball reefs. *V. conspersa* is mostly a habitat generalist. However, it exhibited a small habitat preference for Reef Ball reefs (Chapter 4, Table 5.5). This response may be an example of an adaptive habitat selection. An adaptive habitat selection has been frequently demonstrated previously, when species were specialising in some habitat types that lead to lower mortality outcomes or improved condition due to reduced competition or predation (Morris, 2003; Morris, 2004). Adaptive habitat selection is an important evolutionary driver responsible for specialisation, adaptive radiation and persistence of different species in a constantly changing environment (Morris, 2003; Morris, 2004). An ability to adapt and recognise the negative or positive consequences of human-modified or -introduced habitats may be detrimental to the survival of some species.

A converse response to different habitat types was displayed by *Trinorfolkia clarkei*. Generally, *T. clarkei* individuals were in significantly better condition on artificial reefs compared with natural reefs, especially on new design artificial reefs. This species also did not demonstrate any habitat preferences, likely as it is a habitat (Chapter 4, Table 5.5, Baker *et al.*, 2008; Gomon *et al.*, 2008). This may indicate the possible formation of a perceptual trap for this fish species due to the introduction of an artificial habitat. If, in the case of ecological traps, an individual preferentially (or with equal preference) selects a poor

Table 5. 5 Summary of the habitat selection (Chapter 4) and fitness outcomes for the three study species: *T. caudimaculatus*, *V. conspersa* and *T. clarkei.*

	HSI	**GSI**	***W*rm**	**Survival**	**Habitat selection & recruitment**	**General conclusion**
T. caudimaculatus	No effect	No effect	Context dependant. Location driven. At Frankston highest *W*rm on new design artificial reef.	Highest mortality on Reef Ball reef.	Reef Ball reef - preferred habitat (lab). Highest recruitment on natural reef (field).	Evidence for ecological trap.
V. conspersa	Context dependant. Driven by year. In 2016 highest HSI on Reef Ball reef.	Highest GSI on Reef Ball reefs.	Highest *W*rm on Reef Ball reefs.	No data	Generalist. At Frankston highest recruitment to Reef Ball reef.	Evidence for adaptive habitat selection.
T. clarkei	Context dependant. Driven by year and location. Generally highest HSI on new design artificial reefs.	Context dependant. Driven by location. Highest GSI at Frankston on new design artificial reef. At Altona on Reef Ball reef and natural reefs.	Context dependant. Driven by year and location. Generally highest *W*rm on new design artificial reef.	No data	Generalist.	Evidence for perceptual trap.

quality habitat that leads to lower fitness; in perceptual trap theory, an individual avoids (or does not exhibit a preference) for a habitat that leads to improved fitness (Battin, 2004; Gilroy and Sutherland, 2007). Perceptual traps may lead to the reduction or total loss of positive outcomes of management strategies that rely on the introduction of new artificial habitats for species conservation and habitat restoration, meaning individuals may avoid high quality habitat that have been improved through conservation efforts. Consequently, significant financial losses and decline of stakeholder support may result due to the lack or insignificance of expected positive effects.

The different responses of each fish species to the three habitat types may be attributed to the ecology of each fish species. *Trachinops caudimaculatus* is a shoaling, diurnal, planktivorous fish species. Their fitness has been associated with density dependent effects, as well as availability of the refuge sites (Ford and Swearer, 2013a; Ford and Swearer, 2013b). While this species exhibits positive density-dependent effects due to its shoaling behaviour, these effects may be reversed once densities reach certain thresholds (Ford and Swearer, 2013a; Ford and Swearer, 2013b). Increased habitat complexity may reduce competition (Hixon and Menge, 1991; Almany, 2004), hence diminishing negative density-dependent effects at high densities (Ford and Swearer, 2013a; Ford and Swearer, 2013b). Moreover, Ford *et al.* (2016) showed that habitat quality may be the major predictor of the survival of this fish species. The present results do not contradict previous findings. Generally, individuals were in better condition on reefs with lower densities (new design reefs) and the highest survival rates were observed on structurally more complex habitats with good vertical relief (new design reefs and natural reef). Potentially, the cave-like appearance of Reef Ball reefs may appear attractive to both *T. caudimaculatus* and another shoaling species, *V. conspersa*. However, the less structurally complex Reef Ball reefs lead to high mortality rates for small, diurnal *T. caudimaculatus*. As *T. caudimaculatus* needs to catch plankton and hence spends more time in the water column, it may put individuals in the realm of pelagic predators. As their densities decline, *Trachinops caudimaculatus* tend to shoal less and spend more time inside the habitat, they may be more exposed to benthic predators and also receive lower nutrition due to reduced hunting ability (Milinski, 1993; Ford and Swearer, 2013a). These effects are particularly severe on habitats with reduced shelter and shoaling behaviour has been shown to be less beneficial for survival of this species on isolated patch reefs (Osenberg *et al.*, 2002a; White *et al.*, 2010; Ford and Swearer, 2013b), such as Reef Ball reefs. Conversely, *V. conspersa* is larger and may be less affected by benthic predators while hiding inside the habitat. They are also nocturnal and may feed more effectively during this time (Kinloch *et al.*, 2007). It appears that large cave structure of the Reef Ball reefs is beneficial for the fitness of individuals of this species, which they recognise and use. Moreover, Reef Ball reefs are two years older than new design artificial reefs; and therefore, had a more established benthic community, which might have provided better camouflage and food sources for the predatory *V. conspersa*, leading to improved fitness. There was small evidence of improvement in fitness of individuals occupying new design artificial reefs over time, which may suggest that the observed difference in fitness of individuals of this species between three habitats may dissipate or invert as benthic communities develop of younger reefs.

Trinorfolkia clarkei, as most Tripterygiidae, is a small, site-attached and highly territorial fish species (Feary and Clements, 2006; Wellenreuther *et al.*, 2007; Baker *et al.*, 2008; Edgar, 2008; Gomon *et al.*, 2008). Their territorial nature may influence their habitat selection and be the primary reason for their inability to preferentially select a highly suitable habitat. *T. clarkei* clearly demonstrated improved condition when occupying new design artificial reefs over time, which may be attributed to the formation and potential diversification of the benthic community on these new reefs. Again, these effects may be specific to the ecology of this particular species, being a highly benthic associated predator; and therefore, dependent on the benthic community for shelter and camouflage (Feary and Clements, 2006; Wellenreuther *et al.*, 2007; Baker *et al.*, 2008; Edgar, 2008; Gomon *et al.*, 2008). The enhancement in cover of benthic organisms over time may contribute to more successful predation and, hence, improved individual condition .

Both *Trachinops caudimaculatus* and *Trinorfolkia clarkei* also displayed a location effect. In locations where higher quality natural reefs were located (Frankston), individuals displayed better condition on new design artificial reef than other habitats. These effects may be density-dependent, with good quality natural reefs being the most attractive habitats, leading to high fish densities in general and high densities of studied species specifically. Therefore, additional highly complex new habitat that does not yet support particularly high densities (being new) leads to improved individual fitness. The close proximity of a good quality natural reef (being larger and "noisier"; and therefore, more attractive) may contribute to higher detectability of these new habitats. These effects, however, may decline over time as the densities of the individuals grow on small artificial reefs.

My results indicate that individual responses to different types of artificial habitats are greatly species-, location- and habitat-specific. This is the first study to demonstrate the formation of ecological traps in the marine environment for at least one of the studied species. However, artificial reefs may have positive and negative effects on fish populations depending on the species in question and the surrounding environment. These effects may also differ between artificial reef types. Generally, more complex artificial reefs would more likely have positive effects on fish populations. However, they may not possess the necessary cues for the individuals of some species to recognise their value, leading to the formation of undervalued resources, also known as perceptual traps. Furthermore, the design or size of some artificial reefs may be ecologically insufficient to lead to positive management outcomes. Due to high habitat specialisation of many marine fish species (Munday *et al.*, 1997; Bean *et al.*, 2002; Munday, 2004; Gardiner and Jones, 2005; Wellenreuther *et al.*, 2007; Wilson *et al.*, 2008), singular artificial reef design used in one area may be insufficient and less effective than a mixed artificial reef that combines multiple artificial reef designs. As for the selection of suitable sites for marine protected areas, it is vital to consider the condition, size and structure of the adjacent natural reef and also general habitat availability. Natural reefs may be more attractive habitats due to their size, and already established benthic and fish community. However, these natural reefs may be less suitable in some locations due to lower complexity or high numbers of competitors. In these areas, well designed artificial reefs may be particularly beneficial. When habitat is limiting and/or of poor quality due to degradation, an addition of any type of artificial structure may lead to some increase in fish abundances and even diversity. However, with high levels of overfishing in most areas where artificial structures are generally introduced, the habitat is rarely limiting (Jackson *et al.*, 2001; Halpern *et al.*, 2008; Jackson, 2008). If artificial reefs become more attractive than natural reefs but lead to lower fitness advantages, their effect on fish communities may be devastating, causing a reduction in some species abundances and potential local species extinction. Placement of artificial reefs in the marine environment must lead to the improvement of the available habitat and they must function as closely as possible to natural, non-degraded local reefs.

Artificial reefs are excellent management tools of degraded habitats, recreational fisheries and for fish species conservation. However, poorly designed or poorly placed artificial reefs may lead to insufficient positive outcomes or even significant negative impacts on marine communities. Combined with their high costs, these effects may in turn lead to wasted resources and negative attitude of local communities to the new artificial reef placements, which in turn could impede further management and conservation efforts. All marine infrastructure functions as artificial reefs; and therefore, particular attention must be paid to the design and placement of these underwater constructions. With the spread of marine infrastructure and coastal hardening, commonly known as "ocean sprawl", and worldwide loss of natural habitats (Duarte *et al.*, 2013; Heery *et al.*, 2016), it is vital to investigate the species-specific habitat needs and consider these requirements in designs and placement of artificial reefs.

5.6 References

Almany, G. R. (2004) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos*, 106(2), 275-284.

Anderson, M. J., Gorley, R. N. and R, C. K. (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods. *PRIMER-E Ltd: Plymouth, UK.*

Baine, M. (2001) Artificial reefs: a review of their design, application, management and performance. *Ocean & Coastal Management*, 44(3–4), 241-259.

Baker, J., Shepherd, S., Brown, A., Crawford, H. and Muirhead, D. (2008) Uncommon and cryptic reef fishes: results of pilot surveys along Fleurieu Peninsula, Report for Adelaide and Mt Lofty Ranges Natural Resources Management Board.

Battin, J. (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, 18(6), 1482-1491.

Bean, K., Jones, G. P. and Caley, M. J. (2002) Relationships among distribution, abundance and microhabitat specialisation in a guild of coral reef triggerfish (family Balistidae). *Marine Ecology-Progress Series*, 233, 263-272.

Behrents, K. C. (1987) The influence of shelter availability on recruitment and early juvenile survivorship of *Lythrypnus dalli* Gilbert (Pisces: Gobiidae). *Journal of Experimental Marine Biology and Ecology*, 107(1), 45-59.

Branden, K. L., Pollard, D. A. and Reimers, H. A. (1994) A review of recent artificial reef developments in Australia. *Bulletin of Marine Science*, 55(2-3), 982-994.

Brickhill, M. J., Lee, S. Y. and Connolly, R. M. (2005) Fishes associated with artificial reefs: attributing changes to attraction or production using novel approaches. *Journal of Fish Biology*, 67, 53-71.

Campbell, M. D., Rose, K., Boswell, K. and Cowan, J. (2011) Individual-based modeling of an artificial reef fish community: effects of habitat quantity and degree of refuge. *Ecological Modelling*, 222(23–24), 3895-3909.

Carr, M. H. and Hixon, M. A. (1997) Artificial reefs: the importance of comparisons with natural reefs. *Fisheries*, 22(4), 28-33.

Caselle, J. E. (1999) Early post-settlement mortality in a coral reef fish and its effect on local population size. *Ecological Monographs*, 69(2), 177-194.

Clarke, K. R. and Gorley, R. N. (2006) *PRIMER V6: user manual-tutorial*, Plymouth Marine Laboratory.

Dafforn, K. A., Mayer-Pinto, M., Morris, R. L. and Waltham, N. J. (2015) Application of management tools to integrate ecological principles with the design of marine infrastructure. *Journal of Environmental Management*, 158, 61-73.

Dempster, T., Sanchez-Jerez, P., Fernandez-Jover, D., Bayle-Sempere, J., Nilsen, R., Bjørn, P.-A. and Uglem, I. (2011) Proxy measures of fitness suggest coastal fish farms can act as population sources and not ecological traps for wild gadoid fish. *PLoS ONE*, 6(1), e15646.

Doherty, P. J., Dufour, V., Galzin, R., Hixon, M. A., Meekan, M. G. and Planes, S. (2004) High mortality during settlement is a population bottleneck for a tropical surgeonfish. *Ecology*, 85(9), 2422-2428.

Duarte, C. M., Pitt, K. A., Lucas, C. H., Purcell, J. E., Uye, S.-i., Robinson, K., Brotz, L., Decker, M. B., Sutherland, K. R. and Malej, A. (2013) Is global ocean sprawl a cause of jellyfish blooms? *Frontiers in Ecology and the Environment*, 11(2), 91-97.

Edgar, G. J. (2008) Australian marine life: the plants and animals of temperate waters. 2nd ed. *New Holland Publishers, Sydney*.

Fabi, G., Spagnolo, A., Bellan-Santini, D., Charbonnel, E., Çiçek, B. A., García, J. J. G., Jensen, A. C., Kallianiotis, A. and Santos, M. N. d. (2011) Overview on artificial reefs in Europe. *Brazilian Journal of Oceanography*, 59, 155-166.

Feary, D. and Clements, K. (2006) Habitat use by triplefin species (Tripterygiidae) on rocky reefs in New Zealand. *Journal of Fish Biology*, 69(4), 1031-1046.

Firth, L. B., Knights, A. M., Thompson, R., Mieszkowska, N., Bridger, D., Evans, A., Moore, P., O’Connor, N., Sheehan, E. and Hawkins, S. (2016) Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. *Oceanogr. Mar. Biol. Ann. Rev*.

Ford, J. R., Shima, J. S. and Swearer, S. E. (2016) Interactive effects of shelter and conspecific density shape mortality, growth, and condition in juvenile reef fish. *Ecology*, 97(6), 1373-1380.

Ford, J. R. and Swearer, S. E. (2013a) Shoaling behaviour enhances risk of predation from multiple predator guilds in a marine fish. *Oecologia*, 172(2), 387-397.

Ford, J. R. and Swearer, S. E. (2013b) Two's company, three's a crowd: Food and shelter limitation outweigh the benefits of group living in a shoaling fish. *Ecology*, 94(5), 1069-1077.

Fowler, A. M. and Booth, D. J. (2012) How well do sunken vessels approximate fish assemblages on coral reefs? Conservation implications of vessel-reef deployments. *Marine Biology*, 159(12), 2787-2796.

Froese, R. (2006) Cube law, condition factor and weight–length relationships: history, meta- analysis and recommendations. *Journal of Applied Ichthyology*, 22, 241–253.

Gardiner, N. M. and Jones, G. P. (2005) Habitat specialisation and overlap in a guild of coral reef cardinalfishes (Apogonidae). *Marine Ecology Progress Series,* 305, 163-175.

Gilroy, J. J. and Sutherland, W. J. (2007) Beyond ecological traps: perceptual errors and undervalued resources. *Trends in Ecology & Evolution*, 22(7), 351-356.

Gomon, M. F., Bray, D. J. and Kuiter, R. H. (2008) *Fishes of Australia's southern coasts / edited by Martin Gomon, Diane Bray, Rudie Kuiter*, Reed New Holland, Musuem Victoria, Chatswood, N.S.W.

Grove, R. S., Sonu, C. J. and Nakamura, M. (1991) 4 - Design and engineering of manufactured habitats for fisheries enhancement A2 - Seaman, William. In *Artificial habitats for marine and freshwater fisheries* (Ed. L. M. Sprague), Academic Press, San Diego, pp. 109-152.

Hackradt, C. W., Félix-Hackradt, F. C. and García-Charton, J. A. (2011) Influence of habitat structure on fish assemblage of an artificial reef in southern Brazil. *Marine Environmental Research*, 72(5), 235-247.

Hale, R. and Swearer, S. E. (2016) Ecological traps: current evidence and future directions. *Proceedings of the Royal Society B: Biological Sciences*, 283(1824).

Hale, R., Treml, E. A. and Swearer, S. E. (2015) Evaluating the metapopulation consequences of ecological traps. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1804), 20142930.

Hallier, J. and Gaertner, D. (2008) Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Marine Ecology Progress Series*, 353, 255-264.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R. and Watson, R. (2008) A global map of human impact on marine ecosystems. *Science*, 319(5865), 948-952.

Heery, E., Bishop, M., Critchley, L., Bugnot, A., Airoldi, L., Mayer-Pinto, M., Sheehan, E., Coleman, R., Loke, L. and Johnston, E. (2016) Identifying the consequences of ocean sprawl for sedimentary habitats. *Journal of Experimental Marine Biology and Ecology*.

Hixon, M. A. and Beets, J. P. (1989) Shelter characteristics and caribbean fish assemblages: experiments with artificial reefs. *Bulletin of Marine Science*, 44(2), 666-680.

Hixon, M. A. and Beets, J. P. (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs*, 63(1), 77-101.

Hixon, M. A. and Menge, B. A. (1991) Species diversity: prey refuges modify the interactive effects of predation and competition. *Theoretical Population Biology*, 39(2), 178-200.

Hoey, A. S. and McCormick, M. I. (2004) Selective predation for low body condition at the larval-juvenile transition of a coral reef fish. *Oecologia*, 139(1), 23-29.

Jackson, J. B. C. (2008) Ecological extinction and evolution in the brave new ocean. *Proceedings of the National Academy of Sciences*, 105(Supplement 1), 11458-11465.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. and Warner, R. R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293(5530), 629-637.

Jan, R.-Q., Liu, Y.-H., Chen, C.-Y., Wang, M.-C., Song, G.-S., Lin, H.-C. and Shao, K.-T. (2003) Effects of pile size of artificial reefs on the standing stocks of fishes. *Fisheries Research*, 63(3), 327-337.

Kheawwongjan, A. and Kim, D.-S. (2012) Present status and prospects of artificial reefs in Thailand. *Ocean & Coastal Management*, 57, 21-33.

Kingsford, M. J., Leis, J. M., Shanks, A., Lindeman, K. C., Morgan, S. G. and Pineda, J. (2002) Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science*, 70(1), 309-340.

Kinloch, M., Brock, D., Kirkman, H. and Laperousaz, T. (2007) Seagrass biodiversity on Kangaroo Island. *Report No. CMP07/004, Kangaroo Island Natural Resources Management Board Coast and Marine Program, Adelaide*.

Kristan, I. I. I. W. B. (2003) The role of habitat selection behavior in population dynamics: source–sink systems and ecological traps. *Oikos*, 103(3), 457-468.

McArdle, B. H. and Anderson, M. J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, 82(1), 290-297.

Milinski, M. (1993) Predation risk and feeding behaviour. *Behaviour of teleost fishes*, 285-305.

Morris, D. W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, 136(1), 1-13.

Morris, D. W. (2004) Some crucial consequences of adaptive habitat selection by predators and prey: apparent mutualisms, competitive ghosts, habitat abandonment, and spatial structure. *Israel Journal of Zoology*, 50(2-3), 207-232.

Munday, P. L. (2004) Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biology*, 10(10), 1642-1647.

Munday, P. L., Jones, G. P. and Caley, M. J. (1997) Habitat specialisation and the distribution and abundance of coral-dwelling gobies. *Marine Ecology Progress Series*, 152, 227-239.

Osenberg, C. W., St. Mary, C. M., Schmitt, R. J., Holbrook, S. J., Chesson, P. and Byrne, B. (2002a) Rethinking ecological inference: density dependence in reef fishes. *Ecology Letters*, 5(6), 715-721.

Osenberg, C. W., St. Mary, C. M., Wilson, J. A. and Lindberg, W. J. (2002b) A quantitative framework to evaluate the attraction–production controversy. *ICES Journal of Marine Science: Journal du Conseil*, 59(suppl), S214-S221.

Page, H. M., Dugan, J. E., Schroeder, D. M., Nishimoto, M. M., Love, M. S. and Hoesterey, J. C. (2007) Trophic links and condition of a temperate reef fish: comparisons among offshore oil platform and natural reef habitats. *Marine Ecology Progress Series*, 344, 245-256.

Pickering, H. and Whitmarsh, D. (1997) Artificial reefs and fisheries exploitation: a review of the ‘attraction versus production’ debate, the influence of design and its significance for policy. *Fisheries Research*, 31(1), 39-59.

Reubens, J. T., Vandendriessche, S., Zenner, A. N., Degraer, S. and Vincx, M. (2013) Offshore wind farms as productive sites or ecological traps for gadoid fishes? – Impact on growth, condition index and diet composition. *Marine Environmental Research*, 90(0), 66-74.

Robertson, B. A. and Hutto, R. L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, 87(5), 1075-1085.

Schlaepfer, M. A., Runge, M. C. and Sherman, P. W. (2002) Ecological and evolutionary traps. *Trends in Ecology & Evolution*, 17(10), 474-480.

Seaman Jr, W. and Sprague, L. M. (1991) 1 - Artificial habitat practices in aquatic systems. In *Artificial habitats for marine and freshwater fisheries*, Academic Press, San Diego, pp. 1-29.

Seto, K. C., Güneralp, B. and Hutyra, L. R. (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, 109(40), 16083-16088.

Sherman, R. L., Gilliam, D. S. and Spieler, R. E. (2002) Artificial reef design: void space, complexity, and attractants. *ICES Journal of Marine Science: Journal du Conseil*, 59(suppl), S196-S200.

Sih, A. (2013) Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour*, 85(5), 1077-1088.

Sih, A., Ferrari, M. C. O. and Harris, D. J. (2011) Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, 4(2), 367-387.

Stunz, G. W. and Minello, T. J. (2001) Habitat-related predation on juvenile wild-caught and hatchery-reared red drum *Sciaenops ocellatus* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, 260(1), 13-25.

Thierry, J.-M. (1988) Artificial reefs in Japan — a general outline. *Aquacultural Engineering*, 7(5), 321-348.

Wellenreuther, M., Barrett, P. T. and Clements, K. D. (2007) Ecological diversification in habitat use by subtidal triplefin fishes (Tripterygiidae). *Marine Ecology Progress Series*, 330, 235-246.

White, J. W., Samhouri, J. F., Stier, A. C., Wormald, C. L., Hamilton, S. L. and Sandin, S. A. (2010) Synthesizing mechanisms of density dependence in reef fishes: behavior, habitat configuration, and observational scale. *Ecology*, 91(7), 1949-1961.

Wilson, S. K., Burgess, S. C., Cheal, A. J., Emslie, M., Fisher, R., Miller, I., Polunin, N. V. and Sweatman, H. (2008) Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology*, 77(2), 220-228.

CHAPTER SIX:
General discussion

Young *D. nicthemerus* occupying Reef Ball reef at Frankston, Port Philip Bay, Victoria, Australia

6.1 Artificial reefs as fish habitat

As human populations continue to grow, the effects of human-induced rapid environmental change (HIREC) are expected to become more prominent and severe (Bos *et al.*, 1992; Halpern *et al.*, 2008; Seto *et al.*, 2012; Sih, 2013). Coastal hardening and the introduction of new artificial structures to marine environments (e.g. wave and wind power generators, oil and gas platforms, fish farms) are also likely to continue to increase (Halpern *et al.*, 2008; Firth *et al.*, 2016). Moreover, with the spread of habitat loss and degradation, either directly through human activities such as marine construction or bottom trawling, or through indirect effects of climate change (e.g. loss of coral cover due to bleaching), specially designed artificial reefs may become a useful management tool for restoring habitats and conserving marine species. Similarly, declines in fisheries yields may require the use of artificial reefs to attract fish to improve small fisheries, or to redirect fishing pressure from vulnerable areas (Bohnsack and Sutherland, 1985; Chou, 1997; Baine, 2001; Claudet and Pelletier, 2004; Fabi *et al.*, 2011). Therefore, it is crucial that we understand the consequences of introducing artificial reefs to the marine environment, their precise function (e.g. shore protection, habitat restoration etc.), and aim to design artificial reefs to maximise their performance and specific purpose.

I present in this thesis a detailed examination of how two artificial reef types provide reef fish habitat, as well as a comprehensive investigation into the potential formation of ecological traps due to artificial reef deployment. This is the first study to my knowledge that demonstrates the formation of an ecological trap in the marine environment. My thesis also clearly reveals the complexity and variety of the effects that artificial reef deployment can have on fish communities, which I've shown is highly location-, species- and time post-deployment dependent.

Generally speaking, Reef Ball reefs supported fish communities that were 20% more rich than those at natural reefs, with the exception of large continuous natural reefs. However, large continuous natural reefs supported over 70% higher fish densities than Reef Ball reefs and small, low laying boulder field natural reefs (Chapter 2). Reef Ball reefs were more similar in fish community structure to small, low laying boulder field natural reefs than to large continuous natural reefs, even though there were large differences in fish community structure across all locations and habitats (Chapter 2). Similar patterns were observed when Reef Ball reefs, adjacent natural reefs and new design artificial reefs were monitored for two sampling seasons after the deployment of new design artificial reefs (Chapter 3). Natural reefs supported significantly higher fish densities than either of the two artificial habitats over time (Chapter 3). However, the differences between Reef Ball reefs and natural reefs in fish species richness were much lower than the differences with new design artificial reefs. New design artificial reefs supported more than twice as many fish species than natural reefs or Reef Ball reefs (Chapter 3). These results are partially consistent with several previous studies. For example, Wilhelmsson *et al.* (1998) investigated differences in fish communities between natural reefs and an artificially constructed mound of dead coral heads, and natural reefs and two shipwrecks, and found higher fish density and species richness on most artificial reefs relative to natural reefs. Folpp *et al.* (2013) documented fish community structure at natural reefs, sand flats and Reef Ball artificial reefs, and reported similar findings. Moreover, studies comparing fish communities between natural and artificial reefs commonly report differences in trophic and community structure between habitats (Hackradt *et al.*, 2011; Simon *et al.*, 2011; Folpp *et al.*, 2013; Simon *et al.*, 2013), with few identifying no differences (Carr and Hixon, 1997). Variability in the results of these comparative studies may be attributed to differences in reef size, distance between study sites, isolation, reef age, geographic location and the study species in question (Milon, 1989; Carr and Hixon, 1997;

Seaman and Jensen, 2000; Baine, 2001). In the Wilhelmsson *et al.* (1998) study, the two artificial reefs that exhibited higher species richness and density compared to nearby (within 50 m) natural reefs were of two different types (shipwreck and mound of dead coral) and were established between eight and ten years prior to the study. The third artificial reef was also a shipwreck, established only two years prior to the study, and did not show such distinct differences in fish community composition (Wilhelmsson *et al.*, 1998). In my study, there was an increase in fish species richness supported by the new design artificial reef within the first three months post deployment. Moreover, the similarity between fish communities on new design artificial reefs and natural reefs also increased over time (Chapter 3). Conversely, the general pattern in fish community structure for Reef Ball reefs remained relatively consistent throughout the survey period. In Folpp *et al.* (2013), where the fish community on Reef Ball reefs was investigated, little information was given on the structure or size of natural reefs. If natural reefs in Folpp *et al.* (2013) are of relatively lower quality with low vertical relief, then the results of their study are not surprising and consistent with the results of my thesis, where Reef Ball reefs were comparable to low lying boulder field reefs in their fish communities.

Generally, higher habitat complexity and diversity of refuge sites is associated with increased fish abundances, density and diversity on natural reefs (Messmer *et al.*, 2011; Komyakova *et al.*, 2013). Enhancement of artificial reef structures through increased vertical relief and small refuge site availability has also been shown to have the same effect (Sherman *et al.*, 2002; Wilhelmsson *et al.*, 2006; Langhamer and Wilhelmsson, 2009). For example, Sherman *et al.* (2002) attempted to increase the small-scale complexity of Reef Ball reefs by adding a concrete block to the void space inside the reef, and increased vertical relief by attaching a 10-m floating line. Reef Ball reefs with the block inside supported higher fish densities and species richness than reefs with the floating line or control reefs (Sherman *et* *al.*, 2002). The new design reefs in this thesis had higher vertical relief and small-scale complexity than Reef Ball reefs. These features are potentially responsible for the apparent better performance of the new design artificial reefs as reef fish habitat. However, it must be noted that effects of increased habitat complexity may be species dependent. For example, Langhamer and Wilhelmsson (2009) demonstrated that the addition of holes to the wave energy foundation had no effect on the associated fish community. However, the abundance of *Cancer pagurus* (edible crab) significantly increased on more complex foundations, while the abundance of spiny starfish declined, potentially due to the increase in predator numbers (*C. pagurus*). Therefore, when designing a new artificial reef, it is important to consider the local natural animal community and the interactions between species in order to design a habitat that provides the closest mimic of local natural reefs,.

Significantly higher fish species richness associated with artificial reefs in comparison to natural reefs could also be due to the more fragmented habitat structure, and increased edge and isolation effects (Bohnsack *et al.*, 1994; Jordan *et al.*, 2005). Jordan *et al.* (2005) demonstrated that increased isolation between experimental reef blocks led to an increase in fish abundance and diversity for most treatments. Fragmented Reef Ball reefs and new design artificial reefs may not only support typical reef-associated species, but also habitat generalists and transient species, boosting fish species richness at these habitats. Indeed, greater transient species abundances have been associated with artificial reefs, where they use these habitats for temporal foraging (Overholtzer-McLeod, 2004; Leitao *et al.*, 2008; Folpp *et al.*, 2011; Simon *et al.*, 2011).

Natural reefs are typically larger than most artificial reefs, and in general, larger habitats are expected to support larger fish populations (Rosenzweig, 1995; Lomolino, 2001; Holbrook *et al.*, 2002). Jordan *et al.* (2005) demonstrated that an increase in the number of reef modules increased the number of fish associated with it, although not in equal proportion. Similar results were reported in another experimental study (Jan *et al.*, 2003). This relationship may be explained by higher resource availability (e.g. prey species or refuge sites) (Hixon and Beets, 1989), which explains the generally higher fish abundances on natural reefs compared to Reef Ball reefs and new design artificial reef (Chapter 3). The discrepancies in the results of this study with other studies that reported higher abundances on artificial reefs (Wilhelmsson *et al.*, 1998; Folpp *et al.*, 2013) may relate to the quality of the examined natural reef.

The size and quality of habitats also plays a role in how attractive it is for new recruits. Generally speaking, large habitats are easier to detect as they are "noisier" and provide bigger targets for settling larval reef fish (Stier and Osenberg, 2010; Morton and Shima, 2013; Piercy *et al.*, 2014; Hale *et al.*, 2015). Natural reefs also support well-established fish and benthic communities, which may play a role in habitat choice, particularly for species that are site-attached or have a strong affinity for con-specifics (Perkol-Finkel *et al.*, 2005; Stier and Osenberg, 2010; Morton and Shima, 2013; Hale *et al.*, 2015; Fobert and Swearer, 2017). Indeed, natural reefs received significantly higher recruit densities of one of the study species (*Trachinops caudimaculatus*) that exhibits strong preference for conspecifics (see Hunt *et al.* (2011), Fobert and Swearer (2017)), while for two generalist species (*V. conspersa* and *T. clarkei*) differences in recruitment were not prominent (Chapter 4).

However, laboratory-based habitat choice experiments, where patch size was controlled and the influence of other variables was removed (e.g. con- and hetero- specifics), revealed contradicting results. While *V. conspersa* exhibited no habitat preferences, *T. caudimaculatus* exhibited a strong preference for the Reef Ball reef over the natural reef and the new design artificial reef (Chapter 4). These results suggest that the structure of Reef Ball reefs may be attractive to *T. caudimaculatus*. Indeed, previous studies have demonstrated that habitat structure, apart from the presence of con-specifics, is one of the primary factors driving habitat choice for this fish species (Hunt *et al.*, 2011; Fobert and Swearer, 2017). Therefore, larger, more continuous Reef Ball reefs that have time to establish fish communities may become equally as attractive or more attractive to *T. caudimaculatus* than local natural reefs. The higher preference (*T. caudimaculatus*) or equal attractiveness (*V. conspersa and T. clarkei*) of some artificial habitats (e.g. Reef Ball reef) may not have a large impact on fish populations in areas where reef habitat is limiting, and any additional habitat should lead to increases in overall population size. However, the majority of fish populations are overfished or in decline due to other factors, such as pollution or the introduction of invasive species (Hughes, 1994; Jackson *et al.*, 2001; Halpern *et al.*, 2008; Jackson, 2008), so habitat may not be limiting in many instances. In such situations, it is possible that new recruits that could have reached and survived on a natural reef are instead attracted to artificial structures causing recruitment redirection (Osenberg *et al.*, 2002; Stier and Osenberg, 2010; Morton and Shima, 2013). Artificial reefs may also be more attractive to predatory fish, leading to high predator abundances in the vicinity of artificial reefs, which in turn may lead to higher mortality rates of prey species (Rooker *et al.*, 1997; Overholtzer-McLeod, 2004; Simon *et al.*, 2011). Little is known about fitness consequences of individuals occupying artificial reefs. Only a handful of studies have conducted comparative investigations on fish fitness between natural and artificial structures (Dempster *et al.*, 2011; Reubens *et al.*, 2013; Fernandez-Jover and Sanchez-Jerez, 2015). These studies detected no difference in individual condition between natural and artificial reefs, or detected increased condition on artificial structures (Dempster *et al.*, 2011; Reubens *et al.*, 2013; Fernandez-Jover and Sanchez-Jerez, 2015), although these effects were species-dependent (Fernandez-Jover and Sanchez-Jerez, 2015). However, these studies investigated fish farms and wind power stations as artificial reefs instead of using specially designed artificial reefs for fisheries enhancement, species protection or habitat restoration. If artificial reefs are more attractive than natural reefs, yet cause lower fitness advantages for the individuals, including increased mortality rates, they may act as ecological traps, leading to negative outcomes for fish populations (Battin, 2004; Robertson and Hutto, 2006; Hale and Swearer, 2016).

6.2 Artificial reefs as ecological traps

This thesis provides the first empirical investigation into differences in individual performance between natural and artificial reefs purposely designed and built for fisheries enhancement, habitat restoration and species conservation. The fitness responses of individuals varied according to species and habitat type. The three study species (*T. caudimaculatus*, *V. conspersa* and *T. clarkei*) demonstrated three different potential outcomes of artificial reef deployment. *T. caudimaculatus* condition was similar between natural and new design artificial reefs, but fortnightly recruitment monitoring data and a VIE tagging study both revealed significantly higher mortality of new recruits on Reef Ball reefs compared with the two other reef types (Chapter 5). Given that *T. caudimaculatus* exhibited a strong preference for Reef Ball reefs in the laboratory (Chapter 4), this study is the first to demonstrate the potential formation of an ecological trap in the marine environment. There have been multiple studies that have documented ecological traps in the terrestrial environment (Hale and Swearer, 2016). However, the few previous marine investigations were unable to find evidence for an ecological trap (Hallier and Gaertner, 2008; Dempster *et al.*, 2011; Reubens *et al.*, 2013). Although some studies suggest negative impacts of artificial structures (e.g. fish farms) for some fish species (Bjørn *et al.*, 2001; Pergent-Martini *et al.*, 2006), others have suggested that these structures may act as population sources for wild fish

(Dempster *et al.*, 2011). The effects of artificial structures on fish populations are likely structure type- and species-dependent. Little evidence for the formation of ecological traps in marine environments may be largely related to the difficulty of investigating this phenomenon in aquatic, three-dimensional environments, where tracking individuals is difficult due to their microscopic nature in the larval stages and high complexity of reef habitat utilised by post-settlement life stages.

V. conspersa in general exhibited higher condition on Reef Ball reefs and, while being a habitat generalist, also showed some preference for Reef Ball reefs (Chapter 4, Table 5.5). This response may be an example of adaptive habitat selection. Adaptive habitat selection has been frequently demonstrated, where species specialised in specific habitat types that lead to lower mortality outcomes or improved condition due to reduced competition or predation (Morris, 2003; Morris, 2004). Adaptive habitat selection is an important evolutionary driver responsible for specialisation, adaptive radiation and persistence of different species in a constantly changing environment (Morris, 2003; Morris, 2004).

Finally, *T. clarkei* were in significantly better condition on artificial reefs compared with natural reefs. However, this species did not demonstrate any habitat preferences (Chapter 4). This may indicate the possible formation of a perceptual trap for this fish species due to the introduction of an artificial habitat (Gilroy and Sutherland, 2007). The term "perceptual trap" is used to describe a situation, when a species actively avoids, or fails to preferentially select a good quality habitat (Gilroy and Sutherland, 2007). Perceptual traps may be more difficult to detect in marine environments than ecological traps, and there are only a few potential examples known in terrestrial environments (Gilroy and Sutherland, 2007), which are still a subject of debate. While the effects of perceptual traps may not be as severe as the effects of ecological traps on animal populations, their formation may greatly impede management and conservation efforts. For example, introducing artificial reefs that fish do not recognise as appropriate habitat and subsequently do not inhabit is a waste of conservation resources. Therefore, identifying if artificial reefs constructed specifically for habitat restoration and fish species conservation can function as perceptual or ecological traps is critical to optimising conservation efforts.

My results, combined with previous studies (e.g. Dempster *et al.* (2011)), indicate that responses to different types of artificial habitats are largely species-, location- and habitat-specific. However, the use of condition indices may be an unreliable proxy of artificial structure performance. Individuals may show higher condition on artificial reefs due to lower population density (Anderson, 1988; Booth, 1995; Koslow *et al.*, 1995; Booth and Wellington, 1998; Ford and Swearer, 2013), which may be a result of increased mortality rates. My results suggest that such compensatory density-dependent effects can occur on artificial reefs, which may have the potential to offset some of the negative effects on reef fish survival. Regardless, my study is the first to demonstrate the potential for the formation of both ecological and perceptual traps in the marine environment. Although I show that habitat modifications through the deployment of artificial reefs can directly lead to traps forming, there are other indirect mechanisms that require further investigation. For example, pollution (chemical, light, etc.) associated with urbanised coastal areas may impact on a fish's sensory abilities, increasing the likelihood of selecting poor-quality habitats (Baker and Montgomery, 2001; Kusch *et al.*, 2008; Ward *et al.*, 2008; Nilsson *et al.*, 2012). This warrants further research into the population-level effects of installing artificial reef structures in urban marine environments.

6.3 Final conclusion

Whether a deployment of an artificial reef is considered to be successful greatly depends on the purposes of that deployment. Designing, constructing and deploying artificial reefs can be a costly endeavour (Thierry, 1988; Seaman Jr and Sprague, 1991; Branden *et al.*, 1994; Baine, 2001; Fabi *et al.*, 2011). If the deployment of artificial reefs is predominantly driven by enhancement of the recreational fishing experience, then most hard structures, which function as fish attraction devices, will fit this purpose. However, if artificial reefs are being constructed for the purposes of biomass enhancement, fish species conservation and habitat restoration, then successful reef design and placement will need to incorporate several factors, such as the type of natural environment, adjacent habitat types, distance from natural reef, geographic location, natural benthic and mobile community composition of the area and species specific habitat requirements. These factors are also important for the construction of artificial structures in the marine environment that have a primary function other than directly as artificial reef (e.g. wind power stations, fish farms, marinas, oil and gas platforms etc.). Without considerable knowledge of the effects of artificial reef deployment, understanding key design principles, and selecting suitable deployment locations, local fish communities/populations may suffer recruitment redirection, a concentration of vulnerable species within the vicinity of artificial reefs making them more accessible by fisheries, the formation of unnatural communities that may cause local shifts in community structure, the formation of ecological and perceptual traps, and even local extinctions (Connell and Glasby, 1999; Baine, 2001; Connell, 2001; Battin, 2004; Simon *et al.*, 2011; Hale and Swearer, 2016). Such effects would greatly impede management and conservation efforts and can result in substantial impacts on local marine ecosystems. To avoid these unintended consequences, future artificial reef research should investigate whether the biotic communities that form on artificial reefs are comparable to local natural reefs, assess the attractiveness of artificial reefs and evaluate the fitness consequences to individuals that select these habitats using a multi-species approach.

6.4 References

Anderson, J. T. (1988) A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fishery Science,* 8, 55-66.

Baine, M. (2001) Artificial reefs: a review of their design, application, management and performance. *Ocean & Coastal Management*, 44(3–4), 241-259.

Baker, C. F. and Montgomery, J. C. (2001) Sensory deficits induced by cadmium in banded kokopu, *Galaxias fasciatus*, juveniles. *Environmental Biology of Fishes*, 62(4), 455-464.

Battin, J. (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, 18(6), 1482-1491.

Bjørn, P., Finstad, B. and Kristoffersen, R. (2001) Salmon lice infection of wild sea trout and Arctic char in marine and freshwaters: the effects of salmon farms. *Aquaculture Research*, 32(12), 947-962.

Bohnsack, J. A., Harper, D. E., McClellan, D. B. and Hulsbeck, M. (1994) Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off Southeastern Florida, U.S.A. *Bulletin of Marine Science*, 55(2-3), 796-823.

Bohnsack, J. A. and Sutherland, D. L. (1985) Artificial reef research: a review with recommendations for future priorities. *Bulletin of Marine Science*, 37(1), 11-39.

Booth, D. J. (1995) Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. *Ecology*, 76(1), 91-106.

Booth, D. J. and Wellington, G. (1998) Settlement preferences in coral ‐ reef fishes: Effects on patterns of adult and juvenile distributions, individual fitness and population structure. *Austral Ecology*, 23(3), 274-279.

Bos, E., Vu, M. T., Levin, A. and Bulatao, R. A. (1992) World population projections 1992-Estimates and projections with related demographic statistics. Baltimore, Maryland, Johns Hopkins University Press, VII, 515 p.

Branden, K. L., Pollard, D. A. and Reimers, H. A. (1994) A review of recent artificial reef developments in Australia. *Bulletin of Marine Science*, 55(2-3), 982-994.

Carr, M. H. and Hixon, M. A. (1997) Artificial reefs: the importance of comparisons with natural reefs. *Fisheries*, 22(4), 28-33.

Chou, L. (1997) Artificial reefs of Southeast Asia-do they enhance or degrade the marine environment? *Environmental monitoring and assessment*, 44(1-3), 45-52.

Claudet, J. and Pelletier, D. (2004) Marine protected areas and artificial reefs: a review of the interactions between management and scientific studies. *Aquatic Living Resources*, 17(2), 129-138.

Connell, S. D. (2001) Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs. *Marine Environmental Research*, 52(2), 115-125.

Connell, S. D. and Glasby, T. M. (1999) Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. *Marine Environmental Research*, 47(4), 373-387.

Dempster, T., Sanchez-Jerez, P., Fernandez-Jover, D., Bayle-Sempere, J., Nilsen, R., Bjørn, P.-A. and Uglem, I. (2011) Proxy measures of fitness suggest coastal fish farms can act as population sources and not ecological traps for wild gadoid fish. *PLoS ONE*, 6(1), e15646.

Fabi, G., Spagnolo, A., Bellan-Santini, D., Charbonnel, E., Çiçek, B. A., García, J. J. G., Jensen, A. C., Kallianiotis, A. and Santos, M. N. d. (2011) Overview on artificial reefs in Europe. *Brazilian Journal of Oceanography*, 59, 155-166.

Fernandez-Jover, D. and Sanchez-Jerez, P. (2015) Comparison of diet and otolith growth of juvenile wild fish communities at fish farms and natural habitats. *ICES Journal of Marine Science: Journal du Conseil*, 72(3), 916-929.

Firth, L. B., Knights, A. M., Thompson, R., Mieszkowska, N., Bridger, D., Evans, A., Moore, P., O'Connor, N., Sheehan, E. and Hawkins, S. (2016) Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. *Oceanogr. Mar. Biol. Ann. Rev*.

Fobert, E. K. and Swearer, S. E. (2017) The nose knows: linking sensory cue use, settlement decisions, and post-settlement survival in a temperate reef fish. *Oecologia*, 1-11.

Folpp, H., Lowry, M., Gregson, M. and Suthers, I. M. (2011) Colonization and community development of fish assemblages associated with estuarine artificial reefs. *Brazilian Journal of Oceanography*, 59, 55-67.

Folpp, H., Lowry, M., Gregson, M. and Suthers, I. M. (2013) Fish assemblages on estuarine artificial reefs: natural rocky-reef mimics or discrete assemblages? *PLoS ONE*, 8(6), e63505.

Ford, J. R. and Swearer, S. E. (2013) Two's company, three's a crowd: food and shelter limitation outweigh the benefits of group living in a shoaling fish. *Ecology*, 94(5), 1069-1077.

Gilroy, J. J. and Sutherland, W. J. (2007) Beyond ecological traps: perceptual errors and undervalued resources. *Trends in Ecology & Evolution*, 22(7), 351-356.

Hackradt, C. W., Félix-Hackradt, F. C. and García-Charton, J. A. (2011) Influence of habitat structure on fish assemblage of an artificial reef in southern Brazil. *Marine Environmental Research*, 72(5), 235-247.

Hale, R. and Swearer, S. E. (2016) Ecological traps: current evidence and future directions. *Proceedings of the Royal Society B: Biological Sciences*, 283(1824).

Hale, R., Treml, E. A. and Swearer, S. E. (2015) Evaluating the metapopulation consequences of ecological traps. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1804), 20142930.

Hallier, J. and Gaertner, D. (2008) Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Marine Ecology Progress Series*, 353, 255-264.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R. and Watson, R. (2008) A global map of human impact on marine ecosystems. *Science*, 319(5865), 948-952.

Hixon, M. A. and Beets, J. P. (1989) Shelter characteristics and caribbean fish assemblages: experiments with artificial reefs. *Bulletin of Marine Science*, 44(2), 666-680.

Holbrook, S. J., Brooks, A. J. and Schmitt, R. J. (2002) Predictability of fish assemblages on coral patch reefs. *Marine and Freshwater Research*, 53(2), 181-188.

Hughes, T. P. (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 265(5178), 1547-1551.

Hunt, T. L., Ford, J. R. and Swearer, S. E. (2011) Ecological determinants of recruitment to populations of a temperate reef fish, *Trachinops caudimaculatus* (Plesiopidae). *Marine and Freshwater Research*, 62(5), 502-509.

Jackson, J. B. C. (2008) Ecological extinction and evolution in the brave new ocean. *Proceedings of the National Academy of Sciences*, 105(Supplement 1), 11458-11465.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. and Warner, R. R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293(5530), 629-637.

Jan, R.-Q., Liu, Y.-H., Chen, C.-Y., Wang, M.-C., Song, G.-S., Lin, H.-C. and Shao, K.-T. (2003) Effects of pile size of artificial reefs on the standing stocks of fishes. *Fisheries Research*, 63(3), 327-337.

Jordan, L. K. B., Gilliam, D. S. and Spieler, R. E. (2005) Reef fish assemblage structure affected by small-scale spacing and size variations of artificial patch reefs. *Journal of Experimental Marine Biology and Ecology*, 326(2), 170-186.

Komyakova, V., Munday, P. L. and Jones, G. P. (2013) Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. *PLoS ONE*, 8(12), e83178.

Koslow, J. A., Bell, J., Virtue, P. and Smith, D. C. (1995) Fecundity and its variability in orange roughy: effects of population density, condition, egg size, and senescence. *Journal of Fish Biology*, 47(6), 1063-1080.

Kusch, R. C., Krone, P. H. and Chivers, D. P. (2008) Chronic exposure to low concentrations of waterborne cadmium during embryonic and larval development results in the long‐term hindrance of antipredator behavior in zebrafish. *Environmental Toxicology and Chemistry*, 27(3), 705-710.

Langhamer, O. and Wilhelmsson, D. (2009) Colonisation of fish and crabs of wave energy foundations and the effects of manufactured holes – a field experiment. *Marine Environmental Research*, 68(4), 151-157.

Leitao, F., Santos, M. N., Erzini, K. and Monteiro, C. C. (2008) The effect of predation on artificial reef juvenile demersal fish species. *Marine Biology*, 153(6), 1233-1244.

Lomolino, M. V. (2001) The species-area relationship: new challenges for an old pattern. *Progress in Physical Geography*, 25(1), 1-21.

Messmer, V., Jones, G. P., Munday, P. L., Holbrook, S. J., Schmitt, R. J. and Brooks, A. J. (2011) Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology*, 92(12), 2285-2298.

Milon, J. W. (1989) Economic evaluation of artificial habitat for fisheries: progress and challenges. *Bulletin of Marine Science*, 44(2), 831-843.

Morris, D. W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, 136(1), 1-13.

Morris, D. W. (2004) Some crucial consequences of adaptive habitat selection by predators and prey: apparent mutualisms, competitive ghosts, habitat abandonment, and spatial structure. *Israel Journal of Zoology*, 50(2-3), 207-232.

Morton, D. N. and Shima, J. S. (2013) Habitat configuration and availability influences the settlement of temperate reef fishes (Tripterygiidae). *Journal of Experimental Marine Biology and Ecology,* 449, 215-220.

Nilsson, G. E., Dixson, D. L., Domenici, P., McCormick, M. I., Sørensen, C., Watson, S.-A. and Munday, P. L. (2012) Near-future carbon dioxide levels alter fish behaviour by interfering with neurotransmitter function. *Nature Climate Change*, 2(3), 201-204.

Osenberg, C. W., St. Mary, C. M., Schmitt, R. J., Holbrook, S. J., Chesson, P. and Byrne, B. (2002) Rethinking ecological inference: density dependence in reef fishes. *Ecology Letters*, 5(6), 715-721.

Overholtzer-McLeod, K. L. (2004) Variance in reef spatial structure masks density dependence in coral-reef fish populations on natural versus artificial reefs. *Marine Ecology Progress Series*, 276, 269-280.

Pergent-Martini, C., Boudouresque, C.-F., Pasqualini, V. and Pergent, G. (2006) Impact of fish farming facilities on Posidonia oceanica meadows: a review. *Marine Ecology*, 27(4), 310-319.

Perkol-Finkel, S., Shashar, N., Barneah, O., Ben-David-Zaslow, R., Oren, U., Reichart, T., Yacobovich, T., Yahel, G., Yahel, R. and Benayahu, Y. (2005) Fouling reefal communities on artificial reefs: does age matter? *Biofouling*, 21(2), 127-140.

Piercy, J. J. B., Codling, E. A., Hill, A. J., Smith, D. J. and Simpson, S. D. (2014) Habitat quality affects sound production and likely distance of detection on coral reefs. *Marine Ecology Progress Series*, 516, 35-47.

Reubens, J. T., Vandendriessche, S., Zenner, A. N., Degraer, S. and Vincx, M. (2013) Offshore wind farms as productive sites or ecological traps for gadoid fishes? – Impact on growth, condition index and diet composition. *Marine Environmental Research*, 90(0), 66-74.

Robertson, B. A. and Hutto, R. L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, 87(5), 1075-1085.

Rooker, J., Dokken, Q., Pattengill, C. and Holt, G. (1997) Fish assemblages on artificial and natural reefs in the Flower Garden Banks National Marine Sanctuary, USA. *Coral Reefs*, 16(2), 83-92.

Rosenzweig, M. L. (1995) *Species diversity in space and time*, Cambridge University Press.

Seaman Jr, W. and Sprague, L. M. (1991) 1 - Artificial habitat practices in aquatic systems. In *Artificial habitats for marine and freshwater fisheries*, Academic Press, San Diego, pp. 1-29.

Seaman, W. and Jensen, A. C. (2000) *Purposes and practices of artificial reef evaluation*, Boca Raton, FL: CRC Press LLC.

Seto, K. C., Güneralp, B. and Hutyra, L. R. (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, 109(40), 16083-16088.

Sherman, R. L., Gilliam, D. S. and Spieler, R. E. (2002) Artificial reef design: void space, complexity, and attractants. *ICES Journal of Marine Science: Journal du Conseil*, 59(suppl), S196-S200.

Sih, A. (2013) Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour*, 85(5), 1077-1088.

Simon, T., Joyeux, J.-C. and Pinheiro, H. T. (2013) Fish assemblages on shipwrecks and natural rocky reefs strongly differ in trophic structure. *Marine Environmental Research*, 90, 55-65.

Simon, T., Pinheiro, H. T. and Joyeux, J.-C. (2011) Target fishes on artificial reefs: Evidences of impacts over nearby natural environments. *Science of The Total Environment*, 409(21), 4579-4584.

Stier, A. C. and Osenberg, C. W. (2010) Propagule redirection: habitat availability reduces colonization and increases recruitment in reef fishes. *Ecology*, 91(10), 2826-2832.

Thierry, J.-M. (1988) Artificial reefs in Japan — A general outline. *Aquacultural Engineering*, 7(5), 321-348.

Ward, A. J., Duff, A. J., Horsfall, J. S. and Currie, S. (2008) Scents and scents-ability: pollution disrupts chemical social recognition and shoaling in fish. *Proceedings of the Royal Society of London B: Biological Sciences*, 275(1630), 101-105.

Wilhelmsson, D., Öhman, M. C., Ståhl, H. and Shlesinger, Y. (1998) Artificial reefs and dive tourism in Eilat, Israel. *Ambio*, 27(8), 764-766.

Wilhelmsson, D., Yahya, S. A. S. and Öhman, M. C. (2006) Effects of high-relief structures on cold temperate fish assemblages: a field experiment. *Marine Biology Research*, 2(2), 136-147.

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